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Cite this article: McNickle GG, Gonzalez-Meler MA, Lynch DJ, Baltzer JL, Brown JS. 2016 The world's biomes and primary production as a triple tragedy of the commons foraging game played among plants. *Proc. R. Soc. B* **283**: 20161993. <http://dx.doi.org/10.1098/rsob.2016.1993>

Received: 9 September 2016
Accepted: 10 October 2016

Subject Areas:
ecology

Keywords:
net primary productivity, evolutionary game theory, tragedy of the commons game, foraging game, vegetation game

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Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.3538887>.

The world's biomes and primary production as a triple tragedy of the commons foraging game played among plants

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Plants appear to produce an excess of leaves, stems and roots beyond what would provide the most efficient harvest of available resources. One way to understand this overproduction of tissues is that excess tissue production provides a competitive advantage. Game theoretic models predict overproduction of all tissues compared with non-game theoretic models because they explicitly account for this indirect competitive benefit. Here, we present a simple game theoretic model of plants simultaneously competing to harvest carbon and nitrogen. In the model, a plant's fitness is influenced by its own leaf, stem and root production, and the tissue production of others, which produces a triple tragedy of the commons. Our model predicts (i) absolute net primary production when compared with two independent global datasets; (ii) the allocation relationships to leaf, stem and root tissues in one dataset; (iii) the global distribution of biome types and the plant functional types found within each biome; and (iv) ecosystem responses to nitrogen or carbon fertilization. Our game theoretic approach removes the need to define allocation or vegetation type *a priori* but instead lets these emerge from the model as evolutionarily stable strategies. We believe this to be the simplest possible model that can describe plant production.

1. Background

Photosynthesis by plants removes CO₂ from the atmosphere and as a result, plants are one of the major players in the Earth's climate system. For example, primary production by plants in the Northern Hemisphere causes intra-annual atmospheric CO₂ fluctuations of approximately 8 ppm, which represents an enormous amount of carbon removed from the atmosphere each year [1]. Further, observed climate change has been less severe than predicted by models, in part because terrestrial plants have captured more anthropogenic CO₂ than was initially expected, and plants remain one of the largest sources of uncertainty in climate models [2–4]. It is, therefore, important to continually refine models of plant production in order to increase the accuracy in forecasting future climate scenarios. Here, we go back to first principles, and develop a simple, and general, game theoretic model of plant production that we believe is the simplest possible mathematical representation of this phenomenon.

One of the most common mathematical representations of terrestrial vascular plant production in models is a body that produces leaves, stems, roots and reproductive tissues (e.g. [5–7]). These tissues are the infrastructure that a plant needs to harvest carbon and soil resources which are then used to produce

offspring in the form of seeds and propagules. However, it has not been obvious how to dynamically link these three plant tissues, and as a shortcut most existing models optimize one tissue pool (most commonly leaves), assume constant allocation to other tissues or use discontinuous minimum functions [2–4,8]. However, allocation is not constant and even a casual glance at data suggests that plants produce surprisingly large amounts of roots, leaves and stems relative to their reproductive output. For example, in a global dataset of forest net primary productivity (NPP, [9]), only an average of 9.1% of carbon was allocated to reproductive output, compared with 26.3%, 43.1% and 21.5% to leaves, stems and roots, respectively. These numbers are surprising: why should reproduction be the smallest pool of allocation by a large margin given the central role of reproduction in evolutionary biology? Furthermore, why are stems almost always the largest pool of allocation given that stems do not directly acquire any resources?

Here, we will suggest that plants produce leaves, stems and roots partially because these structures increase an individual's harvest of nutrients and carbon, but also because they competitively pre-empt the harvest of others, which provides indirect benefits. To explicitly capture these dual roles, our model considers the plant's foraging economics as an evolutionary game. We call this foraging, because we assume the plants' optimal production of leaves or roots should balance marginal gains with marginal costs [6,10–12]. Under this definition, the majority of existing vegetation models are foraging models. We call this a game because the optimal production of leaves, stems and roots will depend, in part, on the tissue production of the other plants with whom it competes [13–16]. This game theoretic aspect of plant production has been well understood for many years [5,14,15,17], and here we attempt to bring these ideas together into a single, continuously differentiable model of leaf, stem and root allocation.

