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SHORT COMMUNICATION



Future paths for the 'exploitative segregation of plant roots' model

Ciro Cabal ^a, Ricardo Martinez-Garcia ^b, Aurora de Castro ^{c,d}, Fernando Valladares ^{c,e}, and Stephen W. Pacala ^a

^aDepartment of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA; ^bInternational Centre for Theoretical Physics-South American Institute for Fundamental Research - Instituto de Física Teórica da UNESP, São Paulo, Brazil; ^cDepartment of Biogeography and Global Change, National Museum of Natural Sciences MNCN, CSIC, Madrid, Spain; ^dSchool of Applied Sciences, Edinburgh Napier University, Edinburgh, UK; ^eDepartment of Biology, Geology, Physics and Inorganic Chemistry, Rey Juan Carlos University, Móstoles, Spain

ABSTRACT

The exploitative segregation of plant roots (ESPR) is a theory that uses a game-theoretical model to predict plant root foraging behavior in space. The original model returns the optimal root distribution assuming exploitative competition between a pair of identical plants in soils with homogeneous resource dynamics. In this short communication, we explore avenues to develop this model further. We discuss: (i) the response of single plants to soil heterogeneity; (ii) the variability of the plant response under uneven competition scenarios; (iii) the importance of accounting for the constraints and limitations to root growth that may be imposed from the plant shoot; (iv) the importance of root functional traits to predict root foraging behavior; (v) potential model extensions to investigate facilitation by incorporating facilitative traits to roots, and (vi) the possibility of allowing plants to tune their response by accounting for non-self and non-kin root recognition. For each case, we introduce the topic briefly and present possible ways to encode those ingredients in the mathematical equations of the ESPR model, providing preliminary results when possible.

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1. Introduction

Based on a game theory model, the exploitative segregation of plant roots (ESPR)¹ postulates that plants respond to competition with a second individual by over-proliferating roots close to their stems and under-proliferating farther away from it. Hence, pairs of competing plants segregate their root systems from each other and exploit resources more intensely near their stems than isolated plants. When calculating how local under- and over-proliferation balance each other at the level of the whole root system, ESPR predicts that, compared to isolated individuals, competing plants over-invest in roots when growing in crowded populations, yet they under-invest in sparse populations.

This behavioral strategy has important implications for global carbon cycling in climate-change scenarios and for designing agricultural practices that improve crop efficiency.² By adopting a novel conceptual approach that focuses on the individual plants and accounts for explicit space, ESPR also represents a step forward to understand plant community ecology mechanistically.³ However, real-world conditions add many layers of complexity to below-ground competition that might impact the root allocation patterns predicted by ESPR.

In this short communication, we introduce some of the ingredients neglected in the original ESPR model (hereafter ESPRm) and discuss how they might lead to new results. First, we discuss more complex soil resource dynamics; second, uneven interaction scenarios; third, plant constraints from aboveground development; fourth, diversity in plant traits and strategies; fifth, biotic interaction mechanisms other than

competition; and sixth, sensing capacity of plant roots. Our main goal is to discuss how the existing ESPRm could incorporate these elements and how they would produce novel predictions to be tested experimentally.

2. Soil resource dynamics

Cabal et al.¹ developed the ESPRm to investigate the effect of resource competition on plant foraging behavior, but root scientists are also interested in the foraging behavior of plants with no competition. For instance, several studies report higher root allocation in resource-rich environments,⁴ or local root over-proliferation in resource-rich soil patches.⁵ The ESPRm is based on simple resource dynamics, namely a constant input, a density-dependent abiotic decay, and a biotic decay caused by plant root activity. Therefore, the ESPRm can also predict the spatial root distribution of a solitary exploitative plant in scenarios with different resource levels.

