## EVOLUTIONARY ECOLOGY

# Dispersal stabilizes coupled ecological and evolutionary dynamics in a host-parasitoid system

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When ecological and evolutionary dynamics occur on comparable timescales, persistence of the ensuing eco-evolutionary dynamics requires both ecological and evolutionary stability. This unites key questions in ecology and evolution: How do species coexist, and what maintains genetic variation in a population? In this work, we investigated a host-parasitoid system in which pea aphid hosts rapidly evolve resistance to *Aphidius ervi* parasitoids. Field data and mathematical simulations showed that heterogeneity in parasitoid dispersal can generate variation in parasitism-mediated selection on hosts through time and space. Experiments showed how evolutionary trade-offs plus moderate host dispersal across this selection mosaic cause host-parasitoid coexistence and maintenance of genetic variation in host resistance. Our results show how dispersal can stabilize both the ecological and evolutionary components of eco-evolutionary dynamics.

When ecological and evolutionary processes operate on similar timescales, feedbacks occur between trait change, ecological interactions, and selection in what are called eco-evolutionary dynamics (*1–3*). For eco-evolutionary dynamics to be stable in the long term, both ecological (i.e., species) and evolutionary (i.e., genetic) diversity must be maintained, as these are prerequisites for future ecological and evolutionary changes, respectively. In relatively closed systems lacking strong effects of, for example, immigration or de novo mutations, stable eco-evolutionary dynamics require internal processes that both facilitate species coexistence and generate balancing selection. Thus, the persistence of eco-evolutionary dynamics integrates two fundamental questions in ecology and evolution: What facilitates coexistence (*4*), and what maintains genetic variation in a population (*5*)? Despite the growing recognition that eco-evolutionary dynamics affect population, community, and ecosystem processes (*6–9*), few studies have identified or tested mechanisms that maintain ecological and evolutionary diversity and thereby generate stable eco-evolutionary dynamics (*2, 8, 10, 11*). Because ecological and evolutionary processes are intertwined, simultaneously understanding how both are stabilized is key to understanding how eco-evolutionary dynamics persist in nature.

One mechanism that can maintain both ecological and evolutionary diversity is dispersal through heterogeneous space. Dispersal of individuals between habitat patches can theoretically stabilize consumer-resource dynamics through, for example, spatially asynchronous fluctuations that provide temporary refuges for the resource (*12, 13*). Additionally, when selection favors different alleles across space, dispersal can help maintain multiple alleles (*14, 15*). However, dispersal does not necessarily lead to ecological and evolutionary diversity; high levels of dispersal should homogenize populations in space, thereby causing ecological instability and species loss (*12, 16, 17*) and/or swamping local adaptation and genetic variation (*14, 15*).

In this work, we tested whether dispersal can maintain both species and genetic diversity by stabilizing eco-evolutionary dynamics in an insect host-parasitoid system. At our field site (Arlington Agricultural Research Station, Wisconsin, USA), pea aphid (*Acyrthosiphon pisum*) hosts can rapidly evolve resistance to their specialist parasitoid wasp *Aphidius ervi* (*2*). Most of the variation in pea aphid resistance to parasitoids comes from the presence of the bacterial endosymbiont *Hamiltonella defensa* that can confer resistance to parasitism in aphids that harbor it (*18, 19*). Pea aphids reproduce clonally throughout the growing season (with a single sexual generation in the fall), and because *H. defensa* is vertically transmitted to clonal offspring with high fidelity, the symbiont can be considered part of the extended pea aphid genome (*20*). This makes *H. defensa* infection a convenient genetic marker for aphid resistance. Although *H. defensa* increases resistance, it incurs a cost through reduced aphid fecundity (*2, 21*).

Explaining the stability of this system is challenging because it has several attributes that are known to be ecologically and evolutionarily destabilizing. Ecological interactions between hosts and specialized parasitoids can lead to unstable population cycles (*22*), and seasonal temperature change is likely to be further destabilizing (*23*). Although there is a resistance-fecundity trade-off that is a necessary condition

to explain evolutionary stability, a trade-off is not a sufficient condition (*2*). Moreover, the overwintering loss of *H. defensa* infection by some aphids (*2*) at most acts as an equalizing, not stabilizing, mechanism (*24*) between resistant and susceptible clones.

