

Population genomics and demographic modeling enhance our understanding of trophic level interactions in biological control

Arun Sethuraman^{a,*}, John J. Obrycki^b

^a Department of Biology, San Diego State University, San Diego, CA, USA

^b Department of Entomology, University of Kentucky, Lexington, KY, USA

HIGHLIGHTS

- Population genomics can elucidate historical and contemporary population dynamics of natural enemies, their pests, conspecific competitors, and parasitoids.
- Demographic models based on genomic data can enhance understanding of trophic level interactions across species.
- In this paper we present a proof of concept using population genomic techniques to complement ecological studies of population dynamics across trophic levels.

ARTICLE INFO

Keywords:

Population demographic models
Population genomics
Intraguild interactions
Trophic connections
Predator population dynamics

ABSTRACT

In this paper, we focus on the application of population genomics, including next-generation sequencing and demographic modeling, to enhance the understanding of historical and contemporary trophic level interactions that are a fundamental basis of biological control. We outline how the integration of ecological approaches with population genomics and demographic modeling can provide additional insights into existing trophic interactions and how natural enemies, their parasitoids, and pest species evolve through these interactions, potentially affecting future levels of biological control. We briefly review and summarize our recent population genomic studies of predatory ladybird beetles and discuss how our results provide guidelines for the use of population genomics techniques and population demographic modeling to enhance our understanding of trophic level interactions. Our intent is to demonstrate as a proof of concept, how these methods can supplement currently used techniques and add a complementary genomic aspect to ecological understandings of trophic level interactions, including estimates of effective population sizes of natural enemies and pest species, examination of correlations between these effective population sizes, and evolutionary changes in natural enemies and pest species which may influence levels of biological control. This in combination with experiments and simulations provide a well-rounded framework for using population genomics to inform multi-tier trophic level interactions.

1. Introduction

In recent years, advances in the analysis of genomic data have greatly improved our ability to understand population-level and trophic-level forces shaping the evolutionary and demographic history of species, including the robust resolution of population structure, the estimation of migration rates, both current and historical, and the detection of shifts in population growth, either through expansions or bottlenecks. While most often applied to the study of population history over relatively long time scales (e.g., the effects of Pleistocene glaciation; Moura et al., 2014; Lanier et al., 2015; Papadopoulou and Knowles, 2015; Lozier et al., 2023), these methods are now being used to elucidate population history

and associated parameters on a very recent time scale, sometimes over a span of just 30–40 generations (Lozier, 2014; McCoy et al., 2014; Rosenthal et al., 2021). The new power of these methods is fueled by the tremendous amount of information available in population genomic data. Plummeting sequencing costs, coupled with the lack of a requirement to invest substantial time and efforts in developing molecular markers for each new species under study, place us at the cusp of developing a new paradigm for improving our understanding of trophic level interactions of biological control species by using comparative genomic analyses.

Direct applications of population genetics to biological control include studies of (a) how local adaptation of biological control

* Corresponding author.

E-mail address: asethuraman@sdsu.edu (A. Sethuraman).

<https://doi.org/10.1016/j.biocontrol.2024.105585>

Received 29 April 2024; Received in revised form 3 July 2024; Accepted 12 July 2024

Available online 14 July 2024

1049-9644/© 2024 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

organisms to their hosts/prey have caused differential fitness, and hence play a role in their effectiveness in biological control – e.g. [Li et al., 2023](#) (evolutionary adaptations and increased fitness of the invasive Harlequin ladybird beetle, *Harmonia axyridis* as imported biological control organisms to novel environments and multiple pest species across the globe), [Jones et al., 2024](#) (evolutionary adaptations to latitudinal variation in reproductive diapause responses to photoperiod, despite little population genetic structure in imported and augmented populations of two co-occurring species of predatory ladybird beetles – *Propylea quatuordecimpunctata* and *Hippodamia variegata*), [Goolsby et al., 2004](#) (erionid mites as natural enemies, adapting to invasive climbing ferns), [Lemausurier and Waage, 1993](#) – braconid wasp, *Cotesia glomerata* used in suppression of *Pieris rapae* (described in [Hufbauer and Roderick, 2005](#), [Hufbauer, 2002](#)), (b) how bottlenecks due to importation of natural enemies affect their fitness – e.g. reduced fitness in populations with reduced neutral variation in braconid wasps (*Aphidius ervi*) – [Hufbauer, 2002](#), [Hufbauer, 2004](#), meta-analysis of 34 studies – [Reed and Frankham, 2003](#), [Sethuraman et al., 2018](#) – on recurrent recent bottlenecks in North American populations of *Harmonia axyridis*, and *Hippodamia convergens*, while demonstrating exponential growth in populations of *Coccinella septempunctata* in similar ranges, [Sethuraman et al., 2024](#) – documenting exponential declines and reduced neutral diversity in imported and augmented populations of *Hippodamia convergens*, (c) how pests evolve in response to biocontrol organisms, and environments – e.g. quantitative genetic variation harbored in pea aphids against parasitism by *A. ervi* – [Hufbauer and Via, 1999](#), polygenic adaptation to insecticides in the Colorado potato beetle (*Leptinotarsa decemlineata*) – [Crossley et al., 2017](#), coevolution and sustainability of importation biological control of the invasive walnut aphid (*Chromaphis juglandicola*), and its parasitoid, *Trioxys pallidus*, resulting in failure of biocontrol in California ([Andersen and Mills, 2018](#)).