The ESPRm can thus conjecture plant foraging strategies of solitary plants (SM 1). For instance, it predicts that plants' response to resource limitation depends on whether it is due to a low resource input or a fast abiotic loss (Figure 1). If decreases in the resource input cause the stress, the ESPRm predicts that plants reduce both their root range and root density within that range. In contrast, when the stress is caused by increasing resource loss rates, it predicts that plants reduce their root foraging range but locally over-proliferate roots close to their stem, potentially yielding higher root biomass. This latter response follows the same rules predicted by ESPR for

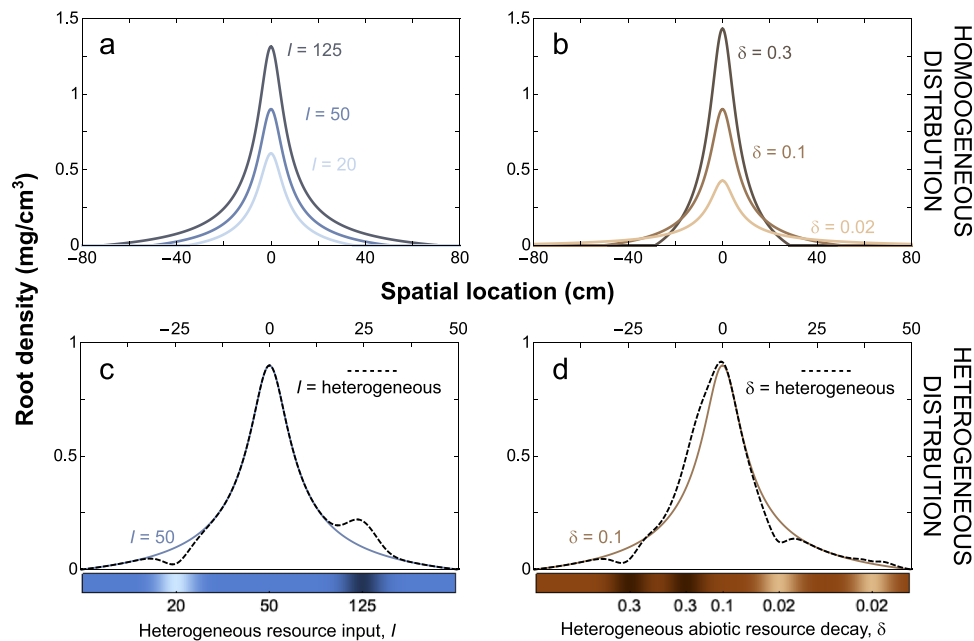


Figure 1. ESPRm predictions for the root density distribution of a single plant centered in the origin of coordinates, in response to different resource dynamics (based in **SM Eq. 4**). Top panels represent cases with spatially homogeneous resources. **a**– Root density increases and the root system expands with increasing resource input (I , mm day^{−1}). **b**– The root system shrinks, but the root density increases close to the plant stem with increasing resource abiotic loss rate (δ , day^{−1}). Bottom panels represent two examples with spatially heterogeneous resource dynamics, showing model predictions in complex scenarios where **c**– resource input is patchy (dashed line), as shown in the bottom color bar, compared to the homogeneous case with $I = 50$ (blue line), or **d**– resource decay rates is patchy in space (dashed line) compared to the homogeneous case $\delta = 0.1$ (brown line). Other parameter values: $\alpha = 1$, $C_b = 5$, $C_t = 0.2$. For parameter descriptions, see SM 1.

competing individuals (i.e., over-proliferation nearby and under-proliferation far away from the stem), highlighting that the exploitative segregation of plant roots may have simply evolved to allow plants to optimize resource uptake and not as a direct response to the presence of neighbors.

An excellent example of how plants may respond differently when soil impoverishment is caused by lower inputs or by higher abiotic loss rates of the resource is given in Cabal & Rubenstein,⁶ who measured savanna grass responses to water stress. They compared differences in root allocation strategies of two C4 grass species growing in two nearby sites with significant water input differences (precipitation) and, within each site, in locations with different abiotic decay rates (evaporation-driven drying rates). Their data show that both species produced more root biomass in the higher precipitation than in the lower precipitation site (significant for one species only), following the predictions shown in **Figure 1(a)** (unpublished results, SM 2). Additionally, in response to higher evaporation, root density increased in the soil surface (0–6 cm depth) but decreased in deeper soil layers. This result agrees with model predictions summarized in **Figure 1(b)**: root density increases close to the plant stem and decreases far from it when abiotic resource loss increases.

