Original Research Article

Habitat complexity, dispersal and metapopulations: Macroscopic study of a predator–prey system

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A B S T R A C T

Habitat complexity is supposed to reduce predation rates by decreasing encounter rates between predators and prey. It is also reasonably true that structural complexity of habitat reduces the available space for interacting species. Traditional mathematical models have understated the role of habitat complexity in understanding predator–prey dynamics. In the first part of this paper, we modify the Rosenzweig–MacArthur predator–prey model phenomenologically by incorporating the effects of habitat complexity on the carrying capacity as well as in the predator's functional response. In the second part, we modify our model system from the point of metapopulation structure in which locally interacting populations are coupled via dispersal. Our results corroborate different observed results of natural systems. Study reveals that predator–prey interaction is stable at the intermediate degree of habitat complexity. The prey density may experience decreasing return at higher degree of habitat complexity. It is also observed that a metapopulation structure increases the stability of the predator–prey interaction in presence of habitat complexity and behaves differently from Rosenzweig–MacArthur model.

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1. Introduction

Lots of theoretical and experimental works have been done to investigate the processes that may shape predator–prey interaction (May, 1973; Hassel, 1978; Begon et al., 1995; Muller and Joshi, 2000). It has been demonstrated that the dynamics of local interacting populations largely depend upon attributes of the local habitats (Johnson, 2006; Anderson, 2001). For example, physical or structural complexity of habitat plays significant role in local population communities (Beukers and Jones, 1997; Grabowski, 2004; Tokeshi and Arakaki, 2012; Johnson et al., 2003; August, 1983; Gratwicke and Speight, 2005; Koivisto and Westerbom, 2010). Habitat structure is defined as any biotic and abiotic physical structure in space, whereas habitat structural complexity refers to the morphological characteristics within a structure itself or the heterogeneity in the arrangement of objects in space (Bell et al., 1991; Lassau and Hochuli, 2004). Habitat complexity is found in almost all ecological systems, whether it is terrestrial or aquatic. Marine habitat, in particular, becomes complex in presence of oyster and coral reefs, mangroves, sea grass beds and salt marshes (Humphries et al., 2011). In lakes, habitat heterogeneity is most

commonly present in the form of littoral zone vegetation or a depth-gradient diversity Eklv (1997). Different field and laboratory experiments confirm that habitat complexity reduces predation rates by decreasing encounter rates between predator and prey (Glass, 1971; Stein and Magnuson, 1976; Saiki and Tash, 1979; Heck and Orth, 1980; Savino and Stein, 1982, 1989a,b; Anderson, 1984; Folsom and Collins, 1984; Persson, 1991, 1993; Persson et al., 1991, 1992; Persson and Eklov, 1995; Christensen and Persson, 1993; Manatunge et al., 2000; Grabowski and Powers, 2004; Canion and Heck, 2009; Humphries et al. 2011; Frederick et al., 2006). Experimentalists have measured the degree of habitat complexity differently according to their needs. For example, marine ecologists measure the degree of habitat complexity by number of sea grass blades per square meter (James and Heck, 1994), amount of shell material in polychaete worm tubes (Bell, 1985) or surface area to volume ratios (Coull and Wells, 1983). In a more recent work, Bartholomew et al. (2000) prescribed two non-dimensional indices C_t/A_t and S_p/P_r to measure the degree of habitat complexity. C_t/A_t measures the amount of cover available within a habitat that interferes with a predator's ability to see a prey within the habitat and S_p/P_r measures the extent to which the structure interferes with predator's ability to move through the habitat in search of a prey. We are trying to incorporate the effects of habitat complexity in a mathematical model by considering the most apparent roles of habitat complexity on predator–prey interaction, and willing to observe the extent to which this complexity drives

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the population dynamics. Our modeling approach is purely phenomenological and the effect of complexity is incorporated in the model system by the nonmechanistic parameters.

The foraging efficiency of predators generally decreases with increasing habitat complexity. Predator's functional response, defined as the amount of prey catch per predator per unit of time, is thus affected by the structure of habitat (Alstad, 2001; Anderson, 2001). The effect of habitat complexity should, therefore, be incorporated in predator's response function. Unfortunately, theoreticians have overlooked this issue and have always studied predator–prey interactions with functional responses that do not consider the effect of habitat complexity. For example, Holling response functions (Holling, 1959), the most commonly used functional responses in predator–prey interactions do not consider the effect of habitat complexity. It is to be mentioned that habitat complexity should not be confused with refuge which has been studied by many authors (Smith, 1974; Murdoch and Oaten, 1975; Chesson, 1978; Sih, 1987; Hassel and May, 1973; Chattopadhyay et al., 2000; Ma et al., 2009). In the later case, preys are completely safe from the predator, and in the former, preys are never safe but encountered by predator at a lower rate. It is, therefore, important to modify traditional functional responses to incorporate the effect of habitat complexity in the predator's response function. Structural complexity not only reduces the predator–prey interaction but also reduces the available space for the interacting species (Meyer and Ausubel, 1999; Freeland and Choquenot, 1990; Li and Wang, 2010). For example, aquatic weeds or submerged vegetations or reefs decrease the predator–prey interaction with its increasing density and reduce the space as well for the interacting species. In other words, structural complexity of habitat reduces both predator's attack rate and the carrying capacity of the environment where they live.

