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Stability via Asynchrony in *Drosophila* Metapopulations with Low Migration Rates

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Very few experimental studies have examined how migration rate affects metapopulation dynamics and stability. We studied the dynamics of replicate laboratory metapopulations of *Drosophila* under different migration rates. Low migration stabilized metapopulation dynamics, while promoting unstable subpopulation dynamics, by inducing asynchrony among neighboring subpopulations. High migration synchronized subpopulation dynamics, thereby destabilizing the metapopulations. Contrary to some theoretical predictions, increased migration did not affect average population size. Simulations based on a simple non–species-specific population growth model captured most features of the data, which suggests that our results are generalizable.

Natural populations often exhibit some degree of spatial structuring into metapopulations: ensembles of local populations (subpopulations) connected by migration (*1*). The effects of migration rate on the dynamics and stability of metapopulations have been extensively investigated theoretically (*1*). Analytical (*2*, *3*) and simulation (*4*) studies have shown that even a simple system, consisting of two subpopulations (modeled by a pair of logistic maps) with a constant rate of to-and-fro migration, can exhibit rich dynamic behavior. In such systems, low, intermediate, and high migration rates have been shown to lead to complex, stable, and unstable dynamics, respectively (*2*–*4*). Similar results have been obtained with a variety of more realistic models (*5*–*8*). Potential stabilizing effects of migration have also been shown in studies on more complex systems (*9*–*12*). Although it has been empirically shown that migration can stabilize dynamics (*13*, *14*), most metapopulation experiments have been carried out within the classical extinction-recolonization framework (*15*), which ignores the dynamics of population size. Thus, rigorous tests of theoretical predictions regarding the effects of migration rate on metapopulation dynamics are rare (*13*). Similarly, despite a large corpus of theoretical studies (*16*–*18*), the effects of migration rates on mean population size have rarely been investigated experimentally (*19*).

Here, we report the effects of low (10%) and high (30%) migration rates on the dynamics of replicated laboratory metapopulations of the fruit fly *Drosophila melanogaster* in a 21-generation experiment (*20*). We quantified constancy stability (*21*) of the metapopulations and subpopulations with the use of a dimensionless measure of amplitude of fluctuation in population size over time (*22*). This statistic, which we call the fluctuation index (FI), is inversely related to stability. We also performed simulations (*20*) using a simple non–*Drosophila*-specific model to test whether the results reflect a simple effect of migration rates on typical population dynamics, or are due to some specific features of the life history and ecology of *Drosophila* cultures.

Metapopulations with low levels of migration (henceforth LMMs) had lower FI values for metapopulation size than did either the control metapopulations (CMs; no migration) or those experiencing high migration levels (HMMs) (Fig. 1A). Nonetheless, the FI for subpopulation size was significantly higher in LMMs than in HMMs or CMs (Fig. 1B). Thus, low levels of migration caused global metapopulation stability, despite increased local instability in the subpopulations. The underlying mechanism was revealed by examining cross-correlations at lag zero of the first differenced time series of log abundance $[\ln(N_{t+1}) - \ln(N_t)$, where N_t is the population size at time t] of all subpopulation pairs in a metapopulation (*23*). The mean cross-correlation across all subpopulation pairs was significantly positive in CMs and HMMs but was close to zero in LMMs (Fig. 2A). This indicates that in CMs and HMMs, the subpopulations tended to reach peak and trough population sizes together, leading to high-amplitude oscillations at the metapopulation level (*20*) (fig. S1). However, there was no such synchrony in subpopulation sizes in LMMs, rendering the metapopulation dynamics relatively more stable.

We further investigated the spatial patterns of subpopulation synchrony by examining the cross-correlations for all nearest neighbor pairs. LMMs showed a significantly negative mean cross-correlation (Fig. 2B), indicating that immediate neighboring subpopulations were often out of phase; this result confirmed some theoretical predictions (*2*–*4*, *10*). CMs and HMMs, however, showed significantly positive mean cross-correlations between nearest neighbors (Fig. 2B). Although high migration rate is predicted to induce synchrony (positive correlation) between subpopulations (*7*–*9*), zero migration (as in our CMs) is not expected to do so, particularly under constant-environment laboratory conditions. With no migration, the subpopulations are independent of one another, and their dynamics should not become synchronized without external environmental forcing (*24*), which is unlikely under laboratory conditions. However, subpopulations in our CMs suffered frequent extinctions, averaging 3.35 out of 9 subpopulations per generation. Upon extinction, these subpopulations were restarted by introducing eight flies (*25*). Thus, about one-third of the subpopulations in each CM were equalized for population size every generation, potentially leading to artifactual positive cross-correlations among them. Overall, our results on the effects of migration rate on subpopulation synchrony, and therefore