To this end, we present a generalizable foraging game where reproductive output is expressed as a triple optimization of leaf, stem and root production under resource competition. We seek the most competitive strategy for all three tissue pools simultaneously as an evolutionarily stable strategy (ESS). The advantage of expressing each tissue as a variable and employing a triple optimization is that allocation to leaves, stems or roots does not have to be defined *a priori*, and instead emerges dynamically from the structure of the model. This means that the physiognomy of plants (e.g. trees versus shrubs versus herbs) is also not specified *a priori* in our model, but rather arise dynamically from the structure of the model. This produces a model where the actual biome type and plant functional types become continuous variables that emerge as ESS solutions. Perhaps counterintuitively, employing a more complicated game theoretic triple optimization criterion allows us to greatly simplify the modelling problem to just a handful of parameters. As a result much of the complexity of vegetation responses is moved out of the parametrization and into the mathematical solution to the model itself. We compare the model predictions with observed NPP data and ask: (i) does the model predict the trends and magnitudes of total NPP observed in two global datasets when parametrized independent of the data? (ii) Does the model predict absolute and relative allocation to leaves, stems and roots in one global dataset? (iii) Can a model with dynamic allocation predict the global distribution of biomes and plant functional types from first principles?

(iv) Can a model of dynamic allocation capture general ecosystem patterns like progressive nitrogen limitation, response to C and N fertilization and root–shoot allocation patterns across ecotones?

2. Methods

(a) Mathematical model description

Here we detail a general form of the model, and expect that users may supply their own functions depending on their predictive goals (table 1). To generate output, we chose the simplest possible mathematical functions from the plant literature, and these are derived in the electronic supplementary material. These simple functions are likely not appropriate in all modelling situations, but provide a first-order approximation of the utility of the general structure of the game. Our reasoning was that if these simple first-order approximations can describe data reasonably well, then more complex process-based equations should only perform better in future applications of this general game.

For a general version of the game, we need to only define a few variables and functions. For plant i , let u_{il} be leaf production, let u_{is} be stem production (assumed to be proportional to height) and let u_{ir} be root production (units $\text{g dry mass m}^{-2} \text{yr}^{-1}$). The vector $\mathbf{u}_i = [u_{il}, u_{is}, u_{ir}]$ represents the plant i 's strategy. We define vectors that contain the strategies of all competing plants. Thus, for x competitors, let $\mathbf{u}_1 = [u_{i1} \dots u_{ix}]$ be a vector of the leaf production strategies of all competing plants, from plant $i = 1 \dots x$ within the ecosystem. Similarly, let $\mathbf{u}_s = [u_{is} \dots u_{xs}]$ and $\mathbf{u}_r = [u_{ir} \dots u_{xr}]$ be vectors containing the stem production and root production strategies of all interacting plants. For simplicity, we imagine that the plants compete for only C and N, and the reproductive output (i.e. fitness) of plant i is influenced by its growth strategy and the strategies of all of its neighbours, $G_i(u_{il}, u_{is}, u_{ir}, \mathbf{u}_1, \mathbf{u}_s, \mathbf{u}_r)$. We model carbon and nitrogen as interacting essential resources (*sensu* [14]), the harvest of which inputs into fitness and use a Cobb–Douglas production function from economics [18] as an effective means for expressing this nutritional relationship:

$$G(u_{il}, u_{is}, u_{ir}, \mathbf{u}_1, \mathbf{u}_s, \mathbf{u}_r) = \pi_{iC}^\alpha \pi_{iN}^\beta, \quad (2.1)$$

