

A Two-Patch Predator-Prey Metapopulation Model

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Abstract. A minimal model for predator-prey interaction in a composite environment is presented and analysed. We first consider free migrations between two patches for both interacting populations, and then the particular cases where only one-directional migration is allowed and where only one of the two populations can migrate. Our findings indicate that in all cases the ecosystem can never disappear entirely, under the model assumptions. The predator-free equilibrium and the coexistence of all populations are found to be the only feasible stable equilibria. When there are only one-directional migrations, the abandoned patch cannot be repopulated. Other equilibria then arise, with only prey in the second patch, coexistence in the second patch, or prey in both patches but predators only in the second one. For the case of sedentary prey, with predator migration, the prey cannot thrive alone in either of the two environments. However, predators can survive in a prey-free patch due to their ability to migrate into the other patch, provided prey is present there. If only the prey can migrate, the predators may be eliminated from one patch or from both. In the first case, the patch where there are no predators acts as a refuge for the survival of the prey.

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1. Introduction

Habitat fragmentation is one of the major sources of biodiversity loss, which frequently occurs in nature due to natural causes or human activities [23]. A population originally thriving in an undisturbed environment may become partitioned into two or more patches (subpopulations) after a catastrophic event, and may continue to thrive independently in the particular patches where the living conditions are favourable. However, due to the reduced size or lesser resources of their smaller new environments they may then be extremely sensitive to adverse conditions, so that habitat fragmentation can ultimately lead

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to species extinction. Metapopulation theory is an instrument devised to understand the associated dynamical processes [22]. One of its major achievements has been to demonstrate that in some circumstances a population can persist globally while the local populations become extinct [5, 9, 11, 22, 24]. Data collection, especially to assess migration rates, is not an activity generally undertaken by field scientists due to its intrinsic difficulty [5, 9] so the role of models is especially important [13]. Metapopulation models distinguish patches and paths by selecting the most favourable populated habitats as patches, with the remaining less populated ground in between regarded as inter-patch migration routes [10].

Successful examples where metapopulation dynamics has been applied are models for the mountain or bighorn sheep (*Ovis canadensis*) and the spotted owl (*Strix occidentalis*) [10]. The bighorn sheep *Ovis canadensis* has several predators — including the wolf (*Canis lupus*), coyote (*Canis latrans*), bear (*Ursus*), Canada lynx (*Lynx canadensis*), mountain lion (*Puma concolor*) and golden eagle (*Aquila chrysaetos*) [6]. Among the main predators of the spotted owl are the great horned owl *Bubo virginianus* — but at the same time *Strix occidentalis* hunts mainly small rodents, so can be viewed as an intermediate trophic level in a food web. Another example where the metapopulation approach to habitat fragmentation may be useful is the predator-prey system of the red fox *Vulpes vulpes* (L.) and rabbit *Oryctolagus cuniculus* (L.). Lepidoptera also play an important role in the development of Metapopulation theory. In Finland *Melitaea cinxia* has been studied using the concept of an incidence function [12], and also other species [16, 17]. Lepidoptera predators are mainly birds, bats, parasitoids, small mammals, reptiles and insects such as ants and dragonflies [2, 3]. Mainly larvae are hunted; this occurs especially for some particular species such as *Parus caeruleus*, *P. major* [4]. Genetic analysis tools have been used to prove that coral reef species may experience population reductions or extinctions at the local level [1]. These contribute to enhance overall meta-population genetic differentiations. A fairly recent review of modelling work on the consequences of habitat loss and fragmentation on interacting populations provides a set of testable hypotheses for experimentalists [18].

From the mathematical modelling viewpoint, nonlinear migrations depending on population growth rates that may lead to sustained population oscillations have been investigated [8]. Modifying the migration rates using concepts such as predator pursuit and prey evasion leads to reduced spatial synchrony and thus improved metapopulation persistence [14]. Explicit space dependence also leads to pattern formations in the metapopulation context [19]. A discrete version of metapopulation models, including a space description, is available [21]. An analytical formula to calculate the average lifetime of species living in fragmented habitats is provided in Ref. [7], which accounts for networks that are dynamically changing due to the destruction of patches and their reestablishment elsewhere in the landscape.

A recent investigation by one of the present authors concentrated on an extension of these metapopulation models to ecoepidemiology [15], when a disease is superimposed on a demographic system of interacting populations [20]. *Inter alia*, it was found that persistent oscillations in one patch can either carry through to a second patch or be dampened in the more composite environment, and in some cases the coexistence of all the populations