available at www.sciencedirect.com

ScienceDirect

journal homepage: http://www.elsevier.com/locate/ecocom

Local adaptation to biocontrol agents: A multi-objective data-driven optimization model for the evolution of resistance

L. Stevens [a,*], D.M. Rizzo [b,1]

[a] University of Vermont, Department of Biology, 321 Marsh Life Science Building, Burlington, VT 05405, USA
[b] University of Vermont, Department of Civil & Environmental Engineering, 219 Votey Building, Burlington, VT 05405, USA

ARTICLE INFO

Article history:
Received 27 August 2007
Received in revised form
13 March 2008
Accepted 25 April 2008
Published on line 12 June 2008

Keywords:
Biological control
Evolution
Resiliency
Meta-population model
Data-driven model
Multi-objective optimization

ABSTRACT

Spatial and temporal variability in the application of biological control agents such as parasites or pathogenic bacteria can cause the evolution of resistance in pest organisms. Because biocontrol will be more effective if organisms are not resistant, it is desirable to examine the evolution of resistance under different application strategies.

We present a computational method that integrates a genetic algorithm with experimental data for predicting when local populations are likely to evolve resistance to biocontrol pathogens. The model incorporates parameters that can be varied as part of pest control measures such as the distribution and severity of the biocontrol agent (e.g., pathogenic fungi). The model predicts the evolution of pathogen defense as well as indirect selection on several aspects of the organism's genetic system. Our results show that both variability of selection within populations as well as mean differences among populations are important in the evolution of defenses against biocontrol pathogens. The mean defense is changed through the pest organism's genotype and the variance is affected by components of the genetic system, namely, the resiliency, recombination rate and number of genes.

The data-driven model incorporates experimental data on pathogen susceptibility and the cost of defense. The results suggest that spatial variability rather than uniform application of biological control will limit the evolution of resistance in pest organisms.

1. Introduction

Biocontrol agents such as pathogenic fungi (Tucker and Stevens, 2003) and bacteria (Medvinsky et al., 2007) are often used to control pest organisms such as insects. Models exist forc the effect of pathogens on diversity both within and between species (Abell et al., 2005; Laird and Jensen, 2006) and other models consider spatial variation (Medvinsky et al., 2004; Shirley and Rushton, 2005). However, the pest species can evolve resistance to biocontrol agents. In this paper, we examine the evolution of such resistance, along with correlated traits that might co-evolve under different patterns of environmental variation. We develop a model using data on the sensitivity of Japanese beetles, *Popilla japonica* to the entomopathogenic fungus *Metarhizium anisopliae*. Insects commonly defend themselves using melanin to encapsulate organisms that breach the cuticle by activation of the enzyme PO. We used data from four populations of Japanese beetles from across Vermont: two were from locations using the bacterial pathogen *B. thuringiensis* as agents of biological pest control, and two locations did not use biocontrol. Populations from areas with biocontrol exhibited greater PO production and suffered less mortality from pathogen exposure; however, PO levels positively correlate with increased mortality in the absence of parasitism (Tucker and Stevens, 2003). The Japanese beetle system is provides a good model for examin-

* *Corresponding author*. Tel.: +1 802 656 0445; fax: +1 802 656 2914.
E-mail addresses: lxsteven@uvm.edu (L. Stevens), drizzo@cems.uvm.edu (D.M. Rizzo).
[1] Tel.: +1 802 656 1495.

1476-945X/$ – see front matter
doi:10.1016/j.ecocom.2008.04.002

ing adaptation to biocontrol because beetles with higher quantities of PO are known to be more resistant to bacterial and fungal infections.

Biochemical defenses, such as PO, are one of several means of pathogen defense. Other means of defense include: immune, life history, behavioral and structural defenses. Organisms also have several defense mechanisms including continuous/inducible expression of defenses, qualitative changes in elicitors/receptors, and increasing/decreasing defense quantity (Rigby et al., 2002). Immunity includes both cellular components (e.g., phagocytic blood cells to defend against general pathogens such as bacteria) and the adaptive immune system (e.g. the antibodies generated by vaccines). Only vertebrates have adaptive immunity; however most organisms, including insects, have biochemical and cellular defenses, such as the common biochemical defense involving the activation of the enzyme PO. In several species, quantity of PO is correlated with parasite resistance (e.g., Gillespie et al., 2000) and Japanese beetle populations that vary in previous exposure to biocontrol vary in PO quantity (Tucker and Stevens, 2003). When biochemical or cellular defenses depend on the quantity of the defense, they are likely to have constraints based on physiological, energetic, genetic, and/or hormonal correlations (Zera and Harshman, 2001); for example, producing high quantities of PO can use energy that might otherwise be used for reproduction. Japanese beetle populations with high quantities of PO exhibit a trade-off between high quantities of defense and other aspects of fitness (Tucker and Stevens, 2003). Because trade-offs can exist for pathogen defense, spatial variation in susceptibility to pathogens can evolve as a result of biocontrol efforts making the evolution of pathogen defense a complex optimization problem.