Natural environment is generally heterogeneous and is subdivided into smaller habitats with different characters. These smaller habitats or patches play a significant role in the coexistence of interacting local populations and stability of the system (Kuang and Takeuchi, 1994; Zhang and Wang, 2003; Auger et al., 2000; Charles et al., 2002). Existing literatures show that dispersal of species among patches may enhance the stability of a system (Allen (1983, 1987), Holt (1985), Takeuchi (1986), Ylikarjula et al. (2000)), or may reduce fluctuations (Holt, 1985), or may eliminate chaos (Ruxton, 1994). In this paper, we first study a predator–prey interaction by incorporating the effect of habitat complexity. In the second phase, we modify and study our system from the point of view of metapopulation structure.

2. Model with habitat complexity

The most commonly used functional response in a predator–prey interaction is Holling Type II (Holling, 1959) which is mathematically represented by

$$g(x) = \frac{\alpha x}{1 + \alpha h x},$$

where x is the prey population density, α is the attack coefficient and h is the handling time. This response function does not incorporate the effect of habitat complexity. So the formula cannot be used directly as predation formula in presence of habitat complexity. Since habitat complexity is more likely to affect the attack coefficient than the handling time for search (Winfield, 1986), the attack coefficient α has to be replaced by $\alpha(1 - c)$, where $c(0 < c < 1)$ is a dimension less parameter which measures how much encounter rate is reduced due to habitat complexity. For example, $c = 0.1$ implies that predator–prey interaction will be reduced by 10% due to habitat complexity. We call c as the degree

or strength of habitat complexity. Following Kot (2001), the total number of prey caught (V) is then given by

$$V = \alpha(1 - c)T_s x,$$

where

$$T_s = T - hV.$$

Here T is the total time, T_s is the available search time and h is the handling time required per prey. Solving for V, we get

$$V = \frac{T\alpha(1 - c)x}{1 + \alpha(1 - c)hx}.$$

Since predator's functional response is defined as the amount of prey catch per predator per unit of time, so the functional response in presence of habitat complexity will be represented by

$$g(x) = \frac{\alpha(1 - c)x}{1 + \alpha(1 - c)hx}.$$

We call g as the modified Holling Type II predation formula that incorporates the effect of habitat complexity.

Recently, we considered (Bairagi and Jana, 2011, 2012) the following system to study the effect of habitat complexity on predator–prey interaction with other biological attributes:

$$\frac{dx}{dt} = rx(1 - \frac{x}{k}) - g(x)y, \frac{dy}{dt} = \theta g(x)y - dy,$$

where g is the modified Holling Type II response function defined as above. Here r is the intrinsic growth rate of prey population, k is the environmental carrying capacity, $\theta(0 < \theta < 1)$ is the conversion efficiency and d is the food independent death rate of predator. All parameters are positive. This model also assumes that the complexity is homogeneous throughout the habitat.

As mentioned in the introduction that structural complexity of habitat reduces the space for prey population and decreases the prey carrying capacity. Therefore, the environmental carrying capacity should be a decreasing function of habitat complexity. For simplicity, we assume that environmental carrying capacity is reduced linearly with increasing habitat complexity. The effect of habitat complexity on the carrying capacity is measured by the dimensionless parameter $c_1(0 < c_1 < 1)$. Thus, if k be the environmental carrying capacity in absence of habitat complexity then it would be $k(1 - c_1)$ in presence of complexity. Assume that $c_2(0 < c_2 < 1)$ measures the effect of habitat complexity on predator's functional response. The quantitative changes in the modified carrying capacity and the modified functional response with varying degree of habitat complexity can be observed in the Fig. 1. Incorporating the effects of habitat complexity, we can represent the above model as

$$\frac{dx}{dt} = rx(1 - \frac{x}{(1 - c_1)k}) - \frac{\alpha(1 - c_2)xy}{1 + \alpha(1 - c_2)hx},$$
$$\frac{dy}{dt} = \frac{\theta\alpha(1 - c_2)xy}{1 + \alpha(1 - c_2)hx} - dy, \quad (1)$$
$$x(0) > 0, y(0) > 0.$$

We call the model system (1) as modified Rosenzweig–MacArthur model. In absence of habitat complexity, i.e. when $c_1 = 0 = c_2$, the system (1) becomes the well known Rosenzweig–MacArthur model (Rosenzweig and MacArthur, 1963).

2.1. Equilibria and its stability

The system (1) possesses three equilibrium points:
(i) the trivial equilibrium $E_0 = (0, 0)$, (ii) the predator-free equilibrium $E_1 = (x_1, y_1)$, where $x_1 = (1 - c_1)k$, $y_1 = 0$ and (iii) the