### Evidence from the field for stable eco-evolutionary dynamics and a spatiotemporal mosaic of selection for hosts

The role of dispersal in maintaining ecological and evolutionary diversity, and thereby eco-evolutionary dynamics, is suggested by 9 years of field data that show long-term coexistence of pea aphids and *A. ervi* (*2*) (Fig. 1). Rates of parasitism in alfalfa fields can change rapidly, and the proportion of aphid clones carrying *H. defensa* also varies among fields and through time (Fig. 1A). Visualizing the data in space (Fig. 1B) illustrates how changes are not synchronized among fields, thereby generating spatiotemporal variation in selection. An analysis of these data (*25*) showed moderate aphid density–dependent variation and strong aphid density–independent variation in the proportion of aphids parasitized by *A. ervi* (figs. S1 to S3 and table S1). These patterns were likely caused by variation in adult parasitoid abundances; analysis of a separate field experiment that manipulated aphid abundance and systematically sampled adult parasitoids (*26*) found a moderate, positive response of adult parasitoid abundance to aphid density ($P = 0.00016$) and very high variation in parasitoid abundance that was independent of aphid density ($P < 10^{-10}$) (fig. S4 and tables S2 to S4). These results are consistent with high variation in parasitism shown in other host-parasitoid systems (*27*) and imply that adult parasitoid dispersal generates spatial variation in parasitism and selection on aphids.

We used a laboratory experiment and mathematical models to address whether the dispersal of aphids across spatiotemporal variation in parasitoid attacks can explain both host-parasitoid coexistence and maintenance of genetic variation for resistance in aphids. Pea aphids are capable of long-range dispersal as winged adults (*28*), and at our field site, roughly 20% of adults were winged (*29*). We used a mathematical model to design the laboratory experiment to test whether aphid dispersal could create persistent eco-evolutionary dynamics, given that spatial variation in parasitism already exists. We then tested the model predictions with a long-term (250 days) experiment. Lastly, we used the model along with parameter estimates from field experiments to evaluate the potential of spatiotemporal variation in parasitism to stabilize eco-evolutionary dynamics in nature.

### Moderate host dispersal plus spatial variation in parasitism stabilize eco-evolutionary dynamics

We started with a deterministic simulation model to generate qualitative predictions for our

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experiment; this type of a priori forecasting gives a direct test of our understanding of ecological systems (*30*). Our simulated experiment contained two patches, and parasitoids were confined to one patch to generate spatial variation in the parasitoid population. The model included parasitoids and two aphid clones: One had low fecundity and was resistant, and the other had high fecundity and was susceptible. Both aphid clones dispersed by producing offspring with wings at a proportion that was affected by aphid density (*25*); each day, 10% of winged adults were then added to a dispersal pool ($\delta_a = 0.1$) that was evenly redistributed among patches. Both aphid and parasitoid populations were age-structured on a daily timescale so that the model could capture rapid population and evolutionary dynamics. The model was parameterized from previous experiments (*2*, *23*) and tailored for two specific aphid clones by using additional experiments (*25*) (fig. S5 and tables S5 to S8). We simulated 250 days, which is ~80 population doubling periods (*23*).

In the model, when there was no dispersal between patches, the resistant clone was excluded from the no-parasitism patch, and the susceptible clone was reduced from 32 to about 2 aphids in the parasitism patch before the parasitoid population went extinct, after which the susceptible clone slowly rebounded (Fig. 2A). With dispersal, each clone became numerically dominant in one patch, but dispersal between patches caused neither to be excluded from either patch (Fig. 2B and fig. S6). However, an especially high or low starting proportion of aphids with resistance or low starting parasitoid abundance could cause the system to converge to an alternative state in which the resistant clone was excluded (figs. S7 and S8). Therefore, although dispersal of aphids between patches most often maintains both species and genotypic diversity, an alternative stable state without the resistant clone is possible.

The experimental test of the model and role of aphid dispersal in eco-evolutionary dynamics was conducted using seven pairs of 30 × 120 cm cages, one with parasitism and one without. We used an uninfected susceptible clone and a *H. defensa*–infected resistant clone that differed in color, allowing us to visually assess evolution. We confirmed the resistance-fecundity trade-off for the two lines used in the study (*25*) (figs. S9 and S10). To manipulate aphid dispersal, we left three cage pairs isolated from each other but manually dispersed aphids between four pairs of cages. We dispersed aphids by pooling winged adults found on the cage sides or the tops of 25% of plants and redistributing them equally between cages every 3 to 4 days; this resulted in dispersal pool sizes that closely matched our simulations (fig. S11).

