RECONSTRUCTING AN ECOSYSTEM: A THEORY UNIFYING INVASION BIOLOGY AND BIOLOGICAL CONTROL

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ABSTRACT
Invasion biology is centered around two focusing themes – (i) will an invasion result in an establishment, and (ii) does the establishment of a new species result in a threat to existing species or critical community or ecosystem characteristics. In biological control, we are continually faced with two different types of invasions. The first of these is the unintentional (or sometimes intentional!) invasion of a plant or animal species into a new area. The second type is the subsequent, and intentional, invasion of natural enemies introduced for the purpose of ameliorating the negative effects of some previously invasive species that has become a threat to other species or to some characteristic of the invaded ecosystem. This paper presents a theory of interactions, based on both guild structures in a community and on population dynamics, that brings together these two types of invasions and connects invasion biology and biological control. In essence, the connections between these two different types of invasion share common population dynamic structure, and a common guild structure. However, the impact on the ecosystem in which these invasions takes place is vastly different between the unintentional introduction of a damaging species compared with the introduction of a species in a higher trophic level. The theory is presented in both ecosystem structure form and in the form of a model of the population dynamic processes involved. The model outcomes are related to current issues and recent projects in biological control.

INTRODUCTION

First, I would like to express my thanks to the symposium organizers for all their hard work putting together such a wonderful meeting, and secondly I would like to thank them for the opportunity of addressing this august body about some ideas I have relating ecosystem or community disturbance and biological control.

I am strongly of the opinion that biological control is the most powerful ally that a disturbed ecosystem has in the efforts to return it to ecological health. In this paper I will try to demonstrate why I think that this is so by following a path from simple ideas to more complex ones in order to demonstrate the power that biological control may have in helping manage ecosystems at risk from invading species. The path I will take is this: I will look at what happens in nature in biological control programs. I will then show that we can capture what happens in nature in a simple model of population dynamics. Then I will expand the
model to include migration in four different types of ecosystems. In these ecosystems, I will simulate the invasion of a species and its remedy through the introduction of a natural enemy. And in these cases, we find the same power and results in a complex ecosystem as we do in the simpler, two-species cases.

**MATERIALS AND METHODS**

To develop these themes about biological control and ecosystem-wide biology, I am going to draw upon real-world data to first give us an impression of what biological control of arthropods can do in terms of population suppression (Van Driesche & Bellows 1996). Of the some 1200 biological control programs developed against arthropods and other pests, there is relatively little data on what we would consider modern quantitative population dynamics. Early qualitative reports of biological control success were exuberant about their impact. More recently, we can find in the literature (and in our own work) quantitative studies on the impact of natural enemies on harmful invasive species.

Fig. 1 shows a few examples of the impact of introducing a natural enemy into an already established population of a harmful or pest species. In every case we find important and repeated characteristics. Although the figure only indicates three examples, we find throughout the quantitative literature four features common to such programs. One, that whenever an arthropod species invades a new territory in which it can survive and reproduce well, its population grows to a size that occupies all the available resource that is critical for that species (such as leaf area, for example). Second, we find that when an effective natural enemy is introduced, it requires some 10-15 generations for the population of the natural enemy to catch up to the pest species density and exert a sufficient force on it that the pest population collapse. Third, we see that in a biological control program, once the natural enemy’s population density has caught up with the pest, the pest population crashes to phenomenally low densities, typically 4-8 orders of magnitude lower than prior to the natural enemy’s introduction, a control level unsurpassed by any other mechanism or pest control known. The final feature of this control is that it appears permanent. The pest and natural enemies continue to exist at very, very low densities without disruptions or outbreaks.

