Multiscale Modeling of Ecosystem Structure and Function

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The dynamics of biological systems, from cells to communities and ecosystems, have been hypothesized to follow optimal trajectories shaped by selection pressure that force organisms to maximize their fitness and reproductive success. This concept has been particularly successful in explaining the form and function of terrestrial vegetation from eco-hydrological and carbon-economy perspectives, and across spatial and temporal scales. Any optimality model is based on three key ingredients: an objective function that describes the gain that needs to be maximized or loss to be minimized, a control variable that shifts the dynamics in the desired direction, and a set of constraints that account for environmental conditions and conservation laws bounding the system. All three ingredients are difficult to define and quantify - especially in complex biological and ecological systems. Despite these difficulties, optimality approaches may complement process-based approaches when mechanistic knowledge is scarce. At the leaf scale, it is often hypothesized that carbon gain is maximized, thus providing a quantifiable objective for a mathematical definition of optimality conditions. Eco-physiological trade-offs and fluctuating resource availability introduce natural bounds to this optimization process. In particular, carbon uptake from the atmosphere is inherently linked to root-water uptake from the soil. Hence, the multi-scaled fluctuations in soil moisture do constrain the amount of carbon assimilated into new biomass. The problem of maximizing photosynthesis at a given water availability by modifying stomatal conductance, the plant-controlled variable to be optimized, has been traditionally formulated for short time intervals over which soil moisture changes can be neglected. This simplification led to a mathematically open solution, where the undefined Lagrange multiplier of the optimization (equivalent to the marginal water use efficiency) is determined via data fitting in an ad-hoc manner. Here, a set of models based on different assumptions that account for soil moisture dynamics over an individual dry-down are proposed so as to provide closed analytical expressions for the carbon gain maximization problem for varying soil moisture resources, atmospheric CO₂ levels, and vapor pressure deficit. Bridging these theories with widely used empirical formulations of stomatal conductance in climate models are also discussed.