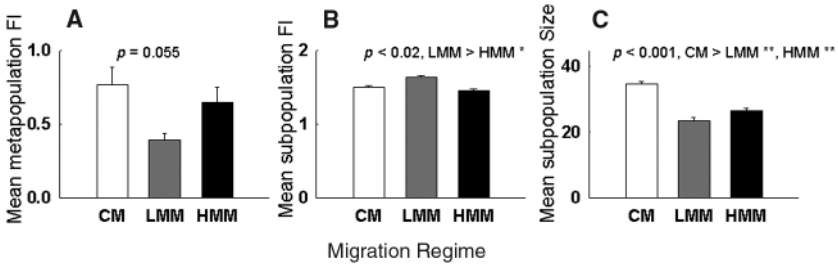

Fig. 1. Experimental results. The *P* values indicate the significance level from the corresponding mixed-model analysis of variance. The inequalities denote the means that were found different at the 0.05 (*) or 0.01 (**) level of significance using Tukey's HSD test. CM, no migration; LMM, low levels of migration (10%); HMM, high levels of migration (30%). Error bars are SEM for four replicate metapopulations. (**A**) Mean fluctuation index (FI) of LMMs is lower than that of either CMs or HMMs, indicating higher constancy stability. (**B**) Mean FI of the subpopulations is highest in the LMMs, suggesting lower stability at that migration rate. (**C**) Mean subpopulation size of CMs is higher than for both LMMs and HMMs, which is unexpected. See text for possible explanations.

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metapopulation stability, seem to confirm the existing theoretical predictions.

Contrary to a previous report that migration leads to increase in population size (*19*), the mean subpopulation and metapopulation sizes of CMs in our study were significantly higher than those of LMMs or HMMs (Fig. 1C). However, the controls used in that study (*19*) underwent no subpopulation extinctions, whereas subpopulations in our CMs frequently went extinct and were restarted (*25*). This influx of flies is the probable reason for increased mean subpopulation size in our CMs. Mean subpopulation size in our LMMs and HMMs did not differ significantly, thus contradicting predictions that local population size should decrease (*17*) or increase (*19*) monotonically with increase in migration rate. This may be attributed to the specific model assumptions and restricted parameter range (*17*), or differences in experimental protocol (*19*), of these studies. Thus, the effects of migration rate on metapopulation and subpopulation size seem to depend critically on model assumptions and the biology of the organisms, making generalized predictions difficult.

The generality of our findings depends largely on whether they reflect a simple effect of migration rates on typical population dynamics, or an interaction of migration rate with some specific features of the life history and ecology of *Drosophila* cultures. One way to address this issue is to simulate the experimental system with a simple model of population dynamics that does not include these specific features of *Drosophila* cultures. Populations with uniform random spatial distribution and scramble competition exhibit simple Ricker dynamics (*26*). Because *Drosophila* cultures more or less satisfy both conditions, we modeled subpopulation dynamics with the one-dimensional, discrete version of the Ricker map (*20*). The qualitative behavior of the Ricker map is determined solely by the intrinsic rate of growth, r, and the model exhibits a period-doubling route to chaos with increase in r (*27*).

The simulation of our experimental system yielded results very similar to the empirical observations. The FI values of LMMs in the simulations were lower than those of both CMs and HMMs (compare Figs. 3A and 1A), whereas at the subpopulation level, FI values for LMMs were the highest (compare Figs. 3B and 1B). The mean all-pair and nearest neighbor cross-correlations were also found to be similar to the experimental data (compare Figs. 2 and 4), with nearest neighbors in LMMs showing significantly negative correlations. However, in the simulations, subpopulation size exhibited the trend CMs < HMMs < LMMs (Fig. 3C), which does not agree with the observed trend in the experiment (CMs > LMMs ~ HMMs). The subpopulation time series revealed that the number of extinctions in the simulations was much less than in the experiment (*28*). The subpopulation extinction criteria for simulations and experiment were zero individuals and the absence of at least one male-female pair, respectively (*20*, *25*). Consequently, there were fewer resets to $N_t = 8$ in the CM subpopulations of the simulations, ultimately leading to lower mean subpopulation size relative to the experiments. Thus, Ricker-based simulations in a biologically meaningful parameter range recovered almost all major features of the experimental data. Scramble competition for resources is experienced across a wide range of animal taxa, including most microbes, invertebrates, fishes, and amphibians, and the Ricker model is known to be a good descriptor of scramble competition–driven dynamics (*26*, *29*, *30*). Our experimental results are therefore likely to hold true for a variety of species.