Environmental resource variations at large scales affect the root density distribution of plants. However, resource availability can also change at spatial scales that are finer than a plant root system range, and root scientists have been interested in understanding how plants can show phenotypically plastic responses to this resource patchiness. Plants adapt their root density to match the local resource availability in poor soils with resource patches.⁷ The ESPR model also works for

heterogeneous soil resource distributions caused by fine-scale variation of resource inputs (**Figure 1(c)**), abiotic decay rates (**Figure 1(d)**), or both.

However, assuming that resource dynamics is governed by a constant input rate and a density-dependent decay at every point of space constitutes an oversimplified picture. Soil resource dynamics might be highly complex, as represented by soil hydrology. The water available in a soil patch depends strongly on the water present in the surrounding compartments through infiltration, lateral diffusion, or evaporation,⁸ all neglected by the original ESPRm. Coupling the ESPRm framework to complex models of resource dynamics that include these additional processes and others, such as vertical gradients of resource availability or soil heterogeneity, will predict the spatial structure of root systems more accurately. For example, the ESPRm can incorporate lateral water transport by adding a diffusion term to the resource dynamics equation. Using Green functions and perturbative calculations⁹ (SM 3), the model is still analytically solvable and predicts that root systems get wider and less densely-populated near the stem as water diffusion gets more intense (**Figure 2**).

3. Uneven interactions

In nature, plant biotic interactions are highly uneven (i.e., each individual interacts with several neighbors of various sizes). Root scientists are interested in understanding how plant response changes in a competitive context where different plant densities¹⁰ or plants with different belowground sizes¹¹ interact, thereby modifying the competitive pressure. A detailed mathematical description of these uneven interactions will very likely

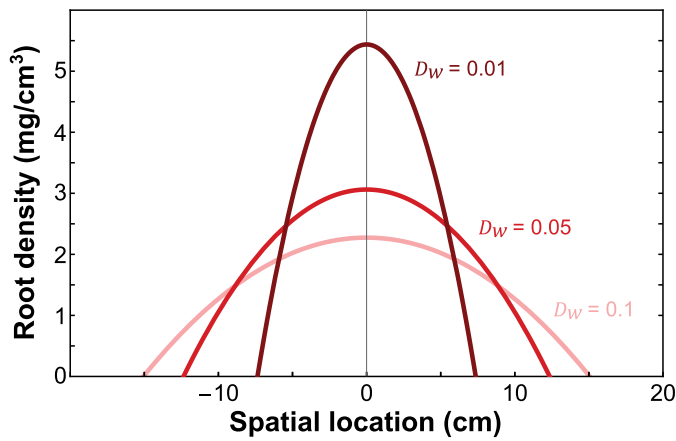


Figure 2. Spatial distribution of root density for three different water diffusion values (D_w , $\text{cm}^2 \text{ day}^{-1}$) (based in **SM 3 Eq. 16**). Other parameter values: $l = 50$, $\alpha = 1$, $\delta = 0.1$, $C_b = 5$, $C_t = 0.1$. For parameter descriptions, see **SM 3**.

result in a less analytically tractable ESPRm. However, as a first approximation to study uneven interactions, we can replace the root density of all non-focal plants with a free parameter that gives the density of non-self roots and solve the model by obtaining the spatial root distribution that maximizes the fitness-generating function as a function of that free parameter (**SM 4**). This spatial root distribution provides a general expression for the exploitative response of the focal plant to any density of non-self roots in the soil (**Figure 3**).

In general, this first approximation to study uneven interactions supports the general predictions of the ESPR for pairs of identical plants, i.e., in the presence of neighbor competitors, plants over-proliferate roots close to their stem and under-proliferate far from it (solid line in **Figure 3**). However, new interesting phenomena also emerge in these uneven scenarios.