where π_{iC} is plant i 's net carbon gain from stem and leaf production; and π_{iN} is plant i 's net nitrogen gain from root production. The Cobb–Douglas production function allows us to link leaf, stem and root production into a single, continuously differentiable fitness function. Reproduction must logically be a product of C and N gain because these resources have a multiplicative effect on plant performance, and it must logically be a weighted product because C and N are not required in equal proportions [19,20]. The exponents α and β are closely related to the plant's ideal homeostatic C:N ratio such that α and β represent the relative proportions of the plant composed of carbon and nitrogen, respectively, where $\alpha + \beta = 1$ which allows constant returns to scale. The restriction to just two nutritional inputs can be relaxed and we show how to include any number of substitutable and essential nutrients in the electronic supplementary material, but the inclusion of additional nutrients quickly increases model complexity.

The net gain functions (π_{iC} , π_{iN}) describe foraging gains minus expenditures. For example, net carbon gain includes the gross amount of carbon harvested through photosynthesis minus the carbon required for respiration and tissue construction. Similarly, net nitrogen gain includes the amount of nitrogen harvested by roots minus the nitrogen required for constructing and maintaining tissues. Thus, a plant's net profit for C and N emerges from (i) the total amount of C and N available to x plants as a function of their combined leaf or root production, multiplied by; (ii) the

Table 1. A generalized game theoretic model of plant production. The model has three output variables per plant: u_{il}^* , u_{is}^* , u_{ir}^* , which are the leaf, stem and root production of plant i ($\text{g m}^{-2} \text{yr}^{-1}$). $\mathbf{u}_l$, $\mathbf{u}_s$, $\mathbf{u}_r$ are vectors of leaf, stem or root production of all competing plants.

main model equations	explanation
$G(u_{il}, u_{is}, u_{ir}, \mathbf{u}_l, \mathbf{u}_s, \mathbf{u}_r) = \pi_C^\alpha \pi_N^\beta$	G is a fitness function for plant i calculated as a weighted product of net C and N harvested. Net harvests are weighted by the stoichiometry of plants, $C/N = \alpha/\beta$ and $\alpha + \beta = 1$
$\pi_C = z(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)H(\mathbf{u}_l) - c_C(u_{il}, u_{is}, u_{ir})$	π_C is the net C harvest of plant i . Calculated from gross photosynthesis (H_C) following the rules of above-ground competition (z) minus the C costs associated with all tissue construction and respiration (c_C)
$\pi_N = f(u_{ir}, \mathbf{u}_r)H(\mathbf{u}_r) - c_N(u_{il}, u_{is}, u_{ir})$	π_N is the net N harvest of plant i . Calculated from gross N uptake (H_N) following the rules of below-ground competition (f) minus the N costs required to construct tissues (c_N)
functions	description
$z_i(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)$	z describes size asymmetric competition which determines the relative harvest of C by plant i compared with all competing plants resulting from stem and leaf production
$f_i(u_{ir}, \mathbf{u}_r)$	f describes size symmetric competition which determines the relative harvest of N by plant i compared with all competing plants resulting from below-ground tissue production
$H_N(\mathbf{u}_r), H_C(\mathbf{u}_l)$	H describes the N and C available to x plants based on total root, or leaf production, and environmental resource availability
$c_C(u_{il}, u_{is}, u_{ir})$	c_C describes the C costs required for tissue production, and respiration by plant i
$c_N(u_{il}, u_{is}, u_{ir})$	c_N describes the N costs required for tissue production by plant i

fraction of the total C and N available that goes to the i th plant based on their competitive ability, minus; (iii) the C and N costs to the i th plant of producing and maintaining its leaves, roots and stems (table 1). Combining these three components:

$$\pi_{iC} = z_i(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)H_C(\mathbf{u}_l) - c_{iC}(u_{il}, u_{is}, u_{ir}) \quad (2.2)$$

and

$$\pi_{iN} = f_i(u_{ir}, \mathbf{u}_r)H_N(\mathbf{u}_r) - c_{iN}(u_{il}, u_{is}, u_{ir}). \quad (2.3)$$