Besides verifying several existing theoretical predictions, our results have potential practical implications. A major concern in conservation biology is the designing of migration corridors for stabilizing the dynamics of populations in isolated, patchy habitats. Our results show that too much migration can actually increase the amplitude of fluctuations in metapopulation size, thus potentially endangering the metapopulation

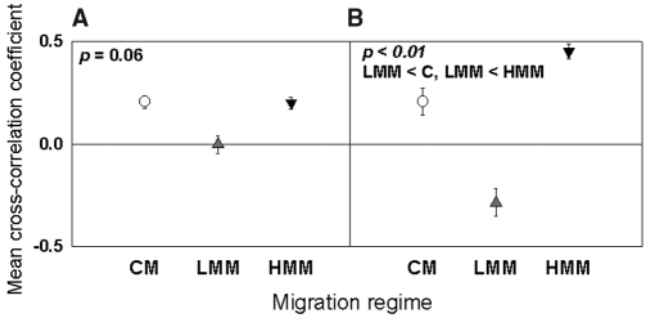

Fig. 2. Mean (±SE) cross-correlation coefficients from the experimental data. (**A**) The means for all possible pairs of subpopulations are positive for CMs and HMMs, indicating synchrony between the subpopulations. (**B**) The mean nearest neighbor cross-correlation coefficient is significantly negative for the LMMs. This indicates that neighboring subpopulations are oscillating out of phase with each other, leading to the observed patterns of stability.

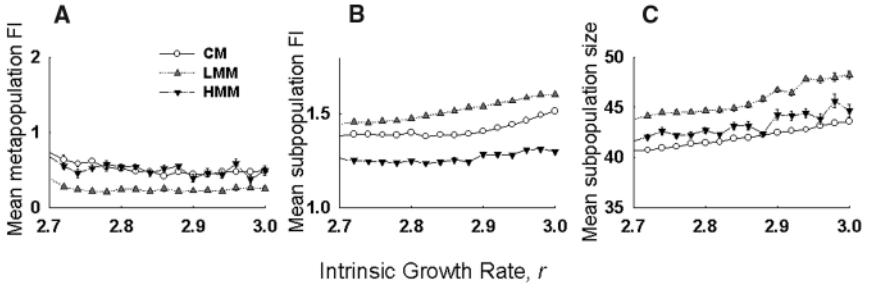

Fig. 3. Simulation results averaged over 10 independent runs (error bars represent SEM). (**A**) Mean metapopulation FI values are lowest for LMMs and are similar for CMs and HMMs (compare Fig. 1A). (**B**) Mean subpopulation FI values are highest for LMMs (compare Fig. 1B). (**C**) The average subpopulation size of CMs is the lowest, contrary to the experimental findings (Fig. 1C). See text for a possible explanation.

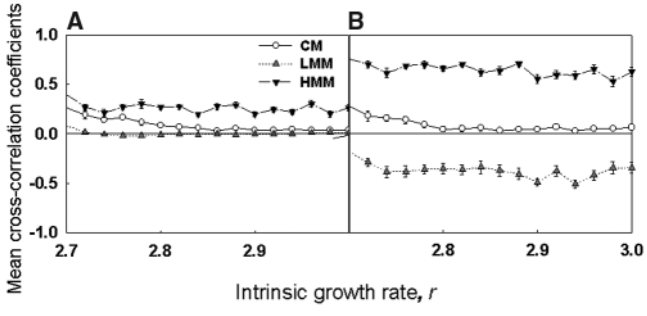

Fig. 4. Mean (±SE) cross-correlation coefficients from the simulations. (**A**) The average cross-correlation coefficient between all possible subpopulation pairs is close to zero for both CMs and LMMs. This indicates an overall lack of synchrony and contradicts the corresponding empirical observation for CMs (compare Fig. 2A). See text for a possible explanation. (**B**) The average cross-correlation coefficient between the nearest neighbors is negative for LMMs but is close to zero for CMs. This shows that although the LMM subpopulations were out of phase with each other, there was little synchrony among the CM subpopulations.

in the long run. However, migration rate in our experiment was density independent and migration was confined to the two nearest neighbors, whereas it is known that the dynamics of a metapopulation can vary depending on the exact form of density dependence (*31*) and scheme of migration (*11*). Moreover, growth rates of *Drosophila* (and most insects, microbes, and fishes) are higher than those of mammals and birds, which are generally of greater concern for conservation. The intrinsic growth rates of subpopulations are also known to interact strongly with migration rate in producing observed metapopulation dynamics (*12*). Therefore, due caution should be exercised when extrapolating our results to natural populations.