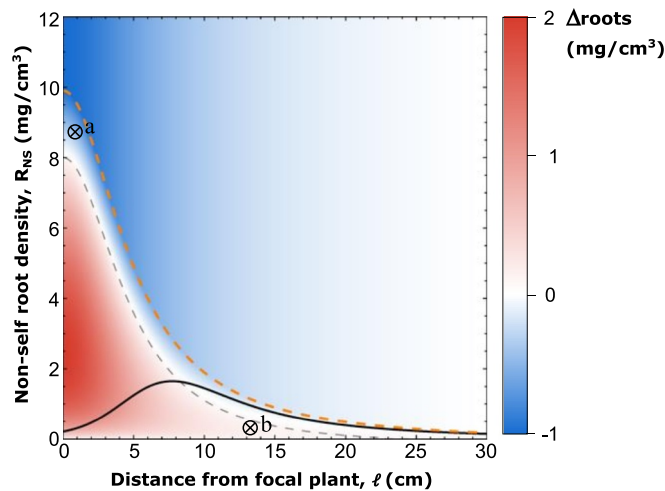


Figure 3. Difference in root production due to competition, $R^*(l; R_{NS}) - R^*(l; R_{NS} = 0)$ (based in **SM Eq. 20**), as a function of the distance to the stem of the focal plant and the density of non-self-roots. The dashed gray line indicates the relation $R_{NS}(l)$ such that competition does not result in differences in root production. The orange dashed line indicates, for each value of l , the minimum density of non-self roots such that $R^*(l; R_{NS}) = 0$. Points **a** and **b** are two specific cases discussed in the text. The solid black line represents the realized combinations of l and R_{NS} in the ESS solution at positive coordinates of Figure 1b in Cabal et al.¹ Parameter values: $l = 50$, $\alpha = 1$, $\delta = 0.1$, $C_b = 5$, $C_t = 0.1$. For parameter descriptions, see **SM 4**.

For instance, the focal plant over-proliferates roots very close to its stem if the density of non-self roots is similar to the optimal density of self roots. However, it can also under-proliferate roots when non-self roots are extremely dense (point **a** in **Figure 3**), a situation that mimics, for instance, a plant growing in a crowded community. Also, under-proliferation dominates far from the stem, but one could observe over-proliferation at very low densities of non-self roots (point **b** in **Figure 3**). This situation could correspond to a large focal plant unwittingly preventing the growth of saplings into big competitors.

A recently published experiment by Lepik *et al.*¹² tested, both in monocultures and species mixtures, the spatial root distribution and root investment of plants growing at different planting densities. Their results showed higher complexity than the basic ESPR predictions for identical pairs of plants. For example, when increasing the number of neighbors, the authors found higher root segregation both in monoculture and species mixtures. These observations coincide with the prediction that, for high non-self root densities, root proliferation should decrease at increasing non-self root densities regardless of the distance from the focal plant (**Figure 3**). In species mixtures with plants of different sizes, Lepik *et al.* generally found that larger plants proliferated roots by their neighbor's insertion point to the substrate. This result seems to agree with the model predicting larger plants over-proliferating roots even far away from their stems as in point **b** (**Figure 3**).

4. Constraints from aboveground

In the previous section, we discussed the case of uneven plant competition, as represented by competing plants of different sizes. We presented a general exploitative model solution that provides the spatial root distribution of the focal plant for any non-self root density. An alternative approach is to implement into the ESPRm, which original version accounts for identical plants, actual plants of different sizes. There are two possible mechanisms leading to different plant sizes. First, plants can have root systems of different sizes if they have different root traits that result in different optima. In the original ESPRm, plants produce any root if it provides a positive net reward to the plant, which limits the range of the root system. We will address this case in the next section. Alternatively, external factors can limit plant size to match plant shoot development. In this case, allometry rather than the root optimum determines root size.¹³ Indeed, the root absorbing surface of plants correlates with its transpiration leaf area to ensure sap flow,¹⁴ and plants with small shoots may have root systems smaller than the root optimum.

