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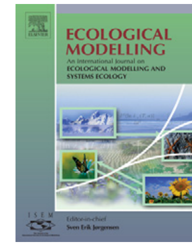

An individual-based model of a tritrophic ecology

*Moshi Arthur Charnell**

Department of Mathematics and Statistics, University of Victoria, P.O. Box 3045 Stn CSC, Victoria, BC, Canada V8W 3P4

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ABSTRACT

A spatially explicit individual-based model for a predator, prey and plant ecosystem is considered. The movement of the individuals is solely based on nearest-neighbour attraction/repulsion and reproduction is asexual. In this simple model emergent spatial organization of the individuals into clusters or groups is present even though all the individuals (predators and prey) are intra-specifically repelled by each other. The model ecosystem was used to determine whether an intra-specific attraction among the prey could increase their individual fitness. The attraction mechanism considered is such that when a prey is not affected by a predator or a plant then this prey is attracted to its nearest-neighbour prey. Under the assumptions of the parameterized model ecosystem, this mechanism seems highly selective on the individual level and it is evident that a population-based model could not assess this attraction mechanism. The main objective of this paper is to formalize mathematically an individual-based model and provide an example of a model tritrophic ecosystem that has the capabilities to assess evolutionary aspects of social behaviour in a prey species.

1. Introduction

The main objective of this paper is to detail a mathematical framework that can assess the evolution of spatial organization and social behaviour of a mobile prey species within an ecological system. An unambiguous mathematically formulated model is presented; implemented as computer code; parameterized for model persistence and plausibility; and used to elicit an evolutionary mechanism that leads to gregarious behaviour in a prey species. The model ecosystem is a strictly deterministic, discrete time, individual-based model of a tritrophic food chain where relationships between individuals are solely based on nearest neighbours and has the novel aspect that the primary resource is confined to an ‘oasis’.

An individual-based model is a system composed of interacting individuals and the system evolves through changes in the properties of the individuals and the relationships between them. Many reviews of the individual-based modelling approach have appeared (Berec, 2002; Breckling et al., 2005; Dumont and Hill, 2004; Grimm, 1999; Huston et al., 1988; Łomnicki, 1992; Uchmański and Grimm, 1996). A critique of ecological modelling gave the conclusion that individual-based models will induce a paradigm shift in ecology towards an ‘ecology of individuals’ (Uchmański and Grimm, 1996).

In the tritrophic ecological model presented in this paper, the characteristics of the individuals (plants, prey, and predators) change in relation to their current states and the states of their nearest-neighbours. When individuals acquire sufficient resources they asexually reproduce by seeding or division (Booth, 1997; Schmitz, 2000). The predators and prey within this model ecosystem have limited vision and are memoryless. Predators chase and consume the nearest prey; and a prey will flee from the nearest predator or move towards and consume the nearest plant. Predators and prey are both repelled by their nearest neighbours within their own species, thereby attempting to maintain a minimum distance between them-

* Tel.: +1 250 360 1397.
E-mail address: moshi@math.uvic.ca.

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selves and other individuals (Beecham and Farnsworth, 1998; Couzin et al., 2002; Flierl et al., 1999; Gueron et al., 1996; James et al., 2004; Kreft et al., 1998; Romey, 1996; Viscido et al., 2005).

Plants are confined to a bounded circular region, the oasis, and arranged hexagonally. A novel aspect to this model is that it is unbounded. Prey feed and reproduce within the oasis and prey can be pushed off the oasis by predators. Predators chase and feed upon the prey within the oasis and can be lead out of the oasis by prey. Since individuals have limited reaction distances, it is possible that these individuals become 'lost', not reacting to other individuals, and eventually die of old age.

In an individual-based model, persistence is an emergent property of the population and can be used to measure the fitness of the population (Booth, 1997; Grimm et al., 1999; Kostova et al., 2004). The persistence of the model ecosystem presented in this paper and its generation of phenomena that appear natural were the measures of success for the model parameters. Nature would tend to select the parameter configurations that produced ecosystems that persisted longer. Parameter values were adjusted by viewing the model output and experimenting with parameter values with the intention to increase the system's persistence and that the behaviour of the individuals were visually realistic. "Natural" group formation was obtained within a system that persisted for many thousands of prey generations and this system was built from assumptions that are well established. The parameterized model ecosystem presented in this paper is a plausible representation of general characteristics of a real ecosystem.