In the experiment, the no-dispersal treatment always resulted in the susceptible clone exclud-

ing or nearly excluding the resistant clone in the absence of parasitism, but in the presence of parasitism either the parasitoids killed all aphids and were then eliminated, or only the resistant clone persisted (Fig. 2C). In the dispersal treatment, neither aphid clone was excluded

for the duration of the experiment, and cage-level extinctions were transient (until alates reestablished that population) and only occurred after parasitoids reached especially high abundances in parasitism cages (Fig. 2D). The influx of resistant aphids into the no-parasitism cages
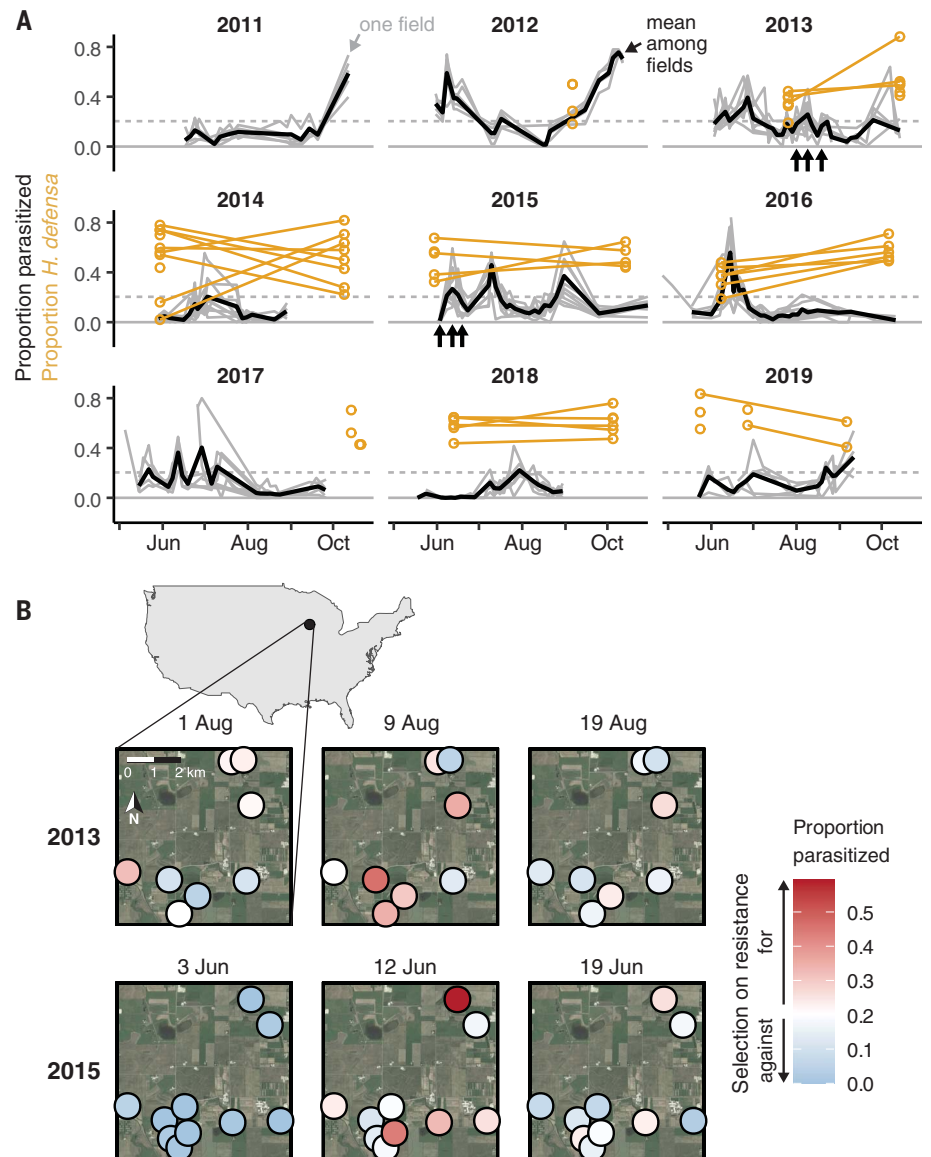


