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Dynamics of Bio-control Agents vis-a-vis Target Pest Populations

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The ultimate goal of biological control is to manipulate and maintain pest populations at low densities and thus prevent problems due to pests. It follows that biological control in long-lived ecosystems can be thought of as a type of ''applied population dynamics" (Murdoch & Briggs, 1996). Information from the majority of population dynamics studies of natural enemies and their interactions with their hosts can have relevance to classical biological control. Information from these studies may also be relevant to conservation biological control in providing the information about correct conditions for optimization of the activity of natural enemies.

Types of Natural Enemies:

The natural enemies used to control invertebrates are taxonomically as well as functionally diverse. They include the functional groups of parasitoids, predators, and pathogens. Taxonomically, groups of natural enemies that are used for biological control range from fish to insects, mites, nematodes, and microorganisms, including bacteria, viruses, fungi, and single-celled organisms. Different groups of natural enemies are emphasized for different control strategies. Classical biological control and conservation have predominantly used insect parasitism and predators and sometimes mites, while all types of natural enemies have been used in undatively. It would be far easier as well as more efficient always to use the same type of natural enemies, but not all groups of natural enemies have members that could provide effective control for each pest. Therefore, biological control practitioners must be trained to work with different types of natural enemies.

Natural Enemy attributes:

Early models suggested several general attributes characterizing successful biological control agents: (1) host specificity, (2) synchrony with the pest, (3) high rate of increase, (4) ability to survive periods with few to no prey, and (5) good searching ability.

Such properties are more important for classical biological control or conservation and are more characteristic of parasitoids than predators or pathogens.

Interaction between the population of natural enemies and target pests:

Biological control does not occur when a few hosts are killed but rather when groups of hosts are killed and their populations remain low. Therefore, it is a phenomenon occurring at the population level. Studying populations that vary in space and time is typically more difficult than studying individual organisms. Progress has been made by studying individuals under controlled situations, followed by controlled studies (often experimental) of combinations of the natural enemy and host individuals in the laboratory and the field. Information on outcomes of studies has been used to derive mathematical models, created to help provide answers about the interactions that cannot be directly gleaned from data collected in the field. This type of approach is required because data from the field are typically influenced by many factors and their complex interactions, and one cannot readily see which are the key factors driving the observed situation. Experiments using mathematical models have been used extensively to investigate the emergent properties of groups of factors acting together. Although there are numerous types of natural enemies, early work in developing ecological theory centred around interactions between predators and prey. An important interaction to be dissected was the response by predators to changes in prey density.

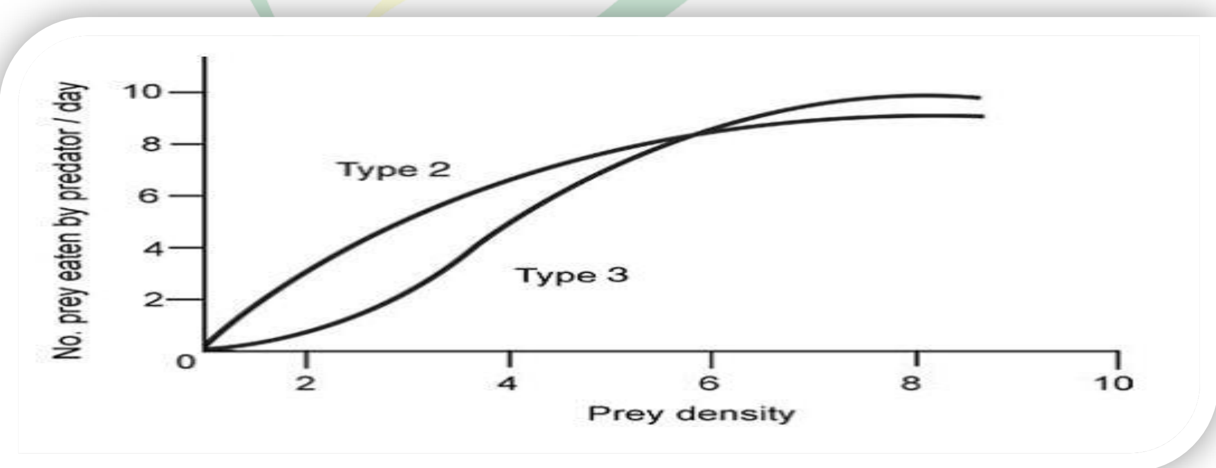

Figure 1 two types of functional responses by predators to changes in prey abundance, with satiation at high prey densities.