Adapting the ESPRm to the constraints from aboveground organs, either dynamically to simulate plant growth or statically if adulthood shoot traits mostly limit the size of a plant species, would require a different approach to solve the model. Instead of calculating the root density that maximizes the net reward in each soil patch, we need to obtain the best root density distribution possible constrained to the total root biomass available. The total root biomass given by this solution is inferior to the optimal, and alternative root distributions for the same plant would still give positive net rewards to plants. This additional constrain to root

growth may produce interesting competition outcomes, different from the ESPR. For instance, ESPR optimizes root density in each soil patch independently, meaning that competition with non-self roots in some portion of its root range should not affect focal plant root density in other soil regions whatsoever. However, plants limited by shoot size can benefit from occupying soil patches free from non-self roots as a response to competition. Therefore, plants in the adapted ESPRm may expand their root ranges toward these free patches when competing.

5. Plant traits and strategies

ESPR assumes that competing plants are identical. However, plants display a substantial between- and within-species diversity of functional traits. Such diversity is fundamental to understanding plant interactions mechanistically.¹⁵ For instance, specific root length has positive effects on plant resource foraging efficiency.¹⁶ To a certain extent, the original ESPRm allows incorporating root phenotypical differences through the parameters that represent the rate of resource absorption per root biomass, the resource-biomass conversion factor, the cost of growing fine, absorbing roots, and the costs of growing thick, transportation roots. By tuning these parameters, we can adapt the ESPRm to describe several plant root physiological and architectural traits. For example, specific root length can be adjusted by parameterizing the costs of fine roots, and the rate of resource absorption per root biomass provided a specific root geometry. Exploring differences in these parameters, researchers could study competition between plants of different species and their plastic responses to different environments from a functional trait approach.

Finally, Cabal *et al.*¹ obtain the spatial root distributions resulting from two possible plant foraging strategies, exploitative and cooperative segregation. The ESPR, corresponding to exploitative segregation, is a selfish strategy expected to evolve in natural populations. Alternatively, the cooperative segregation is an altruistic strategy that results in a root density distribution that optimizes the collective plant yield in crops. In between these two extremes, we can imagine a whole spectrum of intermediate strategies. An interesting experiment would test empirically whether and how human domestication of plants has successfully modified root behaviors toward more cooperative ones. In the experiment by Cabal *et al.*¹ the plant foraging strategy is measured for a traditional Spanish cultivar of pepper plant, finding evidence for the ESPR. Does the wild variety of that same cultivar, *Capsicum annuum* var. *glabriusculum*, show an even more selfish behavior that enhances local root over-proliferation and hence makes a tragedy of the commons¹⁷ more likely? On the other hand, are modern engineered bell pepper varieties more cooperative and therefore more efficient at using soil resources? Is there still room for improvement? These, and related questions asked on other domesticated plants, still lack an answer.

6. Additional interaction mechanisms

The ESPR predicts the foraging behavior of plants that are competing exploitatively for soil resources. There are, nevertheless, many biophysical mechanisms, other than competition, that can determine the net biotic interaction among

plants. Some of these interaction mechanisms may have further negative impacts on plants, such as allelopathy.¹⁸ Others have positive effects and can potentially lead to plant facilitation situations, in which a plant has a positive net effect on its neighbor.¹⁹ The ESPRm can potentially become a standing point to develop more complex plant interaction models (PIMs).³ A PIM is a spatially-explicit model in which plant biotic interactions emerge from a game-theoretical description of the interaction between plants and their environment. Incorporating facilitative traits to the plants in the ESPRm, i.e., traits that lead to microclimatic or soil amelioration at a cost to themselves, is a straightforward way to study plant facilitation following PIM approach.

A good example of plants with facilitative traits are plants able to increase the concentration of a soil resource at the cost of biosynthesizing and exuding chemicals to the soil,²⁰ known as ecosystem engineers. For instance, some plants can stimulate soil microbial activity, which causes an increase in soil nitrogen concentration.²¹ Plants can also increase the availability of some resources directly, for example, by exuding chemicals that mobilize phosphorus (P) in the soil.²² Studies have investigated how a plant can benefit from the presence of neighboring ecosystem engineers able to mobilize P in P-impooverished soils,²³ and how they would alter their spatial root distribution growing more roots toward such plants.²⁴ The ESPRm, extended to become a PIM, could yield accurate predictions for these plant foraging strategies and help to understand theoretically the positive net interactions that have been reported empirically.

