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Branching within branching: A model for host–parasite co-evolution

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Abstract

We consider a discrete-time host–parasite model for a population of cells which are colonized by proliferating parasites. The cell population grows like an ordinary Galton–Watson process, but in reflection of real biological settings the multiplication mechanisms of cells and parasites are allowed to obey some dependence structure. More precisely, the number of offspring produced by a mother cell determines the reproduction law of a parasite living in this cell and also the way the parasite offspring is shared into the daughter cells. In this article, we provide a formal introduction of this branching-within-branching model and then focus on the property of parasite extinction. We establish equivalent conditions for almost sure extinction of parasites and find a strong relation of this event to the behavior of parasite multiplication along a randomly chosen cell line through the cell tree, which forms a branching process in random environment. We then focus on asymptotic results for relevant processes in the case when parasites survive. In particular, limit theorems for the processes of contaminated cells and of parasites are established by using martingale theory and the technique of size-biasing. The results for both processes are of Kesten–Stigum type by including equivalent integrability conditions for the martingale limits to be positive with positive probability. The case when these conditions fail is also studied. For the process of contaminated cells, we show that a proper Heyde–Seneta norming exists such that the limit is nondegenerate.

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Keywords: Host–parasite co-evolution; Branching within branching; Galton–Watson process; Random environment; Infinite random cell line; Random tree; Extinction probability; Extinction–explosion principle; Size-biasing; Heyde–Seneta norming

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1. Introduction and model description

The discrete-time *branching-within-branching process (BwBP)* studied in this paper describes the evolution of generations of a population of cells containing proliferating parasites. In an informal way, its reproduction mechanism may be described as follows:

(1) At time $n = 0$ there is just one cell containing one parasite.
(2) Cells and their hosted parasites within one generation form independent reproduction units which behave independently and in the same manner.
(3) Any cell splits into a random number N, say, of daughter cells in accordance with a probability distribution $(p_k)_{k\geq 0}$.
(4) Then, given N, the hosted parasites, independently and in accordance with the same distribution, produce random numbers of offspring which are then shared into the daughter cells.
(5) All cells and parasites obtained from a cell and its parasites in generation n belong to generation $n + 1$.

We are thus dealing with a hierarchical model of two subpopulations, viz. cells and parasites, with an entangled reproduction mechanism. The hierarchy stems from the fact that cells can survive without parasites but not vice versa.

Proceeding with a more formal introduction, let $\mathbb{V}$ denote the infinite Ulam–Harris tree with root $\varnothing$ and N_{v} the number of daughter cells of cell $\mathsf{v} \in \mathbb{V}$. The $(N_{\mathsf{v}})_{\mathsf{v}\in\mathbb{V}}$ are independent and identically distributed (i.i.d.) copies of the $\mathbb{N}_0$-valued random variable N with distribution $(p_k)_{k\geq 0}$ and finite mean ν, viz. $\mathbb{P}(N = k) = p_k$ for all $k \in \mathbb{N}_0$ and

$$\nu = \mathbb{E}N < \infty.$$

The cell population thus forms a standard *Galton–Watson tree (GWT)* $\mathbb{T} = \bigcup_{n\in\mathbb{N}_0} \mathbb{T}_n$ with $\mathbb{T}_0 = \{\varnothing\}$ and

$$\mathbb{T}_n := \{\mathsf{v}_1 \ldots \mathsf{v}_n \in \mathbb{V} | \mathsf{v}_1 \ldots \mathsf{v}_{n-1} \in \mathbb{T}_{n-1} \text{ and } 1 \leq \mathsf{v}_n \leq N_{\mathsf{v}_1\ldots\mathsf{v}_{n-1}}\}$$

(using the common tree notation $\mathsf{v}_1 \ldots \mathsf{v}_n$ for $(\mathsf{v}_1, \ldots, \mathsf{v}_n)$). Consequently, defining

$$\mathcal{T}_n := \#\mathbb{T}_n = \sum_{\mathsf{v}\in\mathbb{T}_{n-1}} N_{\mathsf{v}} \tag{1}$$

as the *number of cells in the nth generation* for $n \in \mathbb{N}_0$, the sequence $(\mathcal{T}_n)_{n\geq 0}$ forms a standard *Galton–Watson process (GWP)* with reproduction law $(p_k)_{k\geq 0}$ and reproduction mean ν. For basic information on Galton–Watson processes see [12,34].

Let Z_{v} denote the number of parasites in cell $\mathsf{v} \in \mathbb{V}$ and $\mathbb{T}_n^*$ the set of contaminated cells in generation $n \in \mathbb{N}_0$ with cardinal number $\mathcal{T}_n^*$, so

$$\mathbb{T}_n^* := \{\mathsf{v} \in \mathbb{T}_n : Z_{\mathsf{v}} > 0\} \quad \text{and} \quad \mathcal{T}_n^* := \#\mathbb{T}_n^*. \tag{2}$$

We define the *number of parasites process* by

$$\mathcal{Z}_n := \sum_{\mathsf{v}\in\mathbb{T}_n} Z_{\mathsf{v}}, \quad n \in \mathbb{N}_0.$$

After these settings, the BwBP is defined as the pair

$$\left(\mathbb{T}_n, (Z_{\mathsf{v}})_{\mathsf{v}\in\mathbb{T}_n}\right)_{n\geq 0}$$