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Holling (1966) was instrumental in investigating the changes in predator behavior in response to changes in prey density which he called the functional response. The functional response is the behavioural response of predators to host density and should be differentiated from the numerical response, which involves increasing reproduction in response to prey density. Holling found that as prey density increased, the number eaten increased quickly at first but then slowed, to eventually reach a plateau at satiation (Fig. 1, Type 2). Creating models for this response helped to identify the important components: (1) the rate of successful search (orrate of discovering prey), (2) the time available for searching, (3) the handling time (the time it takes the predator to eat that prey item and then be ready to search for another) and(4)predator hunger. This functional response was subsequently found tobe characteristic of many invertebrate predators and parasitoids. Response by vertebrate predators was characterized better by a sigmoid response (Fig. 1, Type 3). With frequent contact with prey, as would occur at higher prey densities, vertebrates could learn how to find, catch, and handle prey and thus respond more quickly, so the slope of the response was steeper although still reaching a plateau. Further studies showed that some invertebrates could also display sigmoid responses, especially those displaying more active searching in areas where more prey occurred. Changing behaviour when prey is more or less dense is only one component of apredator's response. A numerical response refers to the changes in the numbers of predators when prey density changes. One can imagine an immediate increase in the number of natural enemies they gather at an aggregation of prey once it was discovered. For invertebrates, we also commonly see a more delayed response with increases in offspring following an abundance of prey or hosts as a result of increased reproduction. These concepts of functional and numerical responses are central to the development of models describing interactions between predators and prey.

Population regulation:

Exogenous
- Natural enemies (predators, parasites, pathogens)
- Food supply
- Weather
- Shelter

Endogenous
- Sex and age
- Physiology
- Behavior
- Genetics

Figure 2 factors regulating NE populations

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When natural enemies control populations of prey or hosts, this is called population regulation. Populations are generally thought to be controlled by some combination of exogenous factors, factors external to the population such as the effects of natural enemies or climate, and endogenous factors, such as genetic changes in a population or intra specific (within that species) competition (Fig.2). Population regulation has been the subject of many studies and much discussion focused on understanding why natural systems maintain the structures we see. For our purposes, it is important to understand how pest populations are controlled by natural enemies to try to improve biological control success rates. A key question concerns what governs the interactions between natural enemies and hosts to allow their coexistence. Why aren't natural enemies always able to kill all their prey? Several issues, including the effect of the environment on natural enemies and pests, the behaviour of natural enemies and pests, responses of natural enemies to pest density, and actions of natural enemies and hosts on a spatial scale, are central to developing theories regarding how natural enemies coexist with their prey or hosts. Central to the issue of regulation by natural enemies is the concept of density-dependent mortality that mortality inflicted on members of a population which increases about the density of the host or prey population (Fig. 3a). While this type of mortality would increase as the population increases it also decreases as the population as negative feedback. The decrease in mortality of the host at low densities is a critical attribute because in this way the natural enemy does not become extinct (but see below). This concept was central to models created by Nicholson and Bailey (1935), who believed that density-dependent factors regulated populations. Researchers studying natural enemies to try to fit them into models of density dependence soon found that data points often did not fall directly where expected. Instead of being density-dependent, relationships are often 'density vague,' demonstrating that in reality, in all biological systems, responses are often variable but demonstrate general trends. Nevertheless, for many years scientists held that density-dependent responses by natural enemies to hosts or prey were required for successful biological control.

