



Evolutionary response of a native butterfly to concurrent plant invasions: Simulation of population dynamics



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ABSTRACT

The habitat of the green-veined white butterfly *Pieris oleracea* in eastern North America has undergone invasions by the exotic plant garlic mustard (*Alliaria petiolata*), which is replacing native hosts of *P. oleracea* such as *Cardamine diphylla*. *A. petiolata* was originally lethal to most larvae of the native butterfly but during the past 20+ years it has been incorporated successfully into the larval diet, likely through evolutionary change. The region was also invaded by another exotic plant, *Cardamine pratensis*, on which the native butterfly larvae readily develops, allowing the possibility of population rescue. Further complicating the butterfly's reproductive dynamics, it is multigenerational within a summer, and host plant availability and location change during the summer. Our goal is to model the expected dynamics of the native butterfly population in this evolving, dynamic landscape by using a new bio-inspired paradigm known as membrane computing.

In this context, a Probabilistic Guarded Scripted P system has been designed to model and explore the conditions under which an allele conferring ability of *P. oleracea* larvae to develop on *A. petiolata* might have proliferated. The design describes a population dynamics model whose parameter values are derived from experimental and observational data. Our modeling framework is spatially explicit and our model integrates seasonal as well as annual dynamics. The simulation results from our model qualitatively match our field observations and experimental laboratory results, and agree with the results from a previous model on the genotypic adaptation of this butterfly species. From the simulations we identified the likely trajectories for the spatio-temporal distribution of alleles enabling *P. oleracea* to use the invasive plant species across this selective and phenological mosaic.

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1. Introduction

The effects on native herbivorous insects from exotic plant invasions relative to their normal host plants occur at both ecological and evolutionary time scales (Bezemer et al., 2014). These can include “no effect” (e.g. effects of crown vetch *Coronilla* on the native butterfly *Colias philodice* (Karowe, 1990)), to positive effects such as increased population sizes and expanded habitat occupancy in native butterflies using non-native species as larval hosts (e.g. *Speyeria idalia* larvae feeding on non-native *Viola bicolor* (Shuey et al., 2016) or *Euphydryas phaeton* using non-native *Plantago lance-*

olata (Brown et al., 2017)), possibly altered larval or adult defense against predation (e.g. *Anartia jatrophae* larvae using non-native *P. lanceolata*) store some of the iridoid glycosides found in this plant (Knerl and Bowers, 2013), or increasing the number of generations per year (voltinism) (e.g. *Pieris napi* and *Battus philenor* using non-native hosts (Herlihy et al., 2014; Shapiro, 1975a,b; Sims and Shapiro, 1984)). Of concern, however, is that novel exotic plants may present native herbivorous insects with ‘sensory traps’ that are attractive to ovipositing adults but poorly support subsequent larval growth and development (Chew et al., 2012; Harvey et al., 2010; Keeler and Chew, 2008; Keeler et al., 2006).

In natural systems native species may often be exposed to closely sequential or concurrent invasion events from a variety of exotic species with contrasting effects on native species. Predicting the trajectory of a native species' response to such concurrent encounters with exotic species is not straightforward. Further con-

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Fig. 1. Adult *Pieris oleracea* nectaring at flowers of garlic mustard, *Alliaria petiolata*. Photo by F.S. Chew.

tributing to the complexity of effects from concurrent invasion events, a selective spatial and phenological mosaic may be created by the timing and spatial distribution of exotic species as they spread in a region. The trajectory of a native species' response as it encounters exotic species across this mosaic will depend on the details of genetic variation, natural history, life history, chance, and how different parts of the insect population fare in response to dispersal of individuals that survive selective filters in different parts of the mosaic. Here we model a biological system of a native herbivorous insect whose native host plant is being replaced by an exotic invasive plant that has strongly detrimental effects on the native insect, and a closely sequential or possibly concurrent invasion by a second exotic plant with strongly positive effects.

A recovery of population size at our study area (at the nexus of invasions) has already been documented (Chew et al., 2012; Herlihy et al., 2014), as has apparent adaptation of the native insect population to the formerly detrimental exotic plant, whose bolting (flowering) stage but not the rosette stage is now being incorporated into the native insect's diet (Keeler and Chew, 2008). *Alliaria petiolata* M. Bieb. (Cavara & Grande) is present in the system in its rosette stage throughout the entire year, but its bolting stage is present only during the first generation of butterflies each year. Prior stochastic models of this system have explored the competing top-down versus bottom-up influences on population persistence of the native butterfly *P. oleracea* Harris (Lepidoptera: Pieridae) (Keeler et al., 2006) (Fig. 1), and the putative effects of two exotic parasitoid species on population decline and recovery of the butterfly, and an exploration of whether mutation or residual polymorphism is a more probable source for genetic variation (Morton et al., 2015).