The six component functions of the above equations may take a variety of forms based on knowledge and assumptions. Simple benefit minus costs net profit functions form the backbone of previous vegetation models, and we expect users can supply their own pre-existing equations here to transform existing models into game theoretic models. The function $z_i(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)$ should incorporate the asymmetric nature of light competition where the tallest or leafiest plants intercept a disproportionately large share of the light (e.g. electronic supplementary material, figure S1a, [21]). The function $f_i(u_{ir}, \mathbf{u}_r)$ must describe the typically symmetric nature of nutrient competition where plants with the most roots obtain the largest share of available nutrients, but this effect is closely related to their fraction of the total root biomass (electronic supplementary material, figure S1b, [22]). The functions $H_C(\mathbf{u}_l)$ and $H_N(\mathbf{u}_r)$ describing total C and N actually available to the plants should monotonically increase with each plant's leaf and root production, respectively, but cannot exceed what is available in the environment. Finally, the cost functions, $c_{iC}(u_{il}, u_{is}, u_{ir})$ and $c_{iN}(u_{il}, u_{is}, u_{ir})$, should increase monotonically with the production of any tissue. One final assumption is required: the monotonically increasing cost (c) and harvest (H) functions must cross at some point above $u = 0$ production. Otherwise there is no point where marginal benefits will balance marginal costs, and thus there would be no ESS.

The ESS strategy for root, stem and leaf production, $\mathbf{u}_i^* = [u_{il}^*, u_{is}^*, u_{ir}^*]$, can be found by applying the ESS maximum principle [23]. Assuming that all plants produce positive amounts of leaves, shoots and stems at the ESS, then the first-order necessary condition for this ESS requires that the partial of G with respect to each plant's root, stem and leaf production equals 0, and the second-order necessary condition is met if the

second derivatives are negative for all competing plants [23–25]. Our model meets both conditions, and the first-order partial derivatives are given by:

$$\left. \begin{aligned} \frac{\partial G}{\partial u_{ir}} &= \alpha \pi_C^{\alpha-1} \pi_N^\beta \frac{\partial \pi_C}{\partial u_{ir}} + \pi_C^\alpha \beta \pi_N^{\beta-1} \frac{\partial \pi_N}{\partial u_{ir}} = 0, \\ \frac{\partial G}{\partial u_{is}} &= \alpha \pi_C^{\alpha-1} \pi_N^\beta \frac{\partial \pi_C}{\partial u_{is}} + \pi_C^\alpha \beta \pi_N^{\beta-1} \frac{\partial \pi_N}{\partial u_{is}} = 0 \\ \text{and} \quad \frac{\partial G}{\partial u_{il}} &= \alpha \pi_C^{\alpha-1} \pi_N^\beta \frac{\partial \pi_C}{\partial u_{il}} + \pi_C^\alpha \beta \pi_N^{\beta-1} \frac{\partial \pi_N}{\partial u_{il}} = 0. \end{aligned} \right\} \quad (2.4)$$

As a vector-valued triple optimization, this generates three conditions that must be satisfied at the ESS for all plants 1 to x , $\mathbf{u}_1^* \dots \mathbf{u}_x^*$. The partials of the general profit functions are detailed in electronic supplementary material, table S1 and the simple functions implemented for our output are detailed in electronic supplementary material, tables S2–S4.

(b) Validation: model output versus FLUXNET and MOD17

To examine the performance of our general game theoretic framework, we compared output with the FLUXNET and MOD17 datasets. The FLUXNET data are a detailed inventory of NPP estimated from eddy covariance towers, in primarily boreal and temperate forest stands spread around the globe, and for a subset of sites NPP is divided into leaf, stem and root production based on direct on-the-ground observation of each tissue pool [9]. The MOD17 data come from satellite observations primarily of absorbed photosynthetically active radiation which can be converted into total NPP estimates using assumed mathematical transformations, and *a priori* knowledge of the biome type in each grid cell [26,27]. These two datasets represent two independent estimates of NPP at a global scale, using very different methods that come with their own biases and uncertainties. No part of the model equations or the parametrization was derived from, or fit to these data. Instead, the model is parametrized from first principles based on reported maximum and minimum estimates for each parameter in the literature, and a single independent output from the model is compared with both