During the past three decades, examples of other topics in population genetics that have been examined in relation to biological control include: manipulation of genetic variation in natural enemies used in importation biological control ([Hopper & Roush, 1993](#)), discussion of the use of molecular tools in importation biological control ([Unruh & Woolley, 1999](#)), questions related to microevolution in natural enemies ([Hufbauer & Roderick, 2005](#)), detailed examination of the evolutionary concepts in importation biological control ([Roderick & Navajas, 2003](#), [Navajas & Roderick, 2008](#)), and a dedicated volume of the journal, Evolutionary Applications, focused on evolution and biological control ([Roderick et al., 2012](#)). All these papers recognize the influence of new molecular tools on biological control; for example, [Roderick et al. \(2012\)](#) identified next generation sequencing, computational modeling, and bioinformatics as approaches that will add to our understanding of evolution in biological control (summarized in [Hufbauer and Roderick, 2005](#), and in the special issue of Evolutionary Applications (Edited by [Roderick et al., 2012](#)).

Genomic diversity and population structure analysis – Recently, in [Sethuraman et al., 2020](#), we summarized a range of metrics that can be used to provide basic estimates of genomic diversity, including observed heterozygosity, Watterson's Theta (Θ), and nucleotide diversity (π) in both predator, and prey populations. Such measures will allow for simple, but informative comparisons of diversity between populations within species, and among species. Similarly, basic measures of population differentiation and size change include pairwise F statistics ([Weir and Cockerham, 1984](#)), Tajima's D, and Fu and Li's D* statistics ([Ramos-Onsins et al., 2002](#)). Numerous methods exist for these analyses, including the *pegas* R package ([Paradis, 2010](#)) and DNAsp v.5.10 ([Librado and Rozas, 2009](#)). Tajima's D and Fu and Li's D* and F* provide tests of deviation from neutrality and can also serve as indicators of recent population size change (e.g., bottlenecks due to augmentation, population expansion due to invasiveness). Both D* and F* are more sensitive to recent population size expansion ([Ramirez-Soriano et al., 2008](#)), and can help to predict the effects of "invasiveness" in non-native

species, including natural enemies and their prey.

The following examples of the applications of genomics/demographic modeling demonstrate how these methods provide a deeper understanding of trophic interactions related to biological control:

- 1) Understanding of phenotypic and genomic variation – related to trophic level interactions. Examples: Augmentative releases of *Hippodamia convergens* – ([Grenier et al., 2021](#)), Non-native and native populations of *Harmonia axyridis* response to prey species – correlated to genomic variants [Li et al. \(2023\)](#). Genomic studies can provide insights into selective factors influencing the populations of biological control organisms; measure natural selection
- 2) Demographic modeling based on genomic studies can be used to track population dynamics of released species and estimate effective population sizes. For example, [Sethuraman et al., 2018](#) analyzed population trends of two released species of predatory ladybird beetle species and one native species. These studies provide genetic based population estimates to complement ecological studies. A second example is the study of [Jones et al., 2023](#), that examined the population demographic trends and geographical and genomic structure analyses in two released predatory species – *Propylea quatuordecimpunctata* and *Hippodamia variegata*. This study also combined genomic and spatial information using the conStruct tool ([Bradburd et al., 2018](#)) to inform patterns of movement and invasive success.
- 3) Genomics and phenotypic variation in the Braconid parasitoid, *Dinocampus coccinellae*, whose trophic level interaction affects several species of lady beetle predators has been examined ([Vansant et al., 2019](#), [Sethuraman et al., 2022](#), [Tovar et al., 2022](#))
- 4) Genomic studies of natural enemies that are used in conservation biological control can provide data to support practices that have a long-term positive effect on the populations of these natural enemies. For instance, naturally occurring populations of *Hippodamia convergens* (native to Western United States) play a role in conservation biological control across imported and augmented populations of the species in North America ([Sethuraman et al., 2018, 2024](#), [Ang et al., 2024](#))

The anticipated results from these types of studies will help inform (1) standing genomic variation and differentiation among populations of natural enemies and prey species, (2) demographic modeling of population sizes and natural selection which serve as key indicators of the success of biological control and (3) demographic modeling of population sizes, and adaptive evolution of pests, which also serves as indicators of potential changes in trophic level interactions.

Demographic model testing – Characterization of population size changes based on genome-scale data are needed to reach conclusions underlying the population demography of natural enemies and pest species. Genomic diversity and population structure analyses can be used to guide the development of testable population models that will help infer ancient and contemporary demographic histories of natural enemies, their prey, and their parasitoids. For example, based on our population structure analyses across US populations of *H. convergens*, its history could be reflective of a model that involves a deep divergence between eastern and western populations with no successful gene flow into eastern populations, despite augmentative releases ([Sethuraman et al., 2024](#)). Alternatively, eastern populations could represent a successful introduction event into the east from western populations, either without, or with, further gene flow through augmentative release. A model-testing approach provides great flexibility in the ability to explore different scenarios and parameters. For example, we could also explore a model in which structured populations have resulted from serial releases, first with an introduction event from a primary source, followed by another release using individuals from the introduced population. Such a history could apply to both native North American species used via augmentative release, and non-native species that were

initially introduced from Eurasian sources. Finally, we point out that this model-testing framework does not only have to be used in a geographically broad perspective, but can also be used to understand the demographic histories of more focused sets of populations. For example, single populations can be tested for signatures of population expansion or decline against models that maintain stable population sizes. These models are of particular utility to the context of biological control in order to predict successful establishment of imported or augmented species (e.g., *H. convergens*), or invasiveness (e.g., *Ha. axyridis*), in understanding the local population size fluctuations of aphid species in response to predation by natural enemies, and adaptations to local environments, and in modeling demographic history fluctuations of parasitoids (e.g. *Dinocampus coccinellae*) that co-evolve and potentially shift their hosts in response to range expansion.

