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PM

To: "BassiriRad, Hormoz" <hormoz@uic.edu>

Cc: t.buckley@sydney.edu.au

Hi, Hormoz (and Tom, whom I'm copying because he's a great modeler),

Katul has some bright ideas, and the two papers are interesting, I think, for the perspectives paper. I myself have made **optimality models, and they're seductive, but current ones are incomplete**. (Well, all models of the Universe are incomplete. As a friend once said, we can make more and more complete models of the world until we get to the ultimate model, the Universe itself, which is what we couldn't comprehend in the first place. There's a higher optimality in knowing when to stop adding things ad hoc!). I'd like to offer a broad perspective on the use of optimality models.

Maximal growth is only part of the story of natural selection. Models that include **stochastic risk** of herbivory or lethal frost or drought are more realistic (going back to, e.g., Partridge and Denholm, 1965) Also, the seminal optimality model of Cowan and Farquhar that these two papers you sent are built on **counts photosynthesis at any stage as equally useful**, but much more is known by people who look at reproductive stage partitioning, such as nut tree growth modelers. The model also counts **all water as equally accessible**, independent of drought-induced damage to plant organ or even changes in soil-to-root hydraulic resistance or spatial distribution of water in the soil.

Let's not forget the **classic problem of information**: the plant can't sense when and where the water will be, only relying on what its "genetic memory" of past environments were - its response programs were generated by natural selection, with no guarantees that the future is similar. Ask the dinosaurs or the ammonites at the K-T boundary about being made "wrong" for a radically new environment...or even look at the failure of most exotic species (only a few winners get the attention). They don't establish in a new environment, because their responses to resource availability patterns are quite suboptimal; they don't know the neighborhood.

We need an optimality model closest to explaining what natural selection creates. Such a model is one that **deals with, among other things, multiple constraints** - limited water, but also limited N, presence of herbivores, etc. It's hard to do, as shown in the elegant math needed by Tom Buckley or Graham Farquhar or Ülo Niinemets just to incorporate the co-distribution of light and N, water and N, or all 3, even while not addressing risk or the more complex relation of gene success to population-level performance.

Short digression: **even with a single constraint of water, the model requires deep knowledge of the biology and some good math to get a complete answer.** I always point to the tour-de-force of Tom Givnish ((1987) Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. In \fOn the Economy of Plant Form and Function\fR, ed. TJ Givnish. Cambridge University Press, Cambridge, pp. 171-213.). Everyone who uses Cowan and Farquhar's optimality equation assumes that the value of the constant, λ , can be determined – and I take that to mean from biological and physical knowledge, not just curve-fitting. Givnish worked through the biology of, I recall, radish, to calculate the constant - an amazing amount of work. Does the constant vary between species and environments, in a way that **we can predict robustly rather than fit to every new dataset?** One hopes so. After all, our goal even in our one paper is to explain some connections among the variabilities in traits.

Second, what's need is a **model with a mixed objective function** - not total growth in one season, nor even reproductive output in a single season, but multi-year/multi-plant output, which is more complex, esp. for perennials. **The gene is the unit of selection, not the individual plant.** In a mathematical formulation, one approach is to present multiple measures of success (regarding, say, growth per unit of water, growth per unit of nitrogen, growth traded off against herbivory risk as a function on N content, etc.) and give different weights to each. This is a first cut; the combination of individual measures into a final measure need not be a linear combination.

Can anyone build a full model of this type? It's been done for multiple constraints on photosynthetic performance, as in the work on N and water, N and light, or N + water +light that I cited above. However, it's not been done addressing multiple objective functions such as risk distribution, nor information constraints, etc. So, the answer is, not yet, but there are **lots of pieces in the literature, most of them outside of biology at the moment.**

Going back to the formulation of the goal, the objective function: there's much information about managing risk and having systems adopt what are called **mixed strategies** - not always having a fixed response to a given set of conditions, especially by having **multiple copies of a system**, each operating a little differently so that the maximal number of them survives. These ideas come up in communications systems, military systems, etc. but the same thing happens with plants (or other living organisms): the gene is the unit of selection, and any one gene (perhaps controlling part of stomatal conductance, such as by setting mBB) is tossed in with diverse combinations of other genes in the many individuals in a breeding population. We never see a single genotype in a breeding population; nature hedges its bets all around.