**Fig. 1. Field data suggest stable eco-evolutionary dynamics and variation in selection for host resistance through time and space.** (**A**) Proportion of aphids parasitized (gray and black lines) and infected with *H. defensa* (orange points and lines) through time in 5 to 10 alfalfa (*Medicago sativa*) fields at Arlington Agricultural Research Station (AARS), Wisconsin, USA, from 2011 to 2019. Orange lines connect fields sampled for *H. defensa* infection twice in one season. Gray dashed lines represent the lowest parasitism at which resistance should be favored (*2*, *25*). Parasitism is measured as the proportion of dissected aphids containing parasitoid larvae (average 82.4 dissected aphids per sample), and *H. defensa* infection was measured through diagnostic PCR primers (average 45.3 aphids per sample). (**B**) Parasitism through space at AARS for three selected dates each for 2013 (top row) and 2015 (bottom row), where dates within a year are separated by 7 to 10 days and correspond to the black arrows in (A). Point color represents the proportion of aphids parasitized, with colors diverging from where selection for resistance should be neutral; this was calculated as in (A). Points are located at the centroids of associated alfalfa fields, and panel backgrounds show the landscape at AARS. Data for 2011 to 2016 are from reference (*2*). Satellite imagery ©2023 Landsat/Copernicus, Maxar Technologies, USDA/FPAC/GEO.
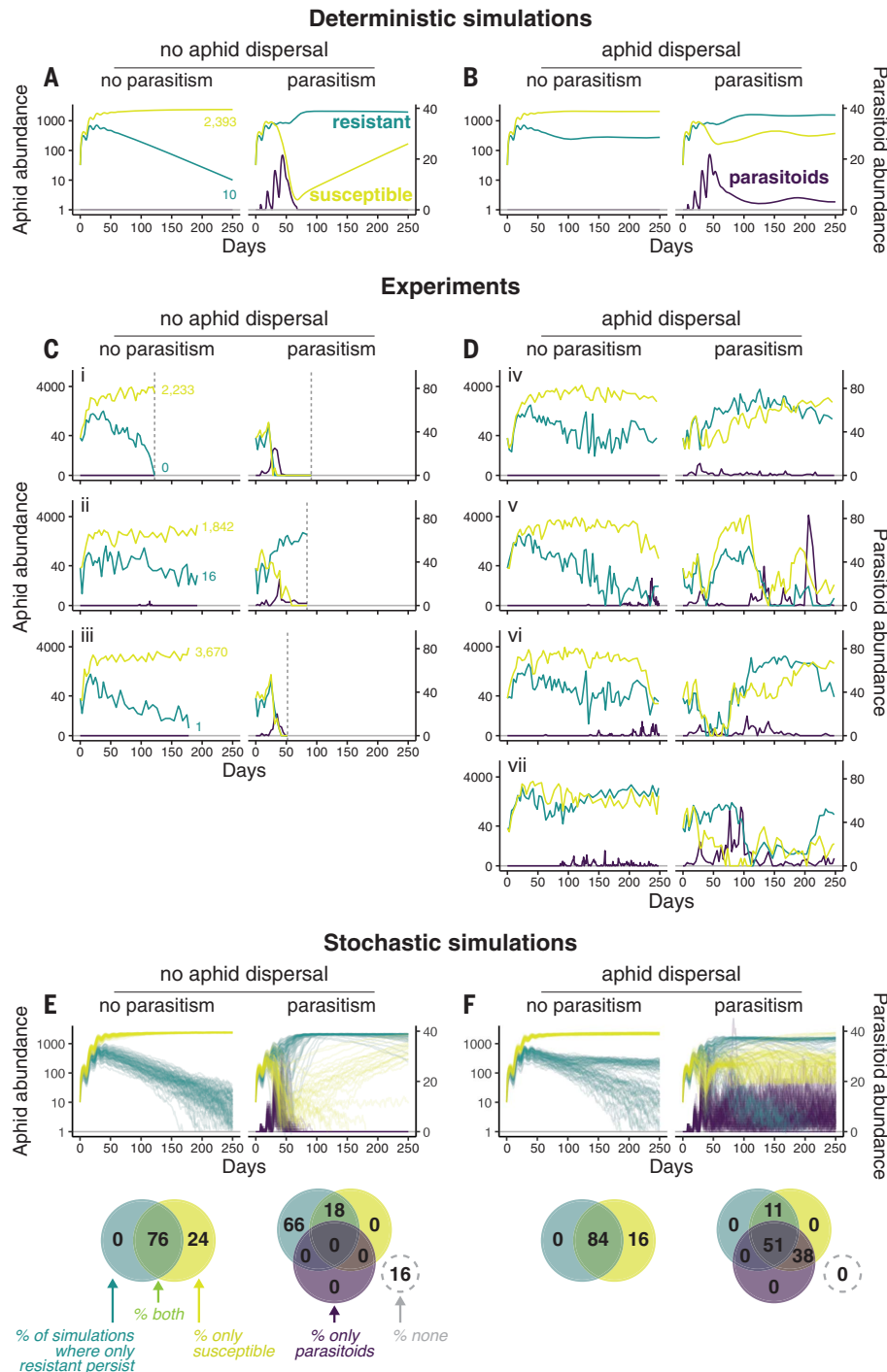
## Deterministic simulations