As a proof of concept to utilize methods for demographic modeling based on genomic data to understand fluctuations in effective population sizes of species at varying trophic levels, here we performed PSMC analyses on two sets of whole genomes: (a) competing conspecifics, *Harmonia axyridis* (assembly: icHarAxyr1, NCBI Accession: GCF_914767665.1, *Coccinella septempunctata* (NCBI Accession: GCF_907165205.1) collected from overlapping ranges in the United Kingdom, and (b) the North American native *Hippodamia convergens* (assembly: HCon1, NCBI Project: PRJNA1017495) and its parthenogenetic parasitoid wasp, *Dinocampus coccinellae* (assembly: Dcocc1, NCBI Project: PRJNA744197), both collected from Lawrence, KS (JJO pers. comm.). Briefly, sequencing reads from each of the above projects were aligned and mapped to their respective reference genomes using bwa-mem2 v.2.2.1 (Vasimuddin et al., 2019), sorted and consensus-called using samtools v.1.16.1 (Li et al., 2009), then analyzed using PSMC (Li and Durbin, 2011). A complete pipeline for these analyses, along with parameters used are available on the manuscript's GitHub page. Results of effective population size variation at different trophic levels were then generated using the *psmc_plot* tool, using a mutation rate of 3.5×10^{-9} , as estimated for insect orders (Liu et al., 2017). Fig. 1 shows the variation in historical effective population sizes (N_e) of conspecific competitors, *Harmonia axyridis* and *Coccinella septempunctata* in the last 100,000 years, replicating declines during the last global glacial cycles, that has been observed in numerous other species. Interestingly, *C. septempunctata* has consistently maintained nearly twice the amount of genetic diversity, compared to *H. axyridis*, indicating a higher degree of competitive success of *C. septempunctata*. Additionally, we also clearly observe that periods of decline in N_e of *C. septempunctata* coincide with

periods of stable N_e in *H. axyridis*, and vice versa, indicative of potential intraguild dynamics in the two competing species over historical time.

Figs. 2(A) and 2(B) are presented separately due to the variation in generation times between the host species, *Hippodamia convergens* (~1 generation per year), versus its parasitoid, *Dinocampus coccinellae* (~likely 4–5 generations per year), and show the estimated variation in historical N_e in both species over the last million years. We clearly observe the small current N_e in *D. coccinellae* (~1000, Fig. 2(B)), as expected by its life history of being a thelytokous, parthenogen (with unfertilized eggs developing into diploid adult females in the absence of males and sexual reproduction). We also note the multi-trophic declines in N_e between *H. convergens* and *D. coccinellae* over historical time, reflective of the life history of *D. coccinellae*, which requires oviposition into adult hosts to complete its developmental cycle.

We acknowledge that the genomes analyzed above are merely to provide a proof-of-concept and might not be entirely representative of the geographical range and genomic diversity of species. We contend, however, that these analyses are extensible as additional population-scale genomic data become available for multiple interacting species. Correlated fluctuations in historical effective population sizes are often indicative of bio-climatic events that could have influenced evolutionary trajectories of co-occurring and interacting species of commensals, mutualists, parasites, and symbionts (e.g. Nikolic et al., 2020, Lu et al., 2022, Kozma et al., 2018). However, correlations are not always causal, and therefore results of PSMC and other related analyses (e.g. MSMC, SMC++) should be considered with caution. It is also important to note that estimates of historical effective sizes are scaled with per site mutation rates, which are often not available for non-model systems (Mather et al., 2020). We therefore recommend multiple types of analyses, including simulations (see section below) to delineate both ancient and contemporaneous evolutionary demographic histories of species.

Simulations – The last section of this paper highlights building extensive predictive models and through computer simulations, generating genome-size data to study predicted genomic diversity, effective population size trajectories, and adaptive and hybridization potentials. Population genomic simulations have been heralded as important tools for understanding and predicting the genome-wide consequences of the complex interplay between demography and selection (Hoban et al., 2012). Powerful backward-time coalescent simulation tools generated for this purpose include *ms* (Hudson, 2002) and its variations such as *msms* (Ewing & Hermisson, 2010), *msprime* (Kelleher and Lohse, 2020)

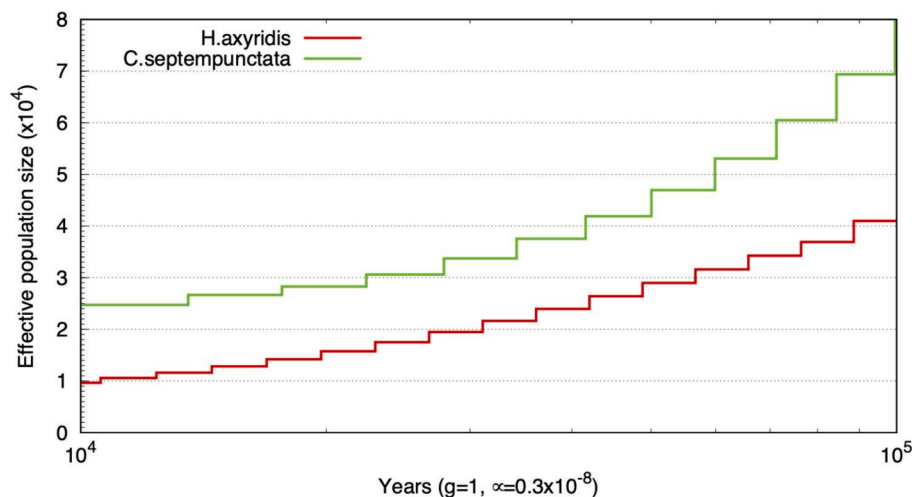


Fig. 1. Historical variation in effective population sizes (N_e) over time (in years before present, up to 100,000 ybp) in two conspecific, competing species of predatory lady beetles, *Harmonia axyridis* (red) and *Coccinella septempunctata* (green) as estimated using PSMC (Li and Durbin 2011) on single whole genomes of both species collected from their Eurasian range. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