These four characteristics of biological control programs and their impact on pest species appear pervasive, and many examples can be found from the biological control of pests in many different environments. This pervasiveness implies that there are intrinsic features of pest-natural enemy systems that are found across many taxa, in many different environments. So a task is set before us to uncover, or at least mimic, what some of these features are, so that we might come closer to an understanding of what makes biological control so powerful in so many different settings. As a beginning, I will present a graphical view of what happens to an ecosystem when it suffers an invasion of a harmful species.
Figure 1. Three examples of biological control outcomes that emphasize the four important points of biological control: first, that an invasive species can reach phenomenal densities. Second, biological control can bring about major suppression of target pest. Third, an expectation that it will take 10 to 15 generations to achieve such suppression, and fourth, that such suppression is permanent. (a), giant whitefly, Bellows unpublished; (b) larch sawfly after Ives 1976; (c), olive scale, after Huffaker 1971.
Figure 2. A fundamental community consists of plant species, herbivore species, and predator or parasitic species.

Figure 3. An ecosystem is composed of many communities operating together in the same space and time. One community may be present in many numbers. There also may be many different communities that interact with one another. An invasion by a species not a member of the ecosystem may reek havoc on ecosystem function.
In Fig. 2 I have characterized the structure and function of a simple, three-species community. Having many such communities, and mixing them with similar communities made up of different species (Fig. 3), provides the basis for an ecosystem in dynamic homeostasis. A major problem arises when a species new to the ecosystem, an invading species, arrives and begins to grow out of control, using up nutrients, or competing for foliage, and changing the homeostasis to the point that the ecosystem can no longer function as is had.

We now need a tool, or a model, that captures the four essential features of a successful biological control campaign. The structure of such models has been the object of much study, from the initial work of Thompson (1924) and Nicholson and Bailey (1933), through to the present day. The simplest and most appropriate form is a pair of difference equations, as shown here:

\[
\begin{align*}
    h(t+1) &= F \cdot h(t) \cdot g(h(t)) \cdot f[h(t), p(t)] \\
    p(t+1) &= h(t) \cdot g(h(t)) \cdot [1 - f[h(t), p(t)]]
\end{align*}
\]

A bit of explanation makes these equations very simple to follow. The herbivore population that is the target of a biological control program is represented by ‘h’. The value of \( t \) is the generation in which the equations are operating, and is iterated or added to each time we use the equations. The symbol \( F \) represents the fecundity of the herbivore. Now we have only the functions \( g \) and \( f \) to deal with. At extremely high densities, the herbivore may run out of resources necessary for optimal reproduction. So the function \( g(h) \) is simply the proportion of offspring that survive in that generation due to any limit placed on the population by lack of resources. The function \( f(g, p) \) tells us the proportion of herbivores that escape parasitism, and hence go on to survive to the adult stage and produce the generation \( h(t+1) \). The proportion that does not escape parasitism (in the second equation) eventually become parasitoid adults, \( p(t+1) \), in the next generation. This pattern repeats itself over and over, generation after generation.

I will not bore you with nearly a hundred years of research trying to find functions for \( g \) and \( f \) that actually describe what we see in biology and in biological control situations. Suffice to say that, after many trials, two have come to be recognized as the most suitable functions. For density dependence in the herbivore population, a model with the necessary properties was provided by Maynard Smith and Slatkin in 1973 (Bellows 1981), where

\[
g(h) = \frac{1}{1 + (ah)^b}
\]

In this model the parameter \( a \) is simply a scaling parameter, helping to fix the equilibrium density of the herbivore population in the absence of any predation or parasitism. The parameter \( b \) has bearing on the degree of severity of the density dependence in the herbivore populations. In most insect populations, density dependence found in nature is mild (Bellows 1981), and in all the simulations reported here \( b \) has the value 1, which represents simple contest competition. The parameter \( a \) was given the value 0.001 for every location, and the fecundity (\( F \)), that is, the number of offspring that do not perish due to density independent causes, was assigned the value 4. This provides an equilibrium herbivore density, in each location (and in the absence of parasitism), of 3000 individuals.
Of the many models employed by many authors for predation or parasitism (function \( f(h,p) \)), only one has emerged that can demonstrate the properties we see in nature: major suppression of an invading species, with stable, continuing populations (May and Hassell 1988). This model employs the negative binomial distribution of attacks by a natural enemy, that is, the attacks tend to be clumped or aggregated (as are also many herbivorous insects in nature). The function takes the form:

\[
\frac{1}{f(h,p)} = 1 + \left(\frac{a'P}{k}\right)^k
\]