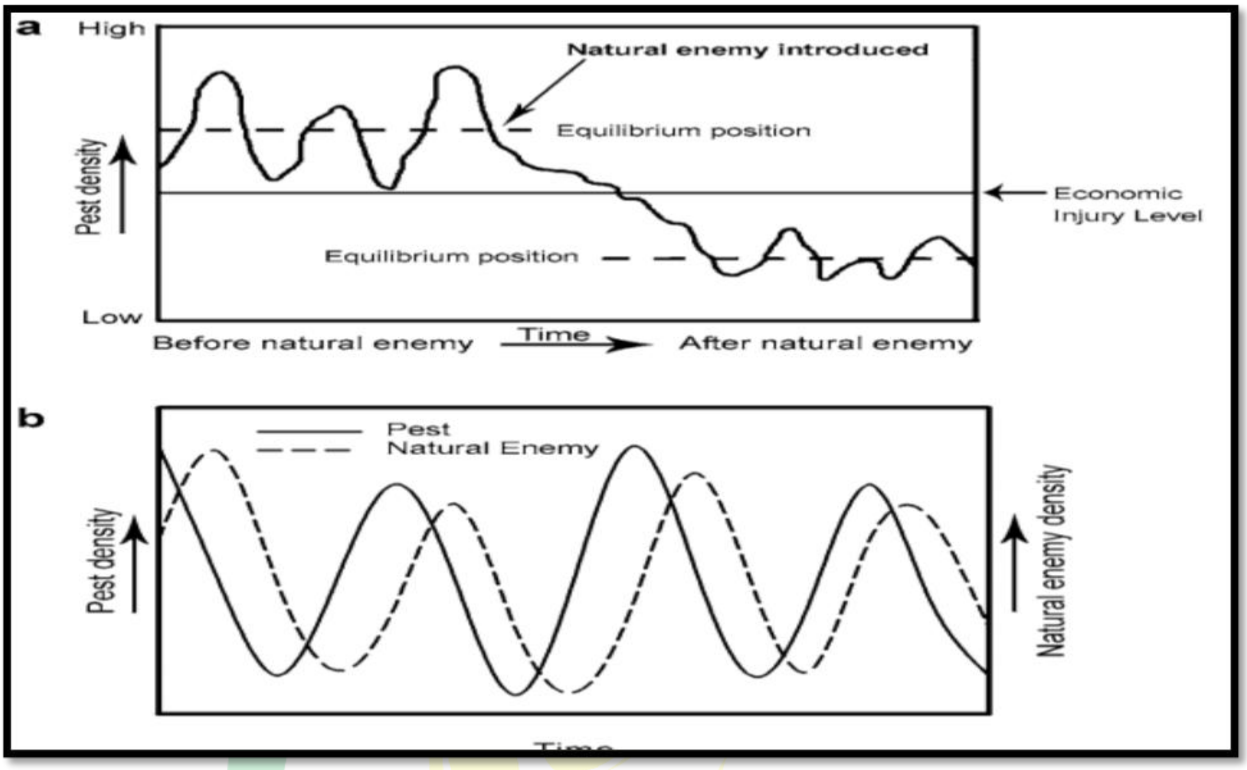

Figure 3 a. Hypothetical results of a classical biological control introduction in which the average abundance of a pest is reduced after the introduction of a natural enemy, demonstrating stable equilibria both before and after the natural enemy are introduced. (From Flint & Dreistadt, 1998.) b. Hypothetical density-dependent relations in a predator-prey (or natural enemy–pest) system with discrete generations.

We can look at density dependence more closely, and classify it into different types of relations. In some systems, there is a time lag after an increase in host density and before mortality increases; this is called delayed density-dependent mortality (Fig. 3b). This can be characteristic of insect populations where a numerical response to increasing host density requires time for a new generation of natural enemies to be produced. For southern pine beetles in loblolly pine stands in Texas, predator-caused mortality demonstrated a delayed response to southern pine beetle populations. Predator-caused mortality was negligible while bark beetle populations increased, then predators increased during the year that the pest population peaked and increased further the next year while the pest populations crashed of course not all mortality is associated with natural enemies or with host density. Density-independent mortality occurs without any relation to density (Fig. 3c). The classic examples of this would be when a weather event negatively affects a population, such as an early freeze causing extensive mortality among non-cold-hardy species, regardless of their density. Among early theorists, some felt that density-independent processes were extremely important and, for a time, the relative importance of density independence versus density dependence in determining host densities was a matter of great debate.

Biological control to be successful, it has long been thought that the natural enemy/host relationship must be stable. This meant that populations of the host would constantly be present and would fluctuate in density around some equilibrium density. After the introduction ofa natural enemy, that equilibrium density would decline to a new stable level at which natural enemy populations would track host populations (Fig. 4). In contrast, in an unstable system, fluctuations could occur with resulting extinctions. Early models by Nicholson and Bailey used discrete generations with one generation of host and parasitoids per year but the results from this model were unstable and fluctuated wildly through time before the host and natural enemy became extinct. This model was based on encounters between the host and parasitoids that occurred randomly. Once natural enemies in the model could search specifically for the host so that parasitoids could respond to the host's high densities, the model's results became stable.

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