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Finslerian Volterra–Hamilton systems in Clementsian forest succession

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Abstract

Use is made of F.E. Clements' classification scheme for forests to model succession. We apply an approximation procedure which allows concentration on dominant and codominant species in the model forest. Volterra–Hamilton systems (a special sort of second-order ode system) are used to model the dynamics of modular populations after J.L. Harper, who conceived of a plant as a collection of populations of various modular units (leaves, roots, flower parts, etc.). There are two timescales, one the ecological (real) one, involving classical competitive, parasitic, commensal, and mutualistic interactions in what we term an ecoscene, and a much longer timescale of primary production towards climax. The climax arises as a result of transformations along a sere. These carry one ecoscene into another, perhaps far removed in real time from the first. Mathematically, these transformations are semi-projective, consisting of a projective time-sequencing change part and an environmental part, after Clements' ideas. The main result is that there are eight types of climax ecoscenes our model allows for dominant/codominant forestry. Each conserves its primary production cost functional. All are Jacobi stable and steady states are linearly stable.

Keywords: Forest; Succession; Finsler geometry; Clements

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1. Introduction

In 1915, the American ecologist F.E. Clements conceived of a forest as a superorganism with a characteristic development analogous to the embryological development of an individual. Each has a time sequence of events: *succession* being a series of ecological stages, which we here and from now on in this paper call *ecoscenes*, that a forest goes through until it reaches a *climax*, whereas a series of ontogenetic stages culminates in an adult phenotypic individual. This climax forest would be optimal for the ambient climate.

Previous work of ours on both succession in a forest and ontological development in an individual [3,6] has suggested the following: whereas development in an individual may be viewed as a series of genetically controlled events allowing response to environmental influences, no such genetic control is available to a forest as a whole. Moreover, the concept of time-sequencing changes in the development of an individual, called *heterochrony*, is an important evolutionary process and evidence for it is found in the fossil record [15,16]. But, for a forest, the notion of a phyletic line of fossils must be replaced by the concept of a *sere*, which is a progressive series of ecoscenes. For a sere the ecological/physiological interactions between populations of plants in an ecoscene are transformed into a new interaction pattern in a new *ecoscene*. The ecoscene in Clements' view is a product of the climate and is controlled by it. The new interactions may be very different, but eventually the climax formation is reached. This is analogous to the adult stage in the development of an individual. No further major changes in community structure occur in Clements' *monoclimax* theory. For a historical account, see [21,8,20].

2. Clements' concept of succession

Herein, we quote freely from *Plant Ecology* by J.E. Weaver and F.E. Clements [11]. As vegetation develops in an area, that area becomes successively occupied by different plant communities, each an ecoscene, in our terminology. Within a region, the final stage or climax results from a series of successive stages, and regardless of whether it starts in open water, solid rock or denuded land, the resulting climax is the same. Successions beginning in ponds, lakes, marshes or elsewhere in water constitute a hydrosere. The movement from one stage of the sere to the next is usually continuous, but when one dominant group of plants gives way to another, the change is clear. For example, floating plants give way to reeds and rushes. In fact, a hydrosere begins with submerged plants, which are gradually replaced by floating plants, this followed by a sedge meadow, then woodland and finally the climax forest.

The plant *formation* is the major unit of vegetation. It does not include animals; for this the word *biome* is used. The formation can be continental in scope, and is a fully developed climax community of a natural area. The formation is a complex and definite organic entity with a characteristic development and structure. It is a product of the climate and is controlled by it. The deciduous forest of the eastern USA, the coniferous forest of the Great Lakes region, the tundra of the far north of Alaska and Canada, and the grasslands of Saskatchewan and Manitoba are all examples. A formation arises, grows, matures and finally dies. It is able to reproduce itself, as may be seen after fire, lumbering or other catastrophes to vegetation.