The parameter \( a' \) represents the search efficiency of a single female parasitoid, and the parameter \( k \) indicates the degree of aggregation of her attacks. In the simulations reported here, these parameters were given values of 0.1 and 0.5, respectively, indicating a moderately efficient natural enemy with a mild degree of aggregation in her attacks.

Before continuing to explore the simulations of ecosystem-level invasions, we must first determine if the tool, that is, the model, is an effective mimic of what we see in natural invasions followed by a biological control program. In order to do so, I ran simulations of just an isolated pair of populations, one herbivore and one parasitoid. Each simulation ran for 20 generations with only the herbivore. At that time, a single natural enemy was added to the population, which was then run for an additional 15 generations. The outcomes are discussed in the Results section, but suffice to say here that they were in keeping with expectations, and validated the use of the model as a tool to explore more complicated ecosystem-level invasions.

In exploring the potential ecosystem-level impact of a natural enemy working against an invasive species, there are several significant questions to explore. One is to what degree is the invaded species suppressed when it is capable of movement from one part of an ecosystem to another. Another important issue is whether any suppression achieved is stable, or is subject to erratic fluctuations.

In order to explore these issues, I developed a model of an ecosystem which consisted of 400 locations, each adjacent to two or more locations, placed on a square grid of 20 rows and 20 columns (Fig. 5). Each location was characterized by a parameter \( \bar{a} \), which was varied in different ways in the four ecosystems. The parameter \( \bar{a} \) varied from 0 to 1, and was used to characterize the suitability of each location for herbivore reproduction. The parameter \( \bar{a} \) was multiplied into the herbivore reproduction equation:

\[
h(t+1) = \bar{a} \cdot F \cdot h(t) \cdot g(h(t), f(h(t), p(t)))
\]

A location with a value of 1 is highly suitable, and imposes no limit on the herbivore. A location with a lower value of \( \bar{a} \) would limit the potential reproduction of the herbivore.

Using this model ecosystem I investigated four different patterns for the value of the parameter \( \bar{a} \), to represent four different types of ecosystems. In one simulation, all locations in the environment had a value of 1. This, in a way, was the most basic evaluation of the behavior of biological control over a wide, uniform area. In the second simulation type, I placed values of 1 in a regular pattern over the ecosystem, separated by values of 0 (Fig. 5). This might be viewed as representing an orchard, or an urban ecosystem, with each house and yard separated by streets or avenues. In the third simulation, I assigned each location in the
ecosystem a random number between 0 and 1. This is the most diverse and complex system (Fig. 6). In the fourth case, I placed specific areas on the ecosystem map in which the locations had high values of $\tilde{a}$, separated by locations with values of 0. This represents an ecosystem with certain vulnerable habitats, in which conditions allow the invading species to flourish, surrounded by areas where the invading species can not reproduce.

Migration in the ecosystem was handled simply, and in keeping with most of what we know about movement in arthropod populations. The premise I followed was as follows: most offspring tend to stay close to their area of birth and rearing (close at least in the sense of the perceived size of the grid). Hence after herbivore reproduction and parasitism, there was a migration phase in which only half of the surviving individuals in a location remained there. Of the other half, 80% were distributed equally in the locations surrounding the one of their birth, indicating moderate amounts of migration. The remaining 10% were considered “far migrators”, and were distributed evenly over the entire ecosystem, into locations from the farthest to the closest to where they were born.