## Experiments



## Stochastic simulations



**Fig. 2. Mathematical simulations and experiments show that aphid dispersal across a selection mosaic can maintain eco-evolutionary dynamics.** (**A** and **B**) In deterministic simulations used to design our experiments, susceptible and resistant aphid clones competed in two patches: one without parasitism (left) and one with (right). Patches were either (A) isolated or (B) connected by aphid dispersal. (**C** and **D**) Experiments designed by using these simulations, with each trial (i to vii) having two cages containing both aphid clones, one of which contained parasitoids, and the other, no parasitoids. Pairs of cages were either (C) isolated or (D) connected by manual aphid dispersal. Dashed, gray vertical lines indicate early termination owing to the extinction of at least one aphid clone. (**E** and **F**) Time series for stochastic simulations designed to closely replicate experiments (100 randomly chosen from 1000 total simulations). Venn diagrams describe how often parasitoids and aphid clones survived across 1000 simulations. [(A) and (C)] Numbers in no-parasitism cages for isolation-treatment simulations and experiments show final clone abundances. [(A) to (F)] Parasitoid abundance refers to adults only.

maintained the resistant clone at low abundance, and susceptible aphids dispersing into the parasitism cage sustained the population of parasitoids that allowed ongoing selection for resistance. Some inconsistencies among replicates occurred owing to differences in our culling of adult parasitoids (fig. S12) and contamination of parasitoids in the no-parasitism cages (fig. S13), but our results were broadly consistent with the model predictions.

Because our a priori model was deterministic, it could not capture the variability among the replicates that we observed. Therefore, we extended the model post hoc to include demographic stochasticity for both aphids and parasitoids as quantified in a separate experiment (*23*). We also added a risk of mortality when aphids drop off plants; aphids defend themselves against parasitism by dropping off plants, and in the experiment, we observed that aphids often could not climb back onto plants and therefore died. Simulations of the stochastic model spanned all experimental outcomes that we observed (Fig. 2, E and F).