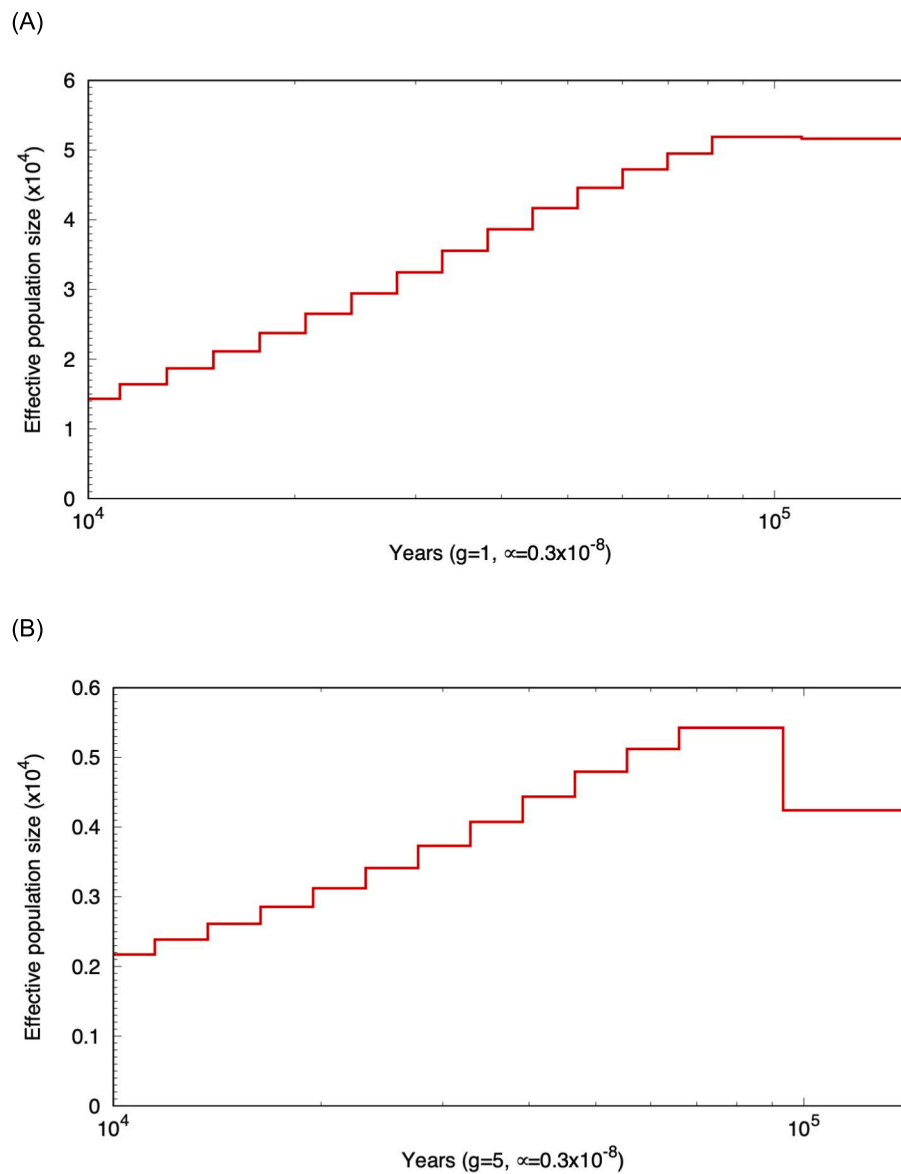


Fig. 2. Historical variation in effective population sizes (N_e) over (in years before present, up to 1,000,000 ybp) in (A) a host predatory lady beetle, *Hippodamia convergens*, and (B) its parasitoid, *Dinocampus coccinellae* as estimated using PSMC (Li and Durbin 2011) on single whole genomes of co-occurring species collected from Lawrence, KS, USA.

as well as forward-time simulators including Easypop (Balloux, 2001), Bottlesim (Kuo & Janzen, 2003), and SLiM (Haller and Messer, 2023), generate genome-wide haplotypic data under a variety of models, including those that include eco-evolutionary dynamics at varying trophic levels. Additional models that can be simulated include the specification of selection regimes (sweeps due to positive Darwinian selection on adaptive traits, and purifying/background selection against migrant alleles through augmentation, and intra-guild predation). Data simulated can mimic the size of data normally generated by a genotyping-by-sequencing (GBS) experiment (of the order of a few thousand SNP's, a few hundred haplotypes), or chromosome-scale genome assemblies. Additional predator-prey dynamics and census/effective size fluctuations can also be simulated to directly complement field experiments. These simulations form the basis of our ability to (1) analyze changes in effective population sizes, (2) examine correlations between predator and prey populations to assess the strength of trophic level interactions, and (3) provide complementary data on predator-prey population dynamics in support of ecological studies.

As a proof of concept of utilizing simulations to understand

contemporary population-scale dynamics of natural predators used in biological control, here we use fastsimcoal28 (Excoffier et al., 2021) to estimate recent demographic parameters of two competing conspecific species in North America – (1) the native lady beetle, *Hippodamia convergens* from its Western range (Sethuraman et al., 2024), and (2) the invasive lady beetle *Harmonia axyridis* from an overlapping range (Li et al., 2023). Briefly, we (i) estimated the site frequency spectrum from SNP data generated via genotyping by sequencing by Sethuraman et al., 2024 and Li et al., 2023, comprised of 9824 SNPs for *Hippodamia convergens* across its geographical range in the Americas and 7824 SNPs for *Harmonia axyridis* across its global range, filtering for genotyping quality (PHRED $Q < 33$), minor allele frequency ($MAF < 0.05$), Hardy-Weinberg Equilibrium, and linkage disequilibrium (Benjamini-Hochberg corrected p -value < 0.05), (ii) simulated 10 runs of 100,000 replicate site frequency spectra under a model of a single-population undergoing a recent bottleneck, (iii) estimated parameters such as effective population sizes pre- and post-bottleneck and time of the bottleneck. Our results (Table 1) indicate several interesting relationships of these two competing conspecific species – (a) a smaller current effective

Table 1
Effective population sizes (Ne) and times of estimated bottleneck events in native Western United States populations of *Hippodamia convergens* and co-occurring invasive United States populations of *Harmonia axyridis*, as estimated using demographic simulations of the site frequency spectra using fastsimcoal28.