RESULTS

TWO SPECIES, SINGLE LOCATION MODEL

Validating a tool such as a model for use in exploring the potential impact of an invading species requires that we examine the behavior of the model in its simplest possible form, and compare the model outcomes with what we know occurs in nature. If the model passes such a test, then it may be useful to generate hypotheses about what may happen in a larger context, that is, in our study what may happen in an ecosystem. Of course, if the model cannot capture the essentials of natural populations, it is an untrustworthy tool and another one must be sought for use in its place.

Of the four essential and common features of an invading species, a biological control program, and the impact on the two populations involved, we can examine each one in turn after conducting simulation studies with the proposed model. I conducted several such studies, with varying values for the parasitoid search parameters and the herbivores growth parameters. One such simulation study, the results of which were typical of all the trials I ran, is shown in Fig. 4.

In this study, we see the rapid rise in density of the invading species, reaching its carrying capacity in just 5 generations. This is equivalent to the invading species occupying all the available resources, as is common when a species is adventive to an area and has no effective natural enemies. In the absence of natural enemies, it rapidly reaches the environmental limit of its growth, and the population is limited by its own density dependence. Here, the model mimics the first of the four common features of a biological control program.

In generation 18, when the invaded species had reached its equilibrium density of 3000 individuals, 10 parasitoids were added to the system. These parasitoids amounted to 0.3% of the host population. But such is often the case in biological control – by the time a natural enemy has been located, screened for safety, and rearing has begun, the invaded species which is its target has been reproducing without limit for many generations. So the entry of 10 adult
parasitoids into the system is typical of such programs. As the impact of 10 natural enemies on a population of 3000 herbivores is nearly undetectable, these releases are often referred to as “inoculation” releases, with the expectation that their offspring will start a population growth that will eventually catch up to, and then control, the invading species.

In natural systems where such data are available, approximately 10-15 generations pass before the density of the invader begins to decline, and when it does so, it does so very rapidly. If a sample is taken at the right time, one can often find a leaf covered with the invading herbivore, together with very large numbers of the natural enemy. Here the model appears to be slightly more efficient than what data we have on such matters, bringing the invaded species density down dramatically within five generations.

The last two matters, the degree of suppression and the stability of that suppression, we also see in the modeled populations. The average density of the invaded species after the suppression (generations 36-40) is 31.2, a drop of two orders of magnitude below its previous high level. The standard deviation of this mean population level is 0.95, which is 3% of the mean, and indicates a very stable population. Clearly the impact of the natural enemy in the model has given us an appropriate decline in density, and maintains it with considerable stability.

Note the major drop in density of the invaded species, followed by a moderately stable and consistently low density of both the herbivore and its natural enemy.

**ECOSYSTEM SIMULATIONS**

Having concluded an evaluation of the model in its simplest setting, we have found that it does have the characteristics and behavior that we see in nature. This does not make the model “correct” in any context – a model is simply an abstract representation a dynamic process. But the fact that the model does capture the dynamical behavior we see among natural populations does give some confidence that we can now apply the model to a wider
scope, and use it to ask questions about the behavior of similar systems, such as an ecosystem which we envisage as a collection of communities each behaving in the manners that the model has been able to replicate. So here we are using the model to explore possibilities, create hypotheses; but we are not attempting to prove something. Hypotheses only get tested by using biological data, and the most useful and related thing a model does is help us create sensible hypotheses to test.

Such testing is beyond the scope of this paper, but we can examine what the model behavior is in the ecosystems that I have proposed testing. Two of these are somewhat trivial, and I will present them de novo at the symposium. Two others will suffice to demonstrate what new insight might be awaiting us in the continued study of ecosystems affected by invasive organisms.

The first of these (Fig. 5) represents an ecosystem that has areas suitable for the reproduction of the invading species, separated by regions that are not. Some have termed such a layout an “orchard” model of an agricultural ecosystem (to distinguish it from monocultural agricultural regions). One of the first things we would expect is that the equilibrium density of the invading species should be lower here than in an ecosystem that was uniformly suitable for reproduction, as there is less resource in this ecosystem. Such turns out to be the case, and the equilibrium density for an invading species in this ecosystem is only 36% that of when it is growing in a uniform ecosystem.