Our goals in this model address components that have not yet been modeled, in part because of limitations of the (prior) modeling framework. Specifically, we assess: (a) Effects of simultaneous concurrent invasions of two hosts – one “good” and one initially “bad” – for the native butterfly, and their effects on the proliferation of genotypes adapted to the “initially bad” host plant. (b) Effects of spatially contiguous but ecologically distinct habitats with different suites of potential host plants and thus seasonally and spatially distinct selection regimes within a breeding season that includes up to three generations of the native butterfly. (c) Butterfly population dynamics and evolution between generations within a breeding season and from year-to-year, tracking the proliferation of genotypes adapted to the exotic invasive plant that was a formerly poor host.

These explorations permit us to assess the possible contributions of the “good” exotic host and the successful incorporation of the initially “bad” exotic host into the butterfly diet to population recovery at this site. They further allow us to explore the hypothesis that near-concurrent invasion by the “good” exotic host may have contributed to spread of the genetic adaptation to the formerly “bad” exotic host.

Computational modeling frameworks in population dynamics

Traditionally, the study of complex systems (and population dynamics, in particular) has been addressed by using ordinary differential equations (ODEs). This approach shows in turn some drawbacks when used for discrete and stochastic processes, and poses some inflexibility to changes, that can cause a big impact in the defined equations (Costantino et al., 1997; Grimm, 1999; Grimm et al., 1999; Judson, 1994; Romero-Campero and Pérez-Jiménez, 2008a). Hence, other computational paradigms have been considered to define more accurate models. One example is Petri nets, a non-deterministic model that is well-suited for distributed systems with concurrent events. This model, extended with stochasticity, has been used together with Cellular Automata for event-based modeling of ecological systems (Gronewold and Sonnenschein, 1998). Other examples such as concurrent and process algebras provide tools for modeling parallel events with kinetics functions (normally adopted from the Gillespie algorithm) (Jordán et al., 2011).

Although each of these (extended) computational frameworks has been used as a modeling framework for many scenarios, none of them fully integrates the dynamics and structural details of complex systems (Colomer-Cugat et al., 2014). In this concern, P systems provide the following advantages as a computational modeling framework: (a) flexibility, i.e. minor changes in the system are reflected as minor changes in the model, (b) capability of simultaneous modeling of coexisting species and their interaction with the environment, (c) ability to define spatially-explicit dynamics (Colomer et al., 2013). For all of these, several membrane computing frameworks have been proposed, such as Dynamical Probabilistic P (DPP) systems (Besozzi et al., 2008), Minimal Probabilistic P (MPP) systems (Barbuti et al., 2015) and Population Dynamics P (PDP) systems (Barbuti et al., 2013; Colomer-Cugat et al., 2014). In what follows, we compare them with our proposed PGSP systems.

DPP systems were first introduced for modeling metapopulations (Besozzi et al., 2008). A DPP system consists of a rooted-tree structure with compartments. As in PGP systems, a DPP rule transforms a multiset u in a compartment i into a multiset v , which can be sent to another membrane j . Moreover, a kinetic constant is used to proportionally calculate the probability of application of the rule. The main differences with PGSP systems are: (a) the probabilities are computed per transition step, depending on the amount of objects present in the compartment, what is more computationally expensive for simulators, (b) it uses a rooted-tree structure instead of a directed-graph, and (c) compartments do not have contexts (flags in PGP systems).

MPP systems, introduced in 2015 (Barbuti et al., 2015), have been used to model the ecological problem of stability of European water frog populations. They are flat P systems (i.e. without an associated structure), whose rules have an associated multiset of promoters and a rate function. Rule promoters are used to represent contexts, and they can coexist in the same configuration. The rate function is used to calculate the probabilities for each transition step as a function of the number of individuals. Thus, the main differences with PGSP systems are: (a) no explicit representation of space, (b) probabilities are calculated in each transition step and used to select the sequence of rules to be applied, and (c) multiple promoters can coexist at a given instant. In order to allow

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