Species/Population	N _{current}	N _{ancestral}	N _{bottleneck}	T _{bottleneck}	Maximum Estimated Likelihood	Maximum Observed Likelihood
<i>Hippodamia convergens</i> (Native – Western USA)	90,132	1,046,780	130,002	24	–2713.74	–1453.28
<i>Harmonia axyridis</i> (Invasive – USA)	66,888	1,045,541	99,125	40	–2997.03	–1571.91

population size in the invasive *H. axyridis*, compared to the native *H. convergens* – an observation supported by previous studies by Lom-baert et al., 2011, 2014 which indicate serial founding and bottleneck events across the invasive range of *H. axyridis*, and Sethuraman et al., 2018 which also estimated (b) recent manifold bottlenecks in both species using microsatellite data, albeit more recent than our estimates here using genome-wide SNP data (24–40 years, scaled as 1 generation per year). These estimates of demographic history under a bottleneck model indicate that *H. convergens* underwent a recent bottleneck event, about 24 ybp, while *Harmonia axyridis* underwent a bottleneck around the time of its introduction to the continental United States, about 40 ybp.

While this analysis presents a proof-of-concept under one biologi-cally feasible model, we recommend performing simulations under numerous models (e.g. isolation with migration, allopatry, sympatry, bottlenecks – described in Sethuraman et al., 2020) to explore more complex evolutionary scenarios. A detailed list of methods, their respective assumptions and limitations that can be utilized for simula-tions under a variety of models is presented in Sethuraman et al., 2020.

2. Conclusion/summary

2.1. Contemporary population dynamics

In this paper we have presented proof of concept examples docu-menting how demographic population genomic simulations, in com-bination with ecologically based experimental studies, can provide a well-rounded framework to inform trophic level interactions. The ex-amples presented in this paper expanded upon our recent studies of three species of predatory ladybird beetles (*Coccinella septempunctata*, *Harmonia axyridis*, and *Hippodamia convergens*) and the solitary Braconid parasitoid, *Dinocampus coccinellae*, that attacks over 50 species of predatory Coccinellidae.

Previously (Sethuraman et al., 2018) attempted a first-pass at delineating population genomic diversity and modeling recent popula-tion size change as indicators of the effectiveness of augmented natural enemy populations. In North America, the non-native, introduced species (*Ha. axyridis* and *C. septempunctata*) are expected to be comprised of populations that are largely admixed (owing to augmentation and invasiveness, which have been studied previously in these species (Kajita et al., 2012, Lombaert et al., 2011)). These species are expected to be highly diverse (owing to heterosis, a characteristic of invasive spe-cies), but with signatures of recent bottlenecks (due to their introductory history), followed by large-scale population expansions. Based on a handful of microsatellite and mitochondrial markers, our results indi-cated complex patterns of population size change and diversity across *Ha. axyridis*, *H. convergens*, and *C. septempunctata* (Sethuraman et al., 2018). The former two species showed signatures of massive recent bottlenecks, while populations of *C. septempunctata* were estimated to be growing exponentially across sampled populations in the United States. Based on those genetic studies and the simulations presented in this paper, we now have documented contemporary population-scale dy-namics over approximately the past 40 years for two species of preda-tory ladybird beetles in North America, the native *Hippodamia convergens* and the non-native *Harmonia axyridis*. These simulations indicate a bottleneck in North American *H. axyridis* populations, approximately 40 ybp, soon after its discovery in the United States. Additionally, a bottleneck in populations of the native species, *H.*

convergens was indicated approximately 24 ybp. Additional genomic data is currently being collected for *Coccinella septempunctata* that may provide explanations for its continued increases in population densities in North America during the past four decades (Sethuraman unpubl. data).

Several ecologically based studies conducted during the early 2000s in North America observed declines in local *H. convergens* populations, but intraguild predation involving *Harmonia axyridis* was not one of the primary causes (Li et al., 2021). When additional genomic data for aphid prey species from regions overlapping with the genomic data from these predatory ladybird species becomes available, the possible role of changes in prey densities could be correlated with the times of bottle-necks in predator populations (Sethuraman et al., 2018, Bahlai et al 2015a,b). Currently, the basis of our understanding of trophic level in-teractions is based primarily on population genomic data from predatory species. Additional genomic data for prey species will enhance our ability to describe trophic level interactions over contemporary time scales.

2.2. Variations in ancestral effective population sizes

Analyses of population genomic data from predatory species and parasitoids attacking these natural enemies over longer periods (thou-sands of generations) informs our understanding of contemporary trophic level interactions. In this paper we present analyses of ancestral effective population sizes of (1) *C. septempunctata* and *Harmonia axyridis* from Eurasian populations and (2) *Hippodamia convergens* and the parasitoid *Dinocampus coccinellae* from North American populations. Even though, *C. septempunctata* and *H. axyridis* show similar trends in decreased effective population sizes over time, *C. septempunctata* consistently shows higher genetic diversity and there are observed pe-riods of time when the effective population size of *H. axyridis* remains stable when Ne for *C. septempunctata* declines. These differences might reflect species specific predator–prey interactions and responses to seasonal abiotic factors (Arnold et al., 2023, Hodek et al., 2012a,b). Similarly, effective population sizes of *Hippodamia convergens* and the parasitoid *D. coccinellae* have declined over time, but these declines are more closely tied to each other, based on the parasitoid/host relationship.

Motivated by the abundance of naturally occurring predator–prey species interactions, biological control provides several advantages for pest suppression, including increased environmental and human safety in comparison to the use of chemical pesticides (Bellows and Fisher, 1999). Human-assisted movement, release, and augmentation of insect parasitoids and predatory insects for the suppression of arthropod pests represents one of the most effective and profitable practices of pest management (Hajek and Eilenberg, 2018, O’Neil & Obrycki, 2009). The optimal use of biological control in pest management systems requires adherence to regulatory guidelines and consideration of potential non-target effects (see discussion in Sethuraman et al., 2020).