FLUXNET and MOD17 data (electronic supplementary material, table S2). This imposed a more severe *a priori* test of the capability of our model than a more common fitting exercise would impose. We sought maximum and minimum values for parameters from the literature, and solved the model using a set of 1000 randomized parameter values that led to evolutionarily stable solutions. Within this range we also required that the parametrization met two important benchmarks: (i) maximum total NPP could not exceed observed values (electronic supplementary material, table S5) and (ii) carbon use efficiency was approximately 50% (electronic supplementary material, figure S2). Because the model and data are independent, there are no statistics describing fit, and no paired observations to plot in a simple linear regression. Thus, to assess fit, we used quantile plots and boxplots to visually compare distributions of the observed and predicted distribution in the data.

(c) Validation: biomes, plant functional types and ecosystem responses

The absolute size, and relative allocation of the plants is not specified *a priori*; instead leaf, stem and root production emerge as ESS solutions which allows us to ask whether the model can predict biomes and the physiognomy of plants found within each biome. For this analysis, we chose a single set of parameters and found the surface of ESS solutions across a global gradient of N and C availability. Onto this surface we mapped Whittaker's [28] biome classifications based on the total NPP in each biome. We also examined the physiognomy of the ESS plants from within each biome (defined by NPP) to check if they are representative of the types of plants found in actual biomes (i.e. trees in forests, shrubs in woodland, herbaceous plants in tundra). This is not meant to be a representation of Whittaker's biome plot (though it happens to also be triangle shaped) but rather is meant to show that the model can predict plant functional type as a continuous variable based on N and C availability.

Finally, we examine the behaviour of individual components of the model across this gradient of C and N availability. This demonstrates how the model responds to C and N fertilization and subsequent progressive limitation.

3. Results

(a) Total net primary productivity; model versus MOD17 versus FLUXNET

First, we asked whether the model output could predict observed total NPP from the MOD17 and FLUXNET datasets. On average the model as implemented overpredicts FLUXNET NPP by 1% (figure 1*a,b*) and MOD17 NPP by 15.8% (figure 1*c,d*). The model slightly underestimates the interquartile range in both datasets (figure 1*a–d*). It is not clear why the model performs better on FLUXNET data. These might seem like large deviations, but we note that when FLUXNET and MOD17 are compared with each other, they deviate by an average of 17%, and also disagree about the interquartile ranges even when constrained to the same data range (figure 1*e,f*). Thus, the uncertainty in the model output is similar, and even slightly lower, than the uncertainty in the two independent datasets themselves.

(b) Production of tissues; model versus FLUXNET

Second, because the model can predict NPP allocated individually to leaves, stems and roots, we compared this with the NPP

estimates for these pools produced by FLUXNET. The model predicts quantitative relationships and the ranges in absolute NPP allocated to leaves (figure 2*a*; electronic supplementary material, figure S3*a,b*), stems (figure 2*b*; electronic supplementary material, figure S3*c,d*) and roots (figure 2*c*; electronic supplementary material, figure S3*e,f*) within a wide range of biologically realistic parameter values. The model does well for absolute NPP above-ground, (figure 2*a,b*; electronic supplementary material, figure S3*a–d*), but slightly under-predicts root NPP (figure 2*c*; electronic supplementary material, figure S3*e,f*). For relative allocation the model does reasonably well; however, small departures in absolute production are amplified in the relative production estimates (figure 2*d*; electronic supplementary material, figure S3*g–j*). Generally, more productive systems contain more NPP in each tissue pool, and stems are typically the largest pool of NPP followed by leaves (figure 2). In both the empirical data and model predictions, we observe a strong negative relationship between stem allocation and root allocation, a weaker negative relationship between leaf and root allocation, and generally positive relationship between stem and leaf allocation (figure 2). Again, we emphasize that our goal here was to describe the general form of the model, and we expect future implementations will use process-based physiological functions for leaves and roots which we anticipate will improve fit. We find it remarkable that first-order approximations of the equations for C and N harvest that have just one parameter (electronic supplementary material, table S3) perform as well as they do on data.