References and Notes

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20. In the experiment, the nine subpopulations (single-vial *Drosophila* cultures) were arranged on the periphery of a circle, with each vial exchanging migrants only with its two nearest neighbors (i.e., a one-dimensional array with periodic boundary conditions). In nature, such metapopulations might exist, for example, on the shorelines of lakes or along the edges of ecosystems. The simulations mimicked the experimental system and focused on the behavior of nine coupled Ricker maps, with periodic boundary conditions. See supporting material on *Science* Online.
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22. We define a population whose size fluctuates with higher amplitude across time to be less stable than one that has lower amplitude of fluctuation ["constancy" attribute of stability (*21*)]. We introduce a measure of stability, the fluctuation index (FI) of a series, given as

$$\mathrm{FI} = \frac{1}{T\bar{N}} \sum_{t=0}^{T-1} \mathrm{abs}(N_{t+1} - N_t)$$

where $\bar{N}$ is the mean population size over T generations. FI thus reflects the mean one-step change in population size, scaled by average population size, over the study duration.
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25. In the experiment, a subpopulation was deemed extinct when it did not contain at least one male and one female fly. When a CM subpopulation became extinct, it was restarted using four males and four females from a backup vial. The backup vials were maintained in parallel to the three treatments, under high larval crowding and yeast supplement to the adults. There were no restarts in LMMs or HMMs; extinct subpopulation vials remained empty until recolonized by migrants from a neighboring subpopulation.
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28. For example, in simulations with $r = 2.8$, comparable to the estimated r in our CM subpopulations, the mean extinction rate was 0.75 out of 9 subpopulations per generation, versus 3.35 out of 9 for experimental CMs.
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Supporting Online Material

www.sciencemag.org/cgi/content/full/312/5772/434/DC1
Materials and Methods
SOM Text
Fig. S1
References

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A Plant miRNA Contributes to Antibacterial Resistance by Repressing Auxin Signaling

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Plants and animals activate defenses after perceiving pathogen-associated molecular patterns (PAMPs) such as bacterial flagellin. In *Arabidopsis*, perception of flagellin increases resistance to the bacterium *Pseudomonas syringae*, although the molecular mechanisms involved remain elusive. Here, we show that a flagellin-derived peptide induces a plant microRNA (miRNA) that negatively regulates messenger RNAs for the F-box auxin receptors TIR1, AFB2, and AFB3. Repression of auxin signaling restricts *P. syringae* growth, implicating auxin in disease susceptibility and miRNA-mediated suppression of auxin signaling in resistance.

Plants perceive a 22–amino acid peptide (flg22) from the N terminus of eubacterial flagellin (*1*). In *Arabidopsis*, flg22 triggers rapid changes in transcript levels, including down-regulation of a gene subset, potentially by posttranscriptional mechanisms (*2*). One posttranscriptional mechanism is RNA silencing, a sequence-specific mRNA degradation process mediated by 20- to 24-nucleotide (nt) RNAs known as short interfering RNAs (siRNAs) and microRNAs (miRNAs). Both are made from double-stranded RNA (dsRNA) by the ribonuclease III enzyme Dicer. Four paralogs (Dicer-likes, or DCLs) are found in *Arabidopsis*. DCL2 produces viral-derived siRNAs (*3*) and siRNAs from antisense overlapping transcripts (*4*). DCL3 generates DNA repeat–associated siRNAs (*3*), whereas DCL4 synthesizes trans-acting siRNAs and mediates RNA interference (*5*–*7*). DCL1 excises miRNAs from intergenic stem-loop transcripts to promote cleavage of cellular transcripts carrying miRNA-complementary sequences (*8*).

We examined whether small RNAs—especially miRNAs—contribute to the rapid changes elicited by flg22. We analyzed transgenic *Arabidopsis* expressing the P1-Hc-Pro, P19, and P15 viral proteins that suppress miRNA- and siRNA-guided functions (*9*, *10*), anticipating that transcripts repressed by flg22-stimulated small RNAs would be more abundant in these lines. Comparative transcript profiling of untreated

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