We used the model to investigate in more detail the mechanisms underlying the effect of aphid dispersal to maintain ecological (parasitoids and aphids) and evolutionary (both aphid clones) variation (Fig. 3A). We used the same parameterization of the model used to design the experiment (Fig. 2, A and B) but varied the proportion of the winged aphids that dispersed between cages ($\delta_a$) (Fig. 3A). At the nominal aphid dispersal proportion used for the experiment ($\delta_a = 0.10$), the system contained both a stable and an unstable stationary point (figs. S14 and S15). When the proportion of resistant aphids started below the unstable point, the resistant clone was excluded. This also occurred if the initial proportion was very high; when susceptible aphids were rare, the parasitoid population temporarily crashed, resulting in dominance of the susceptible clone and subsequent recovery of the parasitoid population when the resistant proportion of aphid population was low (fig. S16). As aphid dispersal increased, the population abundances changed little (fig. S17), but the unstable point converged on the stable point, eventually eliminating both points in a saddle-node bifurcation (*31*). For aphid dispersal greater than about 0.258, the system was globally unstable (i.e., the two aphid clones and parasitoid could not all persist). Conversely, as dispersal decreased, the stable point underwent a Neimark-Sacker (Hopf) bifurcation (*31*), leading to permanent cycles when aphid dispersal was less than 0.04. For these low dispersal rates, although the system did not have a locally stable equilibrium point, there was a stable limit cycle whose domain of attraction spanned most but not all of the persistence space of both aphid clones and the parasitoid. As aphid dispersal decreased further, the amplitude of the cycle increased
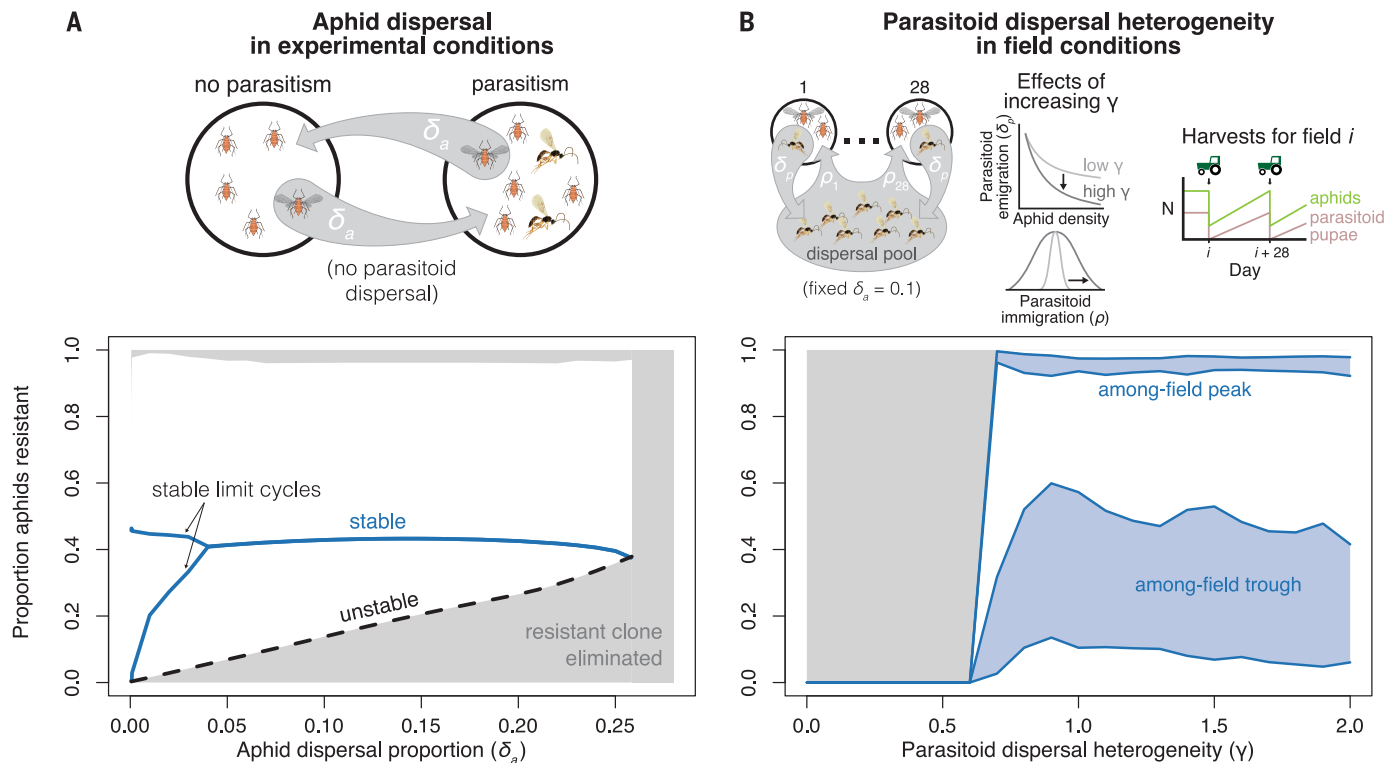
**Fig. 3. Moderate host dispersal and heterogeneous parasitoid dispersal stabilize eco-evolutionary dynamics.** (Bottom) Phase portraits showing how dispersal and the starting proportion of resistant aphids determine the stability of eco-evolutionary dynamics. Dispersal variables are fixed for a given simulation, and only internal, nontrivial states are shown. (**A**) For a given dispersal rate under experimental conditions, if the initial proportion of resistant aphids lies within the white region, the stable point (blue line) is approached through time. If the initial proportion is in the gray area (outside the stable point's domain of attraction), the resistant clone is eliminated. (**B**) Under field conditions, we varied both aphid density–dependent and aphid density–independent sources of parasitoid dispersal heterogeneity through parameter $\gamma$, where $\gamma = 1$ corresponds to field experiment–derived estimates. Because fields vary in their dynamics even as time goes to infinity, the stable state is shown as the range among peak and trough values for all fields (fig. S21). Note that phase portraits are projections of (A) 270- and (B) 3780-dimensional systems onto one dimension and are used as approximate visualizations (*25*); this and the stochastic nature of the field simulation model explain why the lines in (B) are not smooth.

until the parasitoid was eliminated. Thus, in the scenario of the experiment, too-high aphid dispersal causes loss of genetic variation in resistance, whereas too-low dispersal causes loss of the parasitoid and subsequent loss of the resistant aphid clone.