7. Sensing capacity of plant roots

The ESPR does not require any root sensing mechanism, and it relies solely on plant-resource interactions. In the ESPRm, plants adjust their root proliferation in each soil location to the resource availability, determined by the balance between inputs and decay rates. Resource decay has an abiotic component due to physical processes and a biotic component due to the presence of non-self roots that drives plant response to the presence of neighbors. However, the extraordinary ability of plants to identify root tips within a soil patch could have important implications for their root foraging behavior because it allows plants to tune their ESPR response and adopt strategies that may provide higher fitness benefits. Plants use physiological tools, such as root exudates²⁵ or electric signals,²⁶ to detect non-self roots²⁷ and differentiate between kin and non-kin roots.²⁸ Kin recognition gives excellent examples of how plants may adapt their foraging response to their relatedness to competitors.²⁹ Studies have found that, in some cases, kin recognition may explain plant root distributions better than any other competitive mechanism.³⁰ While the ESPRm is purely exploitative, incorporating sensing mechanisms would allow plants to modify their exploitative response to avoid engaging in a losing struggle, preemptively defend a territory, or cooperate with conspecifics.

For instance, we have previously shown that plants in the ESPRm exploitatively underinvest in soil patches with a very high density of non-self roots (point a in Figure 3). Plants benefit from unwittingly retract from these soil patches because

they avoid engaging in competitive behaviors with superior neighbors. Plants able to detect these spots of high non-self root density may actively potentiate that behavior and refrain from engaging in a local competitive race with a strong competitor. Similarly, plants exploitatively overproliferate roots in the surroundings of neighbors with small root systems (point b in Figure 3) –presumably smaller plants–. This behavior may be beneficial for larger plants because it allows them to preemptively terminate seedlings that could become competitors. Like in the latter example, large plants able to sense small neighbors may increment this preemptive over-proliferation of roots and actively hinder their growth. Also, plants could behave more cooperatively when encountering their own offspring's, vegetative clones', or even conspecifics' roots while responding exploitatively to the presence of heterospecific neighbors. The cooperative response, also addressed by Cabal et al.¹ requires sensing non-self roots. Researchers could explore these scenarios by introducing in the model a decision-making process based on explicit plant recognition of root tips.

8. Conclusions

The exploitative segregation of plant roots (ESPR) is a theory based on a simple mathematical model of competition between two identical plants foraging a soil resource. The ESPR is sufficient to trigger a paradigm shift in plant root ecology by proving that previous approaches to below-ground plant foraging, such as root range³¹ and the root investment approach,³² are incomplete. It is only by combining both approaches and studying spatial maps of root density distributions that we will achieve a full understanding of plant foraging behavior and below-ground competition. However, ecosystems are highly complex systems that a simple, analytically tractable model cannot fully explain. Based on empirically supported principles, we have discussed several biotic and abiotic elements that may add further realism and complexity to the ESPR model (ESPRm). While none of these features seem to deny the principle of the ESPR, accounting for them would result in better quantitative predictions of how plants forage in the soil. Plants likely tune their ESPRm response to neighbors depending on other factors, such as soil resource dynamics, constraints from the aboveground, sensing of non-self and non-kin roots, or the phenotypical traits of the interacting individuals. We believe that the progressive addition of these layers of complexity will help develop ESPR as a general theory for root foraging behavior in the coming years.

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Disclosure of interest

The authors report no conflict of interest.

ORCID

Ciro Cabal  <http://orcid.org/0000-0002-7222-1991>
 Ricardo Martínez-García  <http://orcid.org/0000-0003-2765-8147>
 Aurora de Castro  <http://orcid.org/0000-0002-7384-7128>
 Fernando Valladares  <http://orcid.org/0000-0002-5374-4682>
 Stephen W. Pacala  <http://orcid.org/0000-0003-4450-6532>

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