(c) Biomes and plant functional types

As allocation is not constant in this model, but rather emerges dynamically from the game, the model can predict biomes and the physiognomy of the plants found within each biome as a continuum. Remarkably, the output produces distinct regions of total NPP that almost perfectly match the borders of Whittaker's biome types (figure 3*a*; electronic supplementary material, table S5). We show this for one parametrization, but a wide range of parameters can generate this qualitative pattern (not shown). Intuitively, the model predicts that the least productive systems occur where resource availability is lowest, and the most productive systems occur where resource availability is highest.

Within each distinct region of total NPP, the model also predicts the plant functional types found within each of Whittaker's biomes based on their physiognomy (figure 3*b*). For example, when total NPP is similar to that observed in tundra, the model predicts small plants with more allocation to leaves and roots than stems (figure 3*a,b*). Alternatively, when total NPP is similar to that of a tropical forest, the model predicts that the majority of plants will be tree-like, with very high allocation to stems and comparably small allocation to roots (figure 3*a,b*). Just as observed in nature, the model predicts a gradient of increasing allocation to stems and decreasing allocation to roots is along the productivity gradient (figure 3*a,b*). In other words, working from first principles, the model predicts the global distribution of Whittaker's [28] biome types as defined by total NPP, and also predicts the plant functional types found within each biome defined by physiognomy. Our model suggests that plant tissue allocations and even biomes may be the outcome of an ESS to a triple tragedy. Throughout our model, we

Figure 1. Comparison of model output with total NPP in MOD17 and FLUXNET datasets using quantile plots and boxplots. (a,b) Model versus MOD17, (c,d) model versus FLUXNET, (e,f) FLUXNET versus MOD17. In panels (a) and (c) outliers in the datasets lie to the right of the vertical line.

supply just a handful of physiological rates (electronic supplementary material, table S2), and then based on the resource availabilities, plants evolve to their ESS. If the available resources mimic tundra, the ESS evolves to look like tundra plants; if the available resources mimic tropical forest, the ESS looks like tropical forest plants.

(d) Large-scale ecosystem responses to resource availability

Fourth, we asked if the model could predict general patterns in NPP responses to progressive nitrogen limitation and C or N fertilization. Indeed, C fertilization leads to progressive N limitation, and the model predicts modest increases in above-ground production (figure 4b,c) with much larger increases in root production (figure 4d) under C fertilization. Alternatively, N fertilization leads to progressive C limitation and the model predicts large increases in above-ground production (figure 3b,c) with decreases in root production (figure 4d). Both of these effects of C and N fertilization are

commonly reported in empirical studies [2,29] and the model captures these qualitative responses. In our model changes in N availability has a larger effect on total NPP than changes in C. This empirical phenomenon is generally explained as plants being more limited by N than C [30,31], and this happens also in our model, but the game means that increased N also encourages aggressive pre-emption strategies above-ground, based on the C : N ratio. Thus, increasing N also promotes abrupt step-like increases in leaf NPP (figure 4b) and stem NPP (figure 4c) because the plants require additional C to combine with increased N. The asymmetric nature of light competition and the fact that plants require large amounts of C relative to N causes ESSs for leaf and stem production to increase in steps along large resource gradients. These abrupt steps are what appear to define Whittaker's biomes. Importantly, within each step on the total production surface, root NPP (figure 4d) declines with increasing N availability, but this is reset with each shift in plant functional type producing the overall positive trend. That is, within each biome we expect fewer roots at higher

Figure 2. Comparison of the distribution of model output (circles) and the observed empirical FLUXNET data (letters; boreal forest data are shown as 'B' and temperate forest as 'T') for absolute allocation (a–c) and relative allocation (d). The model output is fully independent from the empirical data, and should not be expected to fall on top of each data point. Rather, we highlight that the independently parametrized model output and observed data follow identical quantitative relationships. Electronic supplementary material, figure S3 explicitly compares the distributions of observed and predicted data as QQplots. Model output was based on 1000 model runs using randomly selected parametrization within a conservatively wide, but biologically realistic range of parameters (electronic supplementary material, table S2). Each circle represents output from one different random parametrization. (Online version in colour.)

