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Review

Tragedies and Crops: Understanding Natural Selection To Improve Cropping Systems

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Plant communities with traits that would maximize community performance can be invaded by plants that invest extra in acquiring resources at the expense of others, lowering the overall community performance, a so-called tragedy of the commons (TOC). By contrast, maximum community performance is usually the objective in agriculture. We first give an overview of the occurrence of TOCs in plants, and explore the extent to which past crop breeding has led to trait values that go against an unwanted TOC. We then show how linking evolutionary game theory (EGT) with mechanistic knowledge of the physiological processes that drive trait expression and the ecological aspects of biotic interactions in agro-ecosystems might contribute to increasing crop yields and resource-use efficiency.

Trends

Current increases in crop production are falling below the 2% annual rise needed to maintain global food security, while restrictions on the use of synthetic fertilizers and pesticides are increasing. This calls for new more ecology-based directions in crop breeding and management.

Optimal plant communities with maximum growth or seed production are often not stable against invasion by individuals that invest more in resource harvesting. These effects have been framed as TOCs and conflict with the need in agriculture for increased yields and ecosystem service provisioning.

Recently there is increased interest in assessing how these TOCs arise and how this knowledge in turn may give directions for crop breeding and management. Linking evolutionary game theory (EGT) – the key mathematical tool to analyze natural selection in situations where organisms interact – to our increased understanding of the physiological regulation of trait expression and ecological interactions in agro-ecosystems provides a framework through which this can be achieved.

TOCs in Plants and Links to Crop Management and Breeding

Understanding how properties of plant communities arise from the traits of constituent plants is complicated by the fact that plants interact with each other, as well as with other organisms (e.g., pathogens, herbivores, or **mutualists**; see Glossary). The effect of a given set of traits on plant performance should therefore be viewed in relation to strategies of the other organisms in the system [1]. An issue that is receiving increasing attention in the plant ecological literature is the conflict between individual plant fitness and performance of the vegetation as a whole [2–5]. **Evolutionary game theory** (EGT) studies propose that plant communities with trait values that would maximize community-level performance often cannot resist invasion by plants that invest more in resource harvesting than their neighbors (Table 1). The community might therefore evolve towards a non-optimal state in which all plants overinvest in these functions, but at the expense of fitness-related functions of the population such as reproduction or reduced survival through decreased disease or pest resistance; a phenomenon denoted a **tragedy of the commons** (TOC) [6] (Box 1). The most intuitive example is plant height. Because the costs of support tissue increase with plant height, short stature is optimal in terms of maximum seed production. However, a population of plants with such an optimal allocation to support structures can be invaded by a taller individual because this individual acquires more of the shared resource light [4]. A suite of other traits have been similarly implicated, ranging from above and below ground traits to the interaction with other organisms (Table 1).

Occurrence of TOCs in vegetation stands will have important implications for functioning of managed and natural plant communities [7–9]. Despite these potential implications, EGT analyses of TOCs in plant communities have been mainly limited to theoretical analyses, and implications for real plant-based systems have been poorly quantified (but see [10]).

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Table 1. A List of Traits for Which a TOC Has Been Described in the EGT Literature[a]

Trait	Resource or Service Provider	ESS Relative to Optimum	Explanation
Plant height [4,36]	Light	Taller stature	Shorter plants avoid excessive costs of support or opportunity costs such as lowered defense, but in such a population a taller individual gains advantage by capturing more of the available light
Leaf angle [57]	Light	More horizontal leaves	Vertical leaves facilitate efficient light distribution, but in such a population a plant with more horizontal leaves captures more of the available light
Leaf area [49,52,58,59]	Light	More leaf area	At given nitrogen supply there is a leaf area that optimally balances light capture and leaf N per unit area, but in such a populations a plant with larger leaf area captures more of the available light
Specific leaf area (SLA) [49,60]	Light	Higher SLA	Similar argument as for leaf area, noting that larger leaf areas can be produced by leaves having high SLA
Leaf turnover [61]	Light	Faster leaf turnover	Fast leaf turnover can be wasteful in terms of nutrient losses, but also enables plants to transport nutrients upwards and produce more leaves at the top of the canopy
Root mass [5,28,62]	Soil resources	Larger root mass	There is a size of the root system where the difference between invested plant resources and returns (soil resources) is maximized. However, in such a population a plant with more roots gains a larger share of the available resources
Maximum transpiration [63]	Water	Higher maximum transpiration	Plants with higher transpiration rates take a larger share of the available water, thereby invading a vegetation that would maximize steady-state biomass
Defense [35]	Light or soil resources	Lower defense level	In competition with other plants it pays off for an individual to lower defense because this could entail greater competitiveness
Flower size [2]	Pollinators	Larger flowers	In a population with optimal flower size, an individual with larger flowers attracts a greater share of the available pollinators if these are attracted by the size of floral display
Fruit size [2]	Dispersers	Larger fruits	In a population with optimal fruit size, an individual with larger fruits attracts a larger share of the available dispersers, as such fruits give dispersers a larger reward
Male reproductive parts [64]	Mates	Larger investment	In a population that optimizes allocation between male and female flowers or floral parts, an individual investing more in the male function (pollen production) reaches a larger share of potential mates, and the costs of producing offspring (seeds) is carried by the individuals that produce more female parts
Flowering time [64–66]	Light or soil resources	Flower later	There is a flowering time where the size of the vegetative part and the time left for seed production are optimized, but in such a population a later-flowering plant captures more of the available resources

Glossary

Cheater: an individual that gains a benefit from the collective without investing in the collective itself. These individuals can also be called ‘free riders’ [3].

Cooperation: behavior whose evolutionary stability depends on actual benefits to another [69].

Evolutionary game theory (EGT): the application of game theory to evolving populations of organisms in biology [1]. Distinctions with classic game include considering strategies as inheritable traits rather than as deliberate choices, and the payoff is expressed as Darwinian fitness.

Evolutionarily stable strategy (ESS): a strategy which, if adopted by a population in a given environment, cannot be invaded by any alternative strategy that is initially rare [70].

Jasmonic acid (JA) response pathway: a biosynthetic pathway that is activated in plants in response to attacks by necrotrophic pathogens or chewing insects [40].

Mutualism: a relationship between two species of organisms in which both benefit from the association [44].

Payoff: the overall return on investment gained from a particular strategy or behavior [3].

Rhizobia: soil bacteria that fix atmospheric nitrogen (diazotrophs) after becoming established inside root nodules plants (in the Fabaceae family). To fix nitrogen, rhizobia require a plant host; they cannot independently fix nitrogen [47].

Salicylic acid (SA) response pathway: a biosynthetic pathway that is activated in plants in response to attacks by biotrophic pathogens [40].

Shade-avoidance syndrome (SAS): a suit of traits and responses plants have evolved to escape from shade [39].

Split-root experiments: experiments in which roots of plants are split and the splits can be grown in different pots. As such two plants can have part of their root system in two pots which they share [5].

Tragedy of the commons (TOC): a situation in which individual competition reduces the resource over which individuals compete, resulting in lower overall fitness for all members of a group or population [3].