This current paper highlights the potential for utilizing population genomic studies and demographic modeling, in conjunction with ecological studies, to enhance the effectiveness of human-mediated biological control activities. For example, examination of natural enemy – host genomes followed by demographic modeling of popu-lations in their native ranges, prior to consideration of movement of a natural enemy to a new region for biological control, can provide in-sights to historical population trends that may provide additional

information needed for pre-emptive biological control programs (see special issue of Biological Control).

Data availability

The whole genomes used in the analyses in this paper include: (A) competing conspecifics, *Harmonia axyridis* (assembly: icHarAxyr1, NCBI Accession: GCF_914767665.1, and *Coccinella septempunctata* (NCBI Accession: GCF_907165205.1) collected from overlapping ranges in the United Kingdom, and (B) the North American native *Hippodamia convergens* (assembly: HCon1, NCBI Project: PRJNA1017495) and its parthenogenetic parasitoid wasp, *Dinocampus coccinellae* (Ang et al. 2024) (assembly: Dcocc1, NCBI Project: PRJNA744197), collected in Lawrence Kansas, USA. A complete pipeline for analyses conducted in this paper, along with parameters used are available on the manuscript's GitHub page.

CRedit authorship contribution statement

Arun Sethuraman: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **John J. Obrycki:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This work was supported by NSF ABI 1564659, NSF CAREER 2042516 to AS. This work was funded by the National Institute of Food and Agriculture, U.S. Department of Agriculture, Hatch Program under accession number 1008480 and funds from the University of Kentucky Bobby C. Pass Research Professorship to JJO. This research includes calculations carried out on HPC resources supported in part by the National Science Foundation through major research instrumentation grant number 1625061 and by the US Army Research Laboratory under contract number W911NF-16-2-0189.