Individual-based models have many desirable characteristics, yet there is no standard protocol for describing them (Grimm et al., 2006). Individual-based models have lacked a mathematical formalism that has been well integrated into population-based models (Ginot et al., 2002; Grimm, 1999; Grimm et al., 2006; Kostova et al., 2004; Souissi et al., 2005). The relationships that individual-based models have with population-based models will become clear only when individual-based models are properly defined (Uchmański and Grimm, 1996) and using the language of mathematics to describe individual-based models will allow them to be easily reproduced and increase the success or utility of these models (Grimm et al., 2006).

Kostova et al. (2004) presented a mathematical description of an individual-based ecological model in terms of a discrete-time multidimensional nonlinear map that maps matrices to matrices, yet the presentation did not have the elegance normally attributed to mathematical formalism. The model presented in this paper is mathematically formalized as a discrete-time nonlinear map and uses set theory and difference equations to describe the system's evolution through time. The set notation describes the changes in populations as a result of births and deaths and the difference equations describe the changes in individuals as a result of biological and geographical situations. These two mathematical languages along with a geometry for spatial arguments give a concise framework in which to express an unambiguous spatially explicit individual-based model of a multi-trophic ecosystem.

The modelling assumptions allow the situation that a prey is lost even though there may be another prey within its limited vision. This situation can be used to assess the fitness of gregarious behaviour in a prey species. One of the main emergent properties of the model is that individuals form groups, even though they are not intra-specifically attracted to each other. The benefit of attraction is that prey which are lost can be led back to a plant by prey which are not lost. It is obvious that there is an increase in the reproductive success of a prey having an intra-specific attraction that engages when a prey is not reacting to a predator and cannot see a plant as opposed to having no intra-specific attraction. It is clear that this obvious increase in individual prey fitness could not be considered in a population-based model and the model presented in this paper seems to be as simple as possible and still able to provide evidence for this evolutionary spatial mechanism.

2. The model

The general model framework is defined as a nonlinear map which progresses a collection of sets of vectors discretely through time. The specific model ecosystem is an individual-based tritrophic food chain (plants, prey, and predators) that is spatially explicit in two continuous dimensions using the Euclidean norm, $||\cdot||$, and strictly deterministic. Individuals are represented as dense circular disks where the centres of the plants and their seeds are at discrete locations in a bounded circular area, the oasis, but the predators and prey move in response to nearest-neighbours within a continuous unbounded environment.

The interactions and interrelationships between individuals (Fig. 1) are: plants produce seeds and cannot seed locations that have already been seeded or occupied by plants; seeds produce plants; plants are consumed by prey; prey are attracted to and consume plants; prey reproduce and are repelled by other prey; prey are repelled and consumed by predators; predators are attracted to and consume prey; and predators reproduce and are repelled by other predators. The model is initialized and all individuals will age; die; and have the potential to acquire resources and reproduce.

Plants grow and are consumed by prey. Plants and seeds have very different roles in an ecosystem and as such are different stages in a plant species' life history. Plants grow radially from spatially discrete iso-points and are bounded by non-overlapping equivalent hexagonal regions. Their radial growth rate is constant and there are no environmental limitations, besides area, that restrict growth. Growth also adds weight to a plant and a plant has a maximum weight. Reproduction of

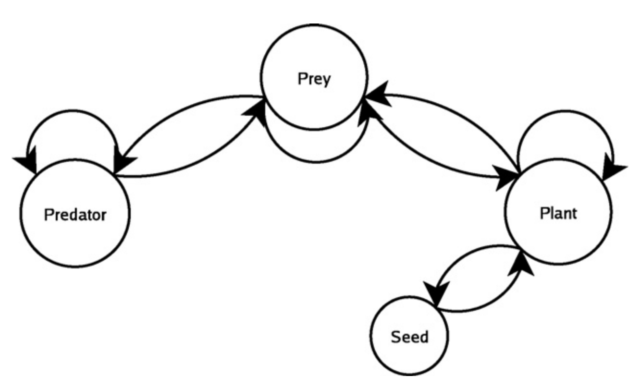

Fig. 1 – Relationships.