Pathogen models have examined uniform and variable environmental effects (Hilker et al., 2006). When selection varies on a spatial scale, adaptation may include not only changes in the mean value of a trait, but also aspects of the variability of the trait; and thus, adaptation is most realistically modeled using multiple traits and a multi-objective optimization approach. Multi-objective optimization problems can be investigated using analytical techniques; however, for more complex situations analytical solutions do not exist. The data-driven nature of evolutionary algorithms make them ideal for analyzing complex multi-objective optimization problems and have many advantages over other optimization techniques for modeling biological adaptation (Foster, 2001) as presented in the following sections.

1.1. *Self-adaptation: indirect selection*

A feature of evolutionary computation that mimics biological processes is that parameters can "self-adapt" or undergo indirect selection (Eiben et al., 1999). Self-adaptation or the "evolution of evolution" occurs when several parameters are incorporated into the evolving fitness of an individual thereby making them subject to evolution.

Adaptation to biocontrol agents can occur by optimizing the mean and variance of a trait. When biocontrol application is unpredictable, it may be advantageous for organisms to produce offspring with a range of phenotypes. In the model presented here, we simulate the simultaneous evolution of the mean *host defense genotype*, as well as two parameters of the organism's genetic system, *recombination rate* and *canalization*, that affect trait variability.

1.2. *Host defense genotype*

Based on empirical studies of plant and animal defenses (Kolb et al., 2001; Pilet et al., 2001; Schneider et al., 2001; Wu et al., 2001), we modeled quantitative (Falconer and Mackay, 1995), polygenic defense genotypes. Most models incorporate haploid organisms (i.e., those having unpaired chromosomes such as bacteria); however, artificial life experiments with haploid organisms that undergo sexual reproduction show that sexual reproduction profoundly influences the evolution of genetic architecture (Misevic et al., 2006). Our model extends previous studies by considering diploid inheritance, which is the more realistic case for animals, plants and fungi.

1.3. *Recombination rate*

The number of chromosomes, $2n$ (two copies of each gene, one from the female parent and one from the male), varies among organisms. We based our model on data from a scarab beetle and $n = 10$, $2n = 20$ for most of this group. If recombination (crossing over between homologous chromosomes during the process of gamete formation when cells go from $2n$ to n) does not occur, the entire intact chromosome inherited from either the female parent or the male parent will end up in the sex cell. With recombination, a novel, hybrid chromosome will result.

The rate of recombination affects the variability of offspring. Recombination rates vary among sexes, populations and species, and can evolve by indirect selection (Uyenoyama and Bengtsson, 1989). Recombination among genes that affect the same trait, such as the multiple defense genes examined in our simulation, affects the ability to form adaptive gene complexes (i.e., genes that work together to perform a particular function) (Palopoli and Wu, 1996). Models have shown that parasites select for recombination in haploid hosts (Hamilton et al., 1990), presumably because recombination generates variability allowing a host to escape attack.

1.4. *Canalization (i.e., resiliency)*

Seventy percent of the variation in PO activity of the caterpillar *Spodoptera littoralis* is estimated to result from environmental factors (Cotter and Wilson, 2002). Several authors have addressed the ability of genotypes, genetically identical at fertilization, to become variable during development (Kaplan and Cooper, 1984; Boldogkoi, 2004) and distinguish between phenotypic plasticity, canalization and adaptive coin flipping. Phenotypic plasticity has been defined as the ability to produce different phenotypes in response to environmental cues (e.g., the number of leaves on a tree). The ability of an organism to produce a constant, stable phenotype regardless of environmental circumstances has been termed canalization. In the numerical computation and artificial life literature, the term