Biologists have to come to grips with more realistic models of optimization. There's lots to gain by **working with people in physics, engineering, and math**, with powerful techniques and with attendant insights coming out. They have to deal with multiple objective functions, multiple constraints, and, sometimes, both. For one thing, they know that **constraints can be holonomic** (expressed as an equation valid for all time, such as a total amount of water available) **or nonholonomic** (expressible only in terms of local changes, not a grand total). **They also know that optimality can be incomputable** – what may be an N,P-complete problem. The only way to find the optimum is to test every possible solution. If you have 20 traits with only 2 values each, high/low, there are $2^{20} = 1,048,576$ combos to test. Nature has even more gene combos to test. **Nature, and engineers, rely on statistical optimization**, genetic recombination (constrained by incompatibility mechanisms, etc.), and engineers rely at times on simulated annealing. It's cool to think of the possibilities

In short, **optimality models are fun**, they appear to address some biological realities, they are mathematically beautiful, often....**but they are very challenging to do right. I'm certainly a partial offender, but I got paroled.** I'd like to go back to them, drawing in the insights from the physicists, engineers, and mathematicians. I'd need another half-lifetime. **There are people who could take this up together.** I'd put Tom Buckley and Graham Farquhar together with Marty Golubitsky (Math, Ohio State), a couple of communications and robotics engineers, and maybe a really good economist.

I would like to put a modest section in the perspectives paper on this topic, perhaps of greatest interest to modelers, but also catching the eye of evolutionary biologists and others.

Cheers,

Vince

Tom
Buckley <t.buckley@sydney.edu.au>
to me, Hormoz

5/5/14

Hi Vince and Hormoz,

Hard to argue with Vince on this.

1. Resource economics is sufficiently difficult to navigate in the context of plant function, with its 10ⁿ simultaneous constraints of physics and history, that few biologists can be trusted with it. I know I can't, and I'd trust myself more than most.

2. Vince asked (rhetorically?) whether anyone can build a full optimisation model. I think not. The logical basis for the approach is that it mimics the history of natural selection that gave rise to extant patterns. But we can't model that history -- we don't know nearly enough, and I doubt that we ever can. Selection is driven by things that have varied dramatically and non-randomly over the recent evolutionary history of land plants.

3. As for current work that is allegedly based on optimisation theory: most of it is really just based on an unfounded assumption about the conservative nature of integrated water loss. There's no economics in it. And the apparent economic foundation is, itself, fatally flawed. See my recent paper with Stan Schymanski, attached.

4. Even at the fairly small scale of a single canopy, and even taking into account as much of the gory detail as current technology allows, it doesn't look like plants come close to optimising resource distribution according to classical definitions. See my other two recent papers, attached. So we're left with a nail, looking for a hammer. It's a bad position to be in.

5. In the end, we have to ask, what do we learn by doing optimisation theory? As a result of all my work in optimisation, I've gained a better understanding of how all the processes link together mathematically, but I can't tell you much more about how plants function. The major take-home messages are (a) everything is co-limiting in the optimum, so questions like, "what is the limitation that causes x?" are ill-posed, and (b) plants generally behave something like optimally, but not exactly, because of various constraints, some of which are poorly known. Item (a) isn't knowledge about plants; it's advice about how to ask questions about plant function. Item (b) is just a re-statement of Darwin. You could argue that item (a) is valuable, but biologists are such reductionists that I doubt they'll ever pay much attention to it. I was practically crucified by 7 different reviewers for trying to publish that point during the 'hydraulic limitations to tree height and NPP' era.

So I'm washing my hands of optimisation theory. You heard it here. It's a bottomless pit filled with circularities and unanswerable questions. Like metabolic scaling theory, it's a great way to get a slew of papers and one's own personal corner of the journal Nature. And it's often very mathematically/aesthetically appealing. But I don't think it adds much value.

Cheers

Tom