Figure 3. The model predicts the global distribution of biomes and plant body types. (a) Total NPP (gC m⁻² yr⁻¹) predicted from the model over a range of N and C availability based on intraspecific competition to demonstrate how one set of parameters (electronic supplementary material, table S2) can evolve into any vegetation type naturally. Isolines and colours represent total NPP, and we have roughly labelled major biomes according to total NPP defined by Whittaker ([28]; electronic supplementary material, table S5). The portion of the plot that corresponds to environments where C is more limiting than N have been omitted because these conditions do not naturally occur on the Earth. (b) Ternary simplex of the fraction of NPP allocated to leaves, stems and roots for a range of total ecosystem NPP. Along a productivity gradient the model predicts the commonly observed shift in body plans that decrease root allocation, and increase in stem allocation (e.g. shift from herbaceous to woody plants). This output is based on our interspecific competition random parametrization algorithm (SI), but to permit visualization of these patterns only the first 100 ESS solutions at each level of total NPP are shown.

nutrient levels, but this negative relationship is a biome specific prediction, not a global prediction.

4. Discussion

The general game theoretic model we have developed provides a simple and surprisingly powerful model of primary

production, allocation, the global distribution of vegetation types and plant responses to C or N fertilization. The model predicts two independent datasets, on average, as well as the datasets predict each other, suggesting that the model uncertainties are no worse than uncertainties associated with measurement error. Considering that our output was based on the simplest first-order approximations of plant function, we find it remarkable that the model performs

Figure 4. Three-dimensional surface plots of NPP versus environmental N and C available for total (a), leaf (b), stem (c) and root (d) production. This is the same output from figure 2a, except it has been plotted as a three-dimensional surface instead and the production of each tissue pool is shown individually. The range of N_{avail} and C_{avail} have also been increased in this figure relative to figure 2a to illustrate how the model predicts NPP to change with changes in resource availability that might occur with global climate change. Increases in C_{avail} are hypothesized to have the largest effects on root production, while increases in N_{avail} are hypothesized to have the largest effects on stem and leaf production. Three anomalous root production values that exceeded $1000 \text{ gC m}^{-2} \text{ yr}^{-1}$ were omitted. (Online version in colour.)

as well as it does. For example, the harvest equations that translate leaf and root production into C and N harvest have just one parameter for the maximum rate of resource encounter. That such a simple model can capture as much variation in the data as it does makes us confident that our general mathematical structure of the game describes something fundamental about plant growth. As a game theory treatment of plant growth and allocation, we argue that it is successful because plant investment into roots, leaves and stems may be a triple tragedy of the commons as plants amplify production of these tissues to pre-empt each other's access to light, water and nutrients and maximize their competitive ability. In other words, if competitive games dictate tissue production and allocation in nature, then explicitly capturing this game theoretic overproduction of tissues in the mathematical structure of the model may turn out to be critical to predicting shifts in NPP and species distributions that are expected under climate change.

Indeed, dramatic shifts in NPP and plant species distributions are anticipated with climate change [2,4,32]. Our model has several advantages beyond its ability to predict empirical data (figure 1). First, allocation is not constant, but rather absolute and relative leaf, stem and root allocation are variables and thus allocation emerges as model predictions (figure 2). Second, the plant functional type does not have to be specified *a priori*, but rather emerges as part of the ESS solution (figure 3). Third, the use of the Cobb–Douglas

production function links above- and below-ground allocation using a continuously differentiable function, rather than a simpler minimum function, or the assumption of constant allocation parameters which allows for prediction of vegetation responses to both C and N limitation (figure 4). Fourth, all of this can be achieved with as few as five parameters (electronic supplementary material, table S2). Taken together, this provides a clear roadmap for how shifts in allocation, total NPP, plant functional type and progressive resource limitation might shape vegetation responses to shifting climate.