Turning to our four expectations from biological control systems, we see that in the absence of natural enemies, the invading species does reach the carrying capacity of this environment quickly. We also note that the population density of the pest falls rapidly following the introduction of the natural enemy, in this case in approximately 7 generations (but this was also the case for this model when evaluated in the simplest trial). The pest population is reduced, and appears to be low and stable for many generations. However, a closer quantitative look shows that the average population density of the invaded species in only 1.5 orders of magnitude lower than its carrying capacity. The standard error of the mean is very low (3% of the mean density), so the new stasis appears very stable. But it does appear that the model does not predict as great a population density reduction as we have seen in many field studies.

Lastly, we turn to an ecosystem that is rather like an abandoned field, or a heterogenous forest, or any other kind of ecosystem that has great variation in its resources over the space it occupies. The average value of the parameter $\alpha$ in this ecosystem is 0.500, thus we might expect that the carrying capacity of the ecosystem would only be half of what we would find in an ecosystem that was uniformly suitable for an invading species. This is indeed the case. But let us turn to our four characteristics and evaluate what the model says about biological control as a tactic in such a diverse system.

We find that an invaded species does indeed climb to the overall carrying capacity very quickly. When the natural enemy is introduced, a new stasis is reached in approximately 10 generations, fitting well with what we see in nature. However, the new equilibrium of the invaded pest is again approximately 1.5 orders of magnitude lower than the environment’s carrying capacity.
Figure 5. An environment with regularly distributed suitability for pest survival, separated by regions where the pest cannot survive. The density of the pest (black) increased until the introduction of the natural enemy (red).
Figure 6. An environment with randomly distributed suitability for survival of an invaded species, and the dynamics of the pest (black) increasing in number until the introduction of the natural enemy (red).
DISCUSSION

When discussing models and their uses, particularly I think in the field of population dynamics, one can be tempted to wax poetic on the charming attributes of this equation or that formulation, or on the elegance of a particular mathematical framework. But jesting aside, models rally only serve two sensible purposes. First, models are of great value when they shed light on some piece of truth that was previously hidden from us. How we can tell whether what the model tells us is true, since we had not discovered it ourselves, is a bit of a philosophical conundrum. But we must pass on and leave the philosophers such puzzles.

Models are also useful to us when we have confidence that they actually capture the essence of an interaction, such as in a host-parasitoid interaction. We can gain such confidence by comparing certain features of a model with similar features of a living system. If the two systems, one living on its own, and the other living in our heads, provide similar answers to questions put to both, then our confidence in the model’s ability grows. It becomes a tool that we can apply to other systems. We can use it to ask questions about bigger, or broader, systems. That is what we did here.

The model that I worked with gave confidence in the beginning because it could readily mimic the behavior of simple real-world systems. This prompts the questions: Can it tell us something we do not know about more complex systems? So I applied it to imaginary ecosystems, with imaginary properties (such as migration), and gathered some new information. The model showed that biological control may well be a phenomenal tool to solving invaded species problems. It indicated that several different kinds of ecosystems that biological control could reduce the density of an invading species from 10-100-fold (although we see values far higher than that in studies of natural systems). The model also indicated that the new lower population density would be extremely stable, and would remain so for a long time. Both of these points are reasons for biological control to stand ready to aid whenever an invasive species problems crops up – not only in our traditional agricultural arenas, but also in urban areas, in forests, in the invasions of wetlands.

The question of whether or not biological control can contribute to restoring ecosystems disturbed by species invasions still needs to be answered in the field. But everything I have found, using tools as disparate as simple populations models to holistic systems analysis, tells me that the answer may well be a resounding yes.

REFERENCES