**Heterogeneity in parasitoid dispersal generates the spatiotemporal variation in parasitism necessary for stable eco-evolutionary dynamics**

We next investigated how heterogeneity in parasitoid dispersal can generate spatiotemporal variation in selection for aphids by using a model tailored to field conditions. Both parasitoids and aphids dispersed among 28 fields, where each field was harvested on a different day so that each field was harvested every 28 days. Harvesting agricultural fields causes high mortality of aphids and parasitoids (stages other than adults) (*32*), so in simulated harvests, mortality for pupal parasitoids was 100%, and for aphids (unparasitized or parasitized), was generated from a uniform distribution

from 96 to 99%. Adult parasitoids can escape through flight, so they were not affected. In contrast to the experiments in which a physical barrier maintained variation in selection for resistance, in this field model, heterogeneity in parasitism was generated by parasitoid dispersal, which we modeled to mimic results from a previous large-scale field experiment (*25*) and analyses of field observations (Fig. 1). Specifically, we included a negative effect of aphid density on emigration and among-field variability in immigration. We estimated both of these sources of heterogeneity from the field (*25*) (table S2), and we combined them to give an overall measure of heterogeneity ($\gamma$); $\gamma = 1$ corresponds to the degree of heterogeneity observed in the field experiment, with larger or smaller values giving greater or lesser heterogeneity. We kept aphid dispersal at its nominal value from the lab experiment ($\delta_a = 0.10$).

At the level of heterogeneity estimated from the field ($\gamma = 1$), the resulting dynamics showed cyclic patterns in abundances of aphids and parasitoids of roughly 170 days (or six harvest-

ing cycles) and had similar magnitudes of greater-than-binomial variation to our field data (fig. S18). If parasitoid dispersal heterogeneity was less than $\gamma = 0.6$, then unstable cycles in parasitoid abundance occurred, which led to parasitoid extinction, followed by the susceptible clone outcompeting the resistant clone (Fig. 3B and fig. S19); a similar threshold occurred at $\gamma = 1.0$ when controlling for the effect of $\gamma$ on the overall parasitoid dispersal rate (fig. S20). Thus, there is a minimum degree of parasitoid dispersal heterogeneity required to stabilize the eco-evolutionary system.

**Conclusions**

Our experimental and theoretical results help explain the maintenance of species and genetic diversity of pea aphid–parasitoid eco-evolutionary dynamics observed in the field (Fig. 1). In both theory (Fig. 2, A, B, E, and F) and experiments (Fig. 2, C and D), aphid dispersal between areas of high and low parasitism was needed. However, if aphid dispersal was too high, genetic variation for resistance was

lost (Fig. 3A). Sufficiently high heterogeneity in parasitoid dispersal allowed parasitoid populations to persist and generated the variation in parasitism required for eco-evolutionary dynamics to remain stable (Fig. 3B). Thus, the maintenance of both ecological and evolutionary components of eco-evolutionary dynamics requires processes that create spatiotemporal heterogeneity across the landscape and moderate dispersal that exposes populations to this heterogeneity without homogenizing them and causing eco-evolutionary dynamics to become unstable.

Aphid resistance to parasitism in our system is conferred by *H. defensa*, and therefore, trait evolution follows a haploid evolutionary model. Although haploid models do not address some of the genetic features that may be important in other models of resistance, such as resistance conferred by recessive alleles in diploid systems (*33, 34*), haploid models nonetheless capture the direction and magnitude of selection for resistance (*35*). Therefore, our results for eco-evolutionary dynamics of pea aphids and *A. ervi* can at least help to understand the stability of eco-evolutionary dynamics in other, nonhaploid systems.

The importance of dispersal and spatial heterogeneity for host-parasitoid coexistence has a long history in ecological theory (*36, 37*), and dispersal between selection regimes is a widely accepted mechanism for maintaining genetic variation (*15, 38, 39*). In this work, we have shown that dispersal can have both of these ecological and evolutionary consequences simultaneously, thereby stabilizing eco-evolutionary dynamics.