References

- Andersen, J.C., Mills, N.J., 2018. Comparative genetics of invasive populations of walnut aphid, *Chromaphis juglandicola*, and its introduced parasitoid, *Trioxys pallidus*, California. *Ecol. Evol.* 8 (1), 801–811.
- Ang, G., Zhang, A., Obrycki, J. and Sethuraman, A., 2024. A High-quality Genome of the convergent lady beetle, *Hippodamia convergens*. *G3: Genes, Genomes, Genetics*, p. jkae083.
- Arnold, M.B., Back, M., Crowell, M.D., Farooq, N., Ghimire, P., Obarein, O.A., Smart, K. E., Taucher, T., VanderJeugd, E., Perry, K.L., Landis, D.A., 2023. Coexistence between similar invaders: The case of two cosmopolitan exotic insects. *Ecology* 104 (4), e3979.
- Bahlai, C.A., Colunga-Garcia, M., Gage, S.H. and Landis, D.A., 2015a. The role of exotic ladybeetles in the decline of native ladybeetle populations: evidence from long-term monitoring. *Biological Invasions*, 17, pp.1005–1024.
- Bahlai, C.A., vander Werf, W., O'Neal, M., Hemerik, L. and Landis, D.A., 2015b. Shifts in dynamic regime of an invasive lady beetle are linked to the invasion and insecticidal management of its prey. *Ecological Applications*, 25(7), pp.1807–1818.
- Balloux, F., 2001. EASYPOP (version 1.7): A computer program for population genetics simulations. *J. Hered.* 92 (3), 301–302.
- Bellows, T.S. and Fisher, T.W., 1999. Handbook of biological control principles and applications of biological control.
- Bradburd, G.S., Coop, G.M., Ralph, P.L., 2018. Inferring continuous and discrete population genetic structure across space. *Genetics* 210 (1), 33–52.
- Crossley, M.S., Chen, Y.H., Groves, R.L., Schoville, S.D., 2017. Landscape genomics of Colorado potato beetle provides evidence of polygenic adaptation to insecticides. *Mol. Ecol.* 26 (22), 6284–6300.
- Ewing, G., Hermisson, J., 2010. MSMS: a coalescent simulation program including recombination, demographic structure and selection at a single locus. *Bioinformatics* 26 (16), 2064–2065.
- Excoffier, L., Marchi, N. and Sousa, V.C., 2021. fastsimcoal ver 2.8 fsc28.
- Goolsby, J.A., Makinson, J.R., Hartley, D.M., Zonneveld, R., Wright, A.D., 2004a. Pre-release evaluation and host range testing of *Floracarus perrepae* (Eriophyidae) genotypes for biological control of Old World climbing fern. In: Cullen, J.M., Briese, D.T., Kriticos, D.J., Lonsdale, W.M., Morin, L., Scott, J.K. (Eds.), *Proceedings of the XI International Symposium on Biological Control of Weeds*. CSIRO Entomology, Canberra, Australia, pp. 113–116.
- Grenier, C., Summerhays, B., Cartmill, R., Martinez, T., Saisho, R., Rothenberg, A., Tovar, A., Rynerson, A., Scott, J., Obrycki, J.J., Sethuraman, A., 2021. Lack of phenotypic variation despite population structure in larval utilization of pea aphids by populations of the lady beetle *Hippodamia convergens*. *Biol. Control* 155, 104507.
- Hajek, A.E., Eilenberg, J., 2018. *Natural enemies: An introduction to biological control*. Cambridge University Press.
- Haller, B.C., Messer, P.W., 2023. SLiM 4: Multispecies eco-evolutionary modeling. *Am. Nat.* 201 (5), E127–E139.
- Hoban, S., Bertorelle, G., Gaggiotti, O.E., 2012. Computer simulations: tools for population and evolutionary genetics. *Nat. Rev. Genet.* 13 (2), 110–122.
- Hodek, I. and E.W. Evans. 2012a. Food Relationships, pp 141–274. In I. Hodek, H.F. van Emden, and A. Honek (eds). *Ecology and Behaviour of the Ladybird Beetles (Coccinellidae)*. Wiley-Blackwell, New York.
- Hodek, Ivo, Alois Honek, and Helmut F. Van Emden, eds. *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. John Wiley & Sons, 2012b.
- Hopper, K.R., Roush, R.T., Powell, W., 1993. Management of genetics of biological control introductions. *Annu. Rev. Entomol.* 38, 27–51.
- Hudson, R.R., 2002. Generating samples under a Wright-Fisher neutral model of genetic variation. *Bioinformatics* 18 (2), 337–338.
- Hufbauer, R.A., 2002. Evidence for nonadaptive evolution in parasitoid virulence following a biological control introduction. *Ecol. Appl.* 12 (1), 66–78.
- Hufbauer, R.A., 2004. Population genetics of invasions: can we link neutral markers to management? 1. *Weed Technol.* 18 (sp1), 1522–1527.
- Hufbauer, R.A., Roderick, G.K., 2005. Microevolution in biological control: Mechanisms, patterns, and processes. *Biol. Control* 35 (3), 227–239.
- Hufbauer, R.A., Via, S., 1999. Evolution of an aphid-parasitoid interaction: variation in resistance to parasitism among aphid populations specialized on different plants. *Evolution* 53 (5), 1435–1445.
- Jones, A.G., Obrycki, J.J., Sethuraman, A. and Weisrock, D.W., 2024. Shared patterns of population genomic variation and phenotypic response across rapid range expansions in two invasive lady beetle species. *Biological Control*, 193, p.105519.
- Kajita, Y., O'Neill, E.M., Zheng, Y., Obrycki, J.J., Weisrock, D.W., 2012. A population genetic signature of human releases in an invasive ladybeetle. *Mol. Ecol.* 21 (22), 5473–5483.
- Kelleher, J., Lohse, K., 2020. Coalescent simulation with msprime. *Stat. Population Genomics* 986, 191–230.
- Kuo, C.H., Janzen, F.J., 2003. bottlesim: a bottleneck simulation program for long-lived species with overlapping generations. *Mol. Ecol. Notes* 3 (4), 669–673.
- Kozma, R., Lillie, M., Benito, B.M., Svenning, J.C., Höglund, J., 2018. Past and potential future population dynamics of three grouse species using ecological and whole genome coalescent modeling. *Ecol. Evol.* 8 (13), 6671–6681.
- Lanier, H.C., Massatti, R., He, Q., Olson, L.E., Knowles, L.L., 2015. Colonization from divergent ancestors: glaciation signatures on contemporary patterns of genomic variation in Collared Pikas (*Ochotona collaris*). *Mol. Ecol.* 24 (14), 3688–3705.
- Le Masurier, A.D., Waage, J.K., 1993. A comparison of attack rates in a native and an introduced population of the parasitoid *Cotesia glomerata*. *Biocontrol Sci. Tech.* 3 (4), 467–474.
- Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R. and 1000 Genome Project Data Processing Subgroup, 2009. The sequence alignment/map format and SAMtools. *bioinformatics*, 25(16), pp.2078–2079.
- Li, H.S., Huang, Y.H., Chen, M.L., Ren, Z., Qiu, B.Y., De Clercq, P., Heckel, G., Pang, H., 2021. Genomic insight into diet adaptation in the biological control agent *Cryptolaemus montrouzieri*. *BMC Genomics* 22, 1–12.
- Li, H., Li, B., Lövei, G.L., Kring, T.J., Obrycki, J.J., 2021. Interactions among native and non-native predatory Coccinellidae influence biological control and biodiversity. *Ann. Entomol. Soc. Am.* 114 (2), 119–136.
- Li, H., Peng, Y., Wang, Y., Summerhays, B., Shu, X., Vasquez, Y., Vansant, H., Grenier, C., Gonzalez, N., Kansagra, K., Cartmill, R., 2023. Global patterns of genomic and phenotypic variation in the invasive harlequin ladybird. *BMC Biol.* 21 (1), 141.
- Librado, P., Rozas, J., 2009. DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics* 25 (11), 1451–1452.
- Liu, H., Jia, Y., Sun, X., Tian, D., Hurst, L.D., Yang, S., 2017. Direct determination of the mutation rate in the bumblebee reveals evidence for weak recombination-associated mutation and an approximate rate constancy in insects. *Mol. Biol. Evol.* 34 (1), 119–130.
- Lombaert, E., Guillemaud, T., Thomas, C.E., Lawson Handley, L.J., Li, J., Wang, S., Pang, H., Goryacheva, I., Zakharov, I.A., Jousset, E., Poland, R.L., 2011. Inferring the origin of populations introduced from a genetically structured native range by approximate Bayesian computation: case study of the invasive ladybird *Harmonia axyridis*. *Mol. Ecol.* 20 (22), 4654–4670.
- Lombaert, E., Guillemaud, T., Lundgren, J., Koch, R., Facon, B., Grez, A., Loomans, A., Malausa, T., Nedved, O., Rhule, E., Staverlokk, A., 2014. Complementarity of statistical treatments to reconstruct worldwide routes of invasion: the case of the Asian ladybird *Harmonia axyridis*. *Mol. Ecol.* 23 (24), 5979–5997.
- Lozier, J.D., 2014. Revisiting comparisons of genetic diversity in stable and declining species: Assessing genome-wide polymorphism in North American bumble bees using RAD sequencing. *Mol. Ecol.* 23 (4), 788–801.