The application of game theory to vegetation modelling is not new, but we have brought together ideas about roots, stems and leaves into a single continuously differentiable function that employs a triple optimization to find the vector-valued ESS solution. We believe our modelling framework has reduced the problem to its simplest possible mathematical structure. For example, Dybzinski *et al.* [5] also modelled NPP as leaf, stem and root production and used a game theoretic optimization criterion. However, their model required 23 parameters, was designed for one vegetation type at a time, predicts monoculture stands and predicts a negative relationship between total and root NPP [5] instead of the positive one observed in the FLUXNET data (figure 2c). We believe that our novel use of the continuously differentiable Cobb–Douglas function to link above- and below-ground processes is what allows our model to generate the correct relationship for roots. However, an important strength of the Dybzinski

et al. [5] model is that it is analytically tractable, while our model can only be solved numerically with difficulty. In the future, it may be possible to combine the mechanistic physiological details captured by Dybzinski *et al.* [5], with the Cobb–Douglas structure of our model to enhance our understanding of the role of mechanistic processes to further improve our understanding of NPP.

5. Conclusion

The general game theoretic model we have presented here is simple but is capable of predicting: (i) the patterns and ranges of total NPP globally in two independent datasets (figure 1); (ii) the absolute and relative allocation relationships in leaf, stem and root production (figure 2; electronic supplementary material, figure S3); (iii) the global distribution of biome types (figure 3*a*) including the types of plants found within each biome from first principles (figure 3*b*) and; (iv) general responses of plants to resource gradients like progressive N limitation, and response to N or C fertilization (figure 4). Our approach removes the need to define vegetation types or allocation *a priori* but instead lets these emerge as ESS solutions via a vector-valued triple optimization. To generate output, we intentionally chose first-order approximations of plant function for the component functions of the model; however, users may implement the general form of the game using their own existing vegetation modules to obtain a dynamic link between above- and below-ground production and a game theoretic optimization criterion. Given the comparisons of output to data shown here, we expect that building upon

this very general game theoretic framework has the potential to greatly improve the representation of vegetation in a variety of the Earth systems models by capturing the triple tragedy of the commons that dictates overproduction of tissues in response to competition.

Data accessibility. The FLUXNET data are publically available at <http://dx.doi.org/10.3334/ORNDAAC/949> [33]. The MOD17 data are publically available at <http://reverb.echo.nasa.gov/reverb/> [26,27]. R code to run and reproduce all model results may be accessed at <https://github.com/ggmcnicle/PlantGames/blob/master/TripleTragedy>.

Authors' contributions. G.G.M. and J.S.B. developed the model equations. All authors contributed to model parametrization and discussion of analyses to perform. G.G.M. and D.J.L. analysed the model output and validation. G.G.M. wrote the manuscript and all authors contributed to revisions.

Competing interests. We have no competing interests.

Funding. This work was funded by a Natural Sciences and Engineering Research Council of Canada Post-Doctoral Fellowship and Banting Post-Doctoral Fellowship to G.G.M. and by the Department of Energy, Terrestrial Ecosystem Science Program (DE-SC 0006607) to M.G.M.

Acknowledgements. We thank FLUXNET for providing their NPP data and thank Ray Dybzinski for advice on FLUXNET data and for many discussions about game theory and plants. The MOD17 data were retrieved from the online Reverb tool, courtesy of the NASA EOSDIS Land Processes Distributed Active Archive Center (LP DAAC), USGS/Earth Resources Observation and Science (EROS) Center, Sioux Falls, South Dakota. We thank Jonathan A. Bennett, Abdel Halloway, R. Julia Kilgour, D. Marc Kilgour, Cory A. Wallace and Christopher J. Whelan for comments and discussion. We thank Ben Bond-Lamberty for suggesting the MOD17 analysis and for comments during review.

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