Available online at www.sciencedirect.com

ScienceDirect

Mathematics and Computers in Simulation 126 (2016) 14–44

MATHEMATICS AND COMPUTERS IN SIMULATION

www.elsevier.com/locate/matcom

Original articles

Metaecoepidemic models with sound and infected prey migration[☆]

Ezio Venturino

Dipartimento di Matematica "Giuseppe Peano", Università di Torino, via Carlo Alberto 10, 10123 Torino, Italy

Received 21 July 2011; received in revised form 10 February 2016; accepted 23 February 2016
Available online 11 March 2016

Abstract

We present a two-patch metaecoepidemic model, in which predators, sound and infected prey occupy the first one. Both kinds of prey can migrate into a second habitat, which constitutes a refuge from the predators. Equilibria of the system and their stability properties are determined analytically and also heavily studied numerically, when too cumbersome. The results indicate that in practical situations it is necessary to carefully assess the environmental state before proceeding to any modification of it, as the consequences might be far from those foreseen.

Keywords: Ecosystems; Fragmentation; Diseases; Predator–prey; Ecoepidemiology

1. Background

In a recent investigation, [31], the author has introduced the concept of metaecoepidemic models. These account for interacting populations affected by a disease and living in separate environments, thereby constituting independent ecoepidemic models, see Chapter 7 of [23], that become interdependent since migration among them is allowed. In [31], only sound prey are assumed to migrate between the different environments, while in [5] predators only do. Here we extend the investigation by allowing also the infected prey to migrate, while at the same time modifying the model, by assuming a Holling type I functional response for the predation instead of a Holling type II. Note that the disease is assumed to propagate by contact among the prey, but it does not affect the predators.

The rationale behind this new concept lies in the investigations on metapopulations, performed since a number of years to study the effects that landscape fragmentation has on ecological communities, [32,33], since the latter may threaten the species survival. In some cases however, persistence in the whole environment can be obtained, although locally populations may experience extinction [8,13,15,32,34].

Heterogeneous environments may arise naturally due to physical unfavorable events, such as landslides, floods and so on, but also human activity is frequently responsible for substantially altering the ecosystems. Construction of roads and human artifacts is the first example, but most agricultural activities cause even more damage to the natural landscape. As a consequence, populations living in the unperturbed environment find themselves partitioned, with one

---

[☆] Part of this research was presented at the DIEMBM 2010 Conference in Samos, Greece; the paper is dedicated to the organizer of the meeting, Athena Makroglou.

E-mail address: ezio.venturino@unito.it.

http://dx.doi.org/10.1016/j.matcom.2016.02.006

subpopulation being cut off from their similar that lie on the other side of the newly arisen barriers, and therefore start to evolve independently of each other, but may become also less apt to survive in adverse conditions. Metapopulations represent a way to investigate the possible evolution in time of such situations, [19]. They have been successfully applied to study a few species, the spotted owl (*Strix occidentalis*), the mountain sheep (*Ovis canadensis*), [14]. In other cases however, the concept of incidence function is used instead, see the case of the butterflies *Melitaea cinxia* and other species in Finland, [16,26,27]. But it is very difficult to collect real data on these models, as remarked in the literature of metapopulation theory, [8,13], so that the importance of mathematical models in this context becomes clear.

Further, ecoepidemic models deal with interacting populations that are affected by a disease. Since the latter occur in nature, they cannot be neglected when studying the dynamics of populations. Furthermore, they must be considered also in metapopulation models. Let us mention in this context the case of mixomatosis, which was humanly inoculated in the wild rabbit, *Oryctolagus cuniculus* (L.), in Australia to try to control its increasing population, [20,21,25,29]. The rabbits are hunted by the red fox *Vulpes vulpes* (L.).

Further examples are provided by *Ovis canadensis*, *Strix occidentalis* and butterflies as mentioned above. The predators of the former are mainly wolf (*Canis lupus*), coyote (*Canis latrans*), bear (*Ursus*), Canada lynx (*Lynx canadensis*), mountain lion (*Puma concolor*), golden eagle (*Aquila chrysaetos*), [9]. Their parasites are mainly nematode lungworms, *Protostrongylus stilesi*, *P. rushi*, *Cysticercus tenuicollis*, *Wyominia tetoni*, *Nematodirus archari*, *N. davtiani*, *Trichostrongylus sp.*, *Protostrongylus rushi*; *Dermacentor albipictus* and *D. venustus*, [4,10]. The principal parasites of *Strix occidentalis* are instead the helminths, which are assumed by predation on small rodents, while the most important predator is the great horned owl, *Bubo virginianus*, which hunts the spotted owl to feed on it but also to eliminate it as a possible competitor for resources, [18]. Lepidoptera are hunted by birds, bats, small mammals, reptiles, and their larvae become the main diet of *Parus caerulens, P. major*, [7]. Butterflies defend themselves by several means: mimetism at the moth stage, diurnal butterflies assume compounds that make them unpalatable for their predators, e.g. *Melitaea cinxia* feeding on *Cotesia melitaearum*, the latter getting alkaloids from the plant on which it feeds, [22]. Other defense mechanisms are shapes, colors or sounds which discourage the predators, [28]. Myrmecophily is an association with ants in which caterpillars find refuge near the ant nests, since they are a predator- and parasitoid-free space, [3]. Parasitoids attack Lepidoptera by implanting in them an egg, which later on kills the host, [12,28]. Lepidoptera are also affected by viruses, for instance nuclear polyhedrosis virus (NPV), cytoplasmatic polyhedrosis virus (CPV), granulosis virus (GV), entomopox virus (EPV), and common bacteria in nature (Bacillaceae), such as *Bacillus thuringiensis* var. kurstaki, which upon ingestion poisons the caterpillars' digestive system.

The previous examples illustrate the necessity of investigating diseases also in the context of metapopulations, extending therefore the concept of ecoepidemics to this wider situation. A first attempt has been made in [31]. With respect to the former study, here we modify the picture by allowing also infected prey to move freely among the patches. Mathematically, this leads to a more complicated system, containing five nonlinear differential equations.

The paper is organized as follows. We introduce the model in the next section. In Section 3 we adimensionalize it and investigate its limiting cases, together with the two systems that possibly constitute the independent patches of the model if communications are interrupted. Section 4 contains the analysis of the simplest possible system's equilibria. The study of the most complicated ones is postponed to the simulations Section 5. The investigation of the effects of parameter changes in the system's dynamics appears in Section 6 and a final discussion of the results concludes the paper.

2. The model

We consider here a two-habitat environment in which two populations coexist, prey and predators. Furthermore, a disease spreads among the prey. In the first patch, both species are present, while in the second one, only the prey, so that the latter can be considered as their refuge, inaccessible by the predators, see Fig. 1.

Migration is allowed between the two patches, both for sound and infected prey subpopulations. The following features on the disease are further assumed. It is transmitted by contact, and it is recoverable. Infected individuals are so weak that they are not able to reproduce, nor to compete for resources with the sound ones, and among themselves. Both disease incidence and recovery rates are independent of the patch. The disease incidence is taken in the simple mass action form.