- Lozier, J.D., Strange, J.P., Heraghty, S.D., 2023. Whole genome demographic models indicate divergent effective population size histories shape contemporary genetic diversity gradients in a montane bumble bee. *Ecol. Evol.* 13 (2), e9778.
- Lu, C.W., Yao, C.T., Hung, C.M., 2022. Domestication obscures genomic estimates of population history. *Mol. Ecol.* 31 (3), 752–766.
- Mather, N., Traves, S.M., Ho, S.Y., 2020. A practical introduction to sequentially Markovian coalescent methods for estimating demographic history from genomic data. *Ecol. Evol.* 10 (1), 579–589.
- McCoy, R.C., Garud, N.R., Kelley, J.L., Boggs, C.L., Petrov, D.A., 2014. Genomic inference accurately predicts the timing and severity of a recent bottleneck in a nonmodel insect population. *Mol. Ecol.* 23 (1), 136–150.
- Moura, A.E., Kenny, J.G., Chaudhuri, R., Hughes, M.A., J. Welch, A., Reisinger, R.R., de Bruyn, P.N., Dahlheim, M.E., Hall, N. and Hoelzel, A.R., 2014. Population genomics of the killer whale indicates ecotype evolution in sympatry involving both selection and drift. *Molecular Ecology*, 23(21), pp.5179-5192.
- Nikolic, N., Liu, S., Jacobsen, M.W., Jónsson, B., Bernatchez, L., Gagnaire, P.A., Hansen, M.M., 2020. Speciation history of European (*Anguilla anguilla*) and American eel (*A. rostrata*), analysed using genomic data. *Mol. Ecol.* 29 (3), 565–577.
- Navajas, M. and Roderick, G., 2008. Molecular diagnosis. In *Encyclopedia of Entomology* (pp. 2449–2455). Springer Netherlands.
- O’Neil, R.J., Obrycki, J.J., Radcliffe, E.B., Hutchison, W.D. and Cancelado, R.E., 2009. Introduction and augmentation of biological control agents. *RADCLIFFE, E.; HUTCHISON, W.*, pp.105-117.
- Papadopoulou, A., Knowles, L.L., 2015. Species-specific responses to island connectivity cycles: refined models for testing phylogeographic concordance across a Mediterranean P leistocene A ggregate I sland C omplex. *Mol. Ecol.* 24 (16), 4252–4268.
- Paradis, E., 2010. pegas: An R package for population genetics with an integrated–modular approach. *Bioinformatics* 26 (3), 419–420.
- Ramírez-Soriano, A., Ramos-Onsins, S.E., Rozas, J., Calafell, F., Navarro, A., 2008. Statistical power analysis of neutrality tests under demographic expansions, contractions and bottlenecks with recombination. *Genetics* 179 (1), 555–567.
- Ramos-Onsins, S.E., Rozas, J., 2002. Statistical properties of new neutrality tests against population growth. *Mol. Biol. Evol.* 19 (12), 2092–2100.
- Reed, D.H., Frankham, R., 2003. Correlation between fitness and genetic diversity. *Conserv. Biol.* 17 (1), 230–237.
- Roderick, G.K., Navajas, M., 2003. Genes in new environments: genetics and evolution in biological control. *Nat. Rev. Genet.* 4 (11), 889–899.
- Roderick, G.K., Hufbauer, R., Navajas, M., 2012. Evolution and biological control. *Evol. Appl.* 5 (5), 419.
- Rosenthal, W.C., McIntyre, P.B., Lisi, P.J., Prather Jr, R.B., Moody, K.N., Blum, M.J., Hogan, J.D., Schoville, S.D., 2021. Invasion and rapid adaptation of guppies (*Poecilia reticulata*) across the Hawaiian Archipelago. *Evol. Appl.* 14 (7), 1747–1761.
- Sethuraman, A., Tovar, A., Welch, W., Dettmers, R., Arce, C., Skaggs, T., Rothenberg, A., Saisho, R., Summerhays, B., Cartmill, R. and Grenier, C., 2022. Genome of the parasitoid wasp *Dinocampus coccinellae* reveals extensive duplications, accelerated evolution, and independent origins of thelytokous parthenogeny and solitary behavior. *G3*, 12(3), p.jkac001.
- Sethuraman, A., Nunziata, S.O., Jones, A., Obrycki, J. and Weisrock, D.W., 2024. Go west: Population genomics reveals unexpected population fluctuations and little gene flow in Western hemisphere populations of the predatory lady beetle, *Hippodamia convergens*. *Evolutionary Applications*, 17(1), p.e13631.
- Sethuraman, A., Janzen, F.J., Rubio, M.A., Vasquez, Y., Obrycki, J.J., 2018. Demographic histories of three predatory lady beetles reveal complex patterns of diversity and population size change in the United States. *Insect Sci.* 25 (6), 1065–1079.
- Sethuraman, A., Janzen, F.J., Weisrock, D.W., Obrycki, J.J., 2020. Insights from population genomics to enhance and sustain biological control of insect pests. *Insects* 11 (8), 462.
- Tovar, A., Monahan, S., Kristan, A., Welch, W., Dettmers, R., Arce, C., Buck, T., Ruben, M., Rothenberg, A., Saisho, R. and Cartmill, R., 2022. Like mother, like daughter? Phenotypic plasticity, environmental covariation, and heritability of size in a parthenogenetic wasp. *bioRxiv*, pp.2022-12.
- UNRUH, T.R., 1999. Molecular methods in classical biological control. *Handbook of Biological Control: Principles and Applications*.
- Vansant, H., Vasquez, Y.M., Obrycki, J.J., Sethuraman, A., 2019. Coccinellid host morphology dictates morphological diversity of the parasitoid wasp *Dinocampus coccinellae*. *Biol. Control* 133, 110–116.
- Vasimuddin, M., Misra, S., Li, H. and Aluru, S., 2019, May. Efficient architecture-aware acceleration of BWA-MEM for multicore systems. In *2019 IEEE international parallel and distributed processing symposium (IPDPS)* (pp. 314–324). IEEE.
- Weir, B.S., Cockerham, C.C., 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 1358–1370.