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Eco-strain in model forests

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Abstract

A new perspective in forest modeling, based on analogies with continuous media physics, is presented. There are two central concepts, one called *eco-strain* in biomass production, and the other *nonlinear allometry*. Previously, it was shown that our models, based on works of the pioneers F. Clements and E. Odum, allow exactly 8 types of schemes for succession in dominant/codominant forestry, which conserve nutrients. It is shown that exactly 5 are eco-strained, including competitive, parasitic and mutualistic schemes, whereas 3 are eco-unstrained, and are reversible deformations of the classical straight-line allometries of Huxley. All are cost-preserving over the longer timescale.

1. Introduction

1.1. A little philosophy of vegetation

The American scientist, F.E. Clements (1874–1926), was the foremost ecologist in North America in the early 20th century [13,16,34,35]. In 1915, Clements conceived of the forest plant community as *an actual organism* having a characteristic development analogous to the embryological development of an individual. For him, each kind of developmental process was to be characterized by a series of events: *succession* being a series of ecological stages *(eco-scenes)* that a community goes through until *climax* is reached, while the series of events during embryogenesis culminates in an adult individual. Nowadays, this view is espoused by Odum [29,28]. We have recently exploited this analogy mathematically and have shed light on both types of processes [5,8,7]. *Heterochrony* or time-sequencing changes of developmental events is a main theme of these works [23,24].

Historians recognize that Clements was influenced by the German tradition known as *naturphilosophie* [12,34,35]. This idealistic European philosophical school started in the late 18th century with J. von Goethe, who thought it necessary to consider the entire life history of a plant and who subsequently strongly influenced A. von Humboldt, the recognized father of Plant Geography. Humboldt searched for mathematical laws in Geography and discovered the "isotherm". He conceived of the Earth as compartmentalized according to types of climate and conditioned by temperature and rainfall. Humboldt perceived a given region of vegetation through the history of its plant forms, via

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the physical influences of climate and mineralogical conditions. His views are close to that of Clements [16,35]. He was succeeded by A. Grisebach, who carried his ideas into the mid-nineteenth century. Grisebach coined the term *formation*, later used by Clements, which further developed Humboldt's idea of *physiognomy*. He demonstrated how physiognomy, the form of plants (needle, leaf, branching and trunk) was determined largely by climate. O. Drude was Professor of Botany at the Dresden Botanical Gardens in the early 20th century [13,34,35]. It is known that works published by Drude, strongly emphasizing *social integration of communities responding to climate*, directly influenced the Clements view of Grassland Ecology [13,34,35]. Furthermore, the German philosopher I. Kant had a powerful influence on all of the above mentioned. His view of a *harmoniously functioning universe, which historically unfolds into its ideal forms*, motivated Goethe and Humboldt to form their own views on plant growth, geographic distribution and community structure [34,35]. Also, in the mathematical theories we use, history plays a central role in that production over a period of time is a basic quantity [4,8,10]. These men may be considered essentially *neo-Lamarkians, rather than neo-Darwinians* (just in terms of ideas, as some pre-dated one or both) in that the relationship between environment and "organism" envisaged by them was direct; the plant community responded with changes in structure, when subjected to the forces in the environment such as temperature, light and moisture.

If the name of the great German poet comes as a surprise in the present biological context, it should be recalled that Goethe made significant contributions to both animal and plant morphology, recognized even today. Goethe postulated a single leaf type (Blatt) for the array of lateral appendages on a stem, such as foliage leaves, sepals, carpals, bracts, and various flower organs. This "Blatt" was useful as a mental means of deriving all appendages from a single *ideal type*, but it carried *no phylogenetic implications*. Nowadays, it is recognized that, *histologically* speaking, all these *modular units*, to use terminology of botanist Harper [18], are the same. Furthermore, there is a suggestive correspondence between Goethe's "Blatt" and Harper's "Modular Unit" (including, as well, shoots, buds and roots). We believe this can serve as a philosophical foundation for the ecological theory of Harper, based on notion that *an individual plant is a set of populations*, each a type of modular unit (see [12]). We have exploited this correspondence with success in [5,8,11,14] and elsewhere.

1.2. A brief history of allometry

In the year 1746, P.-L. de Maupertuis published his *Principle of Least Action* in a precise mathematical form which later was extended by L. Euler, W. Hamilton and J.-L. Lagrange. They based their subsequent development of modern Classical Mechanics on this principle. In fact, Maupertuis believed his principle applied not only to physics but also to biology. He envisaged a specific role for it in plant vegetative growth and the motion of animals, according to historian B. Glass [17].

In regard to plant growth, development and ecology, our previous work indicates that although there are a few examples where the principle actually seems to work, mostly it can *not* be used as a founding principle. Instead, a weaker form of *energy conservation* is to be employed to model, for instance, nutrient cycling in a forest ecosystem [5,7,10,11,14].

In 1936, Sir Julian Huxley introduced the concept of Allometry, or the experimental study of the relative growth of parts of animals, via log–log plots of measurements of morphological characters of individuals in a Euclidean background geometry. These plots resulted in straight lines via the statistical method of least squares [21]. Around the same time, another Englishman, Sir Joseph Needham, did experimental work which seemed to show that straight-line allometries he discovered between amounts of simple chemical compounds found in developing embryos constituted, in his own words, the "chemical ground plan for development" [26].

A. Laird's 1965 experimental work on vertebrate growth ultimately led to Huxley's Allometric law [19]. Both her work and that in the early 1940s by Nobel prize winning physiologist, Sir Peter Medawar, on the experimentally derived concept of "growth energy" for embryonic cells in culture [22,25], indicated that growth processes are described by the Gompertz curve, rather than, say, the logistic curve, although both are S-shaped (see [3]). Laird pointed out that since organs in an individual grow with the *same* constant Gompertz rate, the allometric law logically followed. These Gompertz type results have been central to our mathematical modeling methods [5,8,11,14].

In 1944, the American forester, J. Kittredge, used allometry to estimate the crown biomass of trees in a forest stand by measuring the trunk girth, or diameter at breast height (DBH) [20]. Again, there are the experiments of botanist J. Harper in 1962 who found Gompertz curves to be the best (least squares) fit description of growth of simple aquatic plants (see [18]). Most recently, there is the book *Plant Allometry* by Karl Niklas [27], who records a variety of plant