## REFERENCES AND NOTES

1. N. G. Hairston Jr., S. P. Ellner, M. A. Geber, T. Yoshida, J. A. Fox, *Ecol. Lett.* **8**, 1114–1127 (2005).
2. A. R. Ives *et al.*, *Nat. Ecol. Evol.* **4**, 702–711 (2020).
3. R. D. Bassar, T. Coulson, J. Travis, D. N. Reznick, *Ecol. Lett.* **24**, 623–625 (2021).
4. G. E. Hutchinson, *Am. Nat.* **93**, 145–159 (1959).
5. T. Dobzhansky, *Genetics and the Origin of Species* (Columbia Univ. Press, ed. 3, 1951).
6. T. Yoshida, L. E. Jones, S. P. Ellner, G. F. Fussmann, N. G. Hairston Jr., *Nature* **424**, 303–306 (2003).
7. M. A. Duffy, L. Sivars-Becker, *Ecol. Lett.* **10**, 44–53 (2007).
8. L. R. Schaffner *et al.*, *Nat. Ecol. Evol.* **3**, 1351–1358 (2019).
9. I. M. Ware *et al.*, *Funct. Ecol.* **33**, 31–42 (2019).
10. M. A. Barbour, D. J. Kliebenstein, J. Bascompte, *Science* **376**, 70–73 (2022).
11. R. A. Lankau, S. Y. Strauss, *Science* **317**, 1561–1563 (2007).
12. W. W. Murdoch, C. J. Briggs, R. M. Nisbet, *Consumer-Resource Dynamics*, vol. 36 of Monographs in Population Biology (Princeton Univ. Press, 2003).
13. M. P. Hassell, H. N. Comins, R. M. Mayt, *Nature* **353**, 255–258 (1991).
14. J. Felsenstein, *Annu. Rev. Genet.* **10**, 253–280 (1976).
15. B. Star, R. J. Stoffels, H. G. Spencer, *Genetics* **177**, 1743–1751 (2007).
16. S. P. Ellner *et al.*, *Nature* **412**, 538–543 (2001).
17. A. R. Ives, *Am. Nat.* **140**, 1–29 (1992).
18. K. M. Oliver, N. A. Moran, M. S. Hunter, *Proc. Natl. Acad. Sci. U.S.A.* **102**, 12795–12800 (2005).
19. K. M. Oliver, C. H. Higashi, *Curr. Opin. Insect Sci.* **32**, 1–7 (2019).
20. K. M. Oliver, A. H. Smith, J. A. Russell, *Funct. Ecol.* **28**, 341–355 (2014).
21. A. J. Martinez, M. R. Doremus, L. J. Kraft, K. L. Kim, K. M. Oliver, *J. Anim. Ecol.* **87**, 464–477 (2018).
22. M. P. Hassell, *The Dynamics of Arthropod Predator-Prey Systems*, vol. 13 of Monographs in Population Biology (Princeton Univ. Press, 1978).
23. M. H. Meisner, J. P. Harmon, A. R. Ives, *Ecol. Monogr.* **84**, 457–476 (2014).
24. P. L. Chesson, *Annu. Rev. Ecol. Syst.* **31**, 343–366 (2000).
25. Materials and methods provided as supplementary materials.
26. M. Kishinevsky, A. R. Ives, *Ecosphere* **13**, e4050 (2022).
27. S. W. Pacala, M. P. Hassell, *Am. Nat.* **138**, 584–605 (1991).
28. M. A. H. Smith, P. A. MacKay, *Oecologia* **81**, 160–165 (1989).
29. M. J. Bosch, A. R. Ives, *Ecol. Entomol.* **48**, 597–609 (2023).
30. J. S. Clark *et al.*, *Science* **293**, 657–660 (2001).
31. S. H. Strogatz, *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering* (CRC Press, ed. 2, 2019).
32. K. S. Rauwald, A. R. Ives, *Ecol. Appl.* **11**, 1224–1234 (2001).
33. A. R. Ives, D. A. Andow, *Ecol. Lett.* **5**, 792–801 (2002).
34. M. D. Rausher, *Nature* **411**, 857–864 (2001).
35. J. F. Crow, M. Kimura, *An Introduction to Population Genetics Theory* (Harper & Row, 1970).
36. M. P. Hassell, *J. Anim. Ecol.* **69**, 543–566 (2000).
37. C. J. Briggs, M. F. Hoopes, *Theor. Popul. Biol.* **65**, 299–315 (2004).
38. M. C. Whitlock, *Evolution* **54**, 1855–1861 (2000).
39. M. Slatkin, *Annu. Rev. Ecol. Syst.* **16**, 393–430 (1985).
40. L. A. Nell, lucasnell/gameofclones, v1.0.2, Zenodo (2023); https://doi.org/10.5281/zenodo.8429166.
41. L. A. Nell, lucasnell/gameofclones-data, v1.0.4, Zenodo (2024); https://doi.org/10.5281/zenodo.10570148.

## SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.adg4602
Materials and Methods
Figs. S1 to S21
Tables S1 to S8
References (*42–53*)
MDAR Reproducibility Checklist