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Impacts of dispersal on rapid adaptation and dynamic stability of *Daphnia* in fluctuating environments

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Prior ecological research has shown that spatial processes can enhance the temporal stability of populations in fluctuating environments. Less explored is the effect of dispersal on rapid adaptation and its concomitant impact on population dynamics. For asexually reproducing populations, theory predicts that dispersal in fluctuating environments can facilitate asynchrony among clones and enhance stability by reducing temporal variability of total population abundance. This effect is predicted when clones exhibit heritable variation in environmental optima and when fluctuations occur asynchronously among patches. We tested this in the field using artificial ponds and metapopulations composed of a diverse assemblage of *Daphnia pulex* clones. We directly manipulated dispersal presence/absence and environmental fluctuations in the form of nutrient pulses. Consistent with predictions, dispersal enhanced temporal asynchrony among clones in the presence of nutrient pulses; this in turn stabilized population dynamics. This effect only emerged when patches experienced spatially asynchronous nutrient pulses (dispersal had no effect when patches were synchronously pulsed). Clonal asynchrony was driven by strong positive selection for a single clone that exhibited a performance advantage under conditions of low resource availability. Our work highlights the importance of dispersal as a driver of eco-evolutionary dynamics and population stability in variable environments.

1. Introduction

Increasing anthropogenic impacts on natural systems have increased interest in the role of landscape connectivity and dispersal as drivers of stability and long-term persistence of populations [1–3]. An abundance of metapopulation models show that dispersal can strongly alter the ecological and evolutionary dynamics of populations, influencing population persistence, adaptive evolution and the genetic diversity of local populations. However, consideration of the effects of dispersal on population dynamics and temporal stability, especially in response to short-term environmental perturbations, has focused largely on ecological and demographic processes. This probably stems from the view that adaptive evolution occurs at timescales that are much longer than population dynamics. Thus, while it is widely appreciated that evolutionary responses can enhance the persistence of populations in changing environments [4–8], consideration of their effects on population dynamics and temporal stability has been less frequently explored [9]. Nevertheless, a growing body of research shows that some species can display 'contemporary' or 'rapid evolution' in which microevolutionary responses occur at timescales similar to population and community dynamics [9–11]. Thus, evolutionary responses can alter the dynamics and stability of populations and communities at ecological timescales—what are commonly termed 'eco-evolutionary' dynamics (e.g. [12–16] reviewed in [10,17,18]). The increasing recognition of the importance of rapid adaptive responses in nature suggests that our understanding of dispersal's effects on population dynamic stability may sometimes require consideration of both ecological and evolutionary phenomena.

A characteristic shared by most natural systems is the inconstancy of their environmental conditions over time. Accordingly, topics of enduring interest in ecology are the factors that enhance the temporal stability and persistence of populations that experience recurring environmental perturbations [19,20]. Models of metapopulation dynamics have shown repeatedly that dispersal can be a potent stabilizing mechanism. For instance, dispersal from source populations into poorer sinks can maintain populations that would otherwise face extinction [21]. When applied to temporally varying metapopulations, such source–sink dynamics can stabilize local populations by increasing population abundances under poor environmental conditions via immigration and reducing population abundances during favourable periods via emigration, consequently reducing the magnitude of variability over time [22–24]. Dispersal can also facilitate rapid population recovery as environmental states transition from poor to favourable conditions. The efficacy of dispersal as a stabilizing agent depends greatly on how temporal environmental variation covaries spatially. Spatial asynchrony in temporal heterogeneity ensures that some patches in the metapopulation experience favourable conditions and can act as dispersal sources for patches undergoing periods of low abundance—increasing temporal stability at the local scale [22,23,25,26].

Empirical and theoretical considerations of the effects of dispersal and gene flow on evolution are extensive but fall largely outside the context of dynamic stability. This work has demonstrated that gene flow can be a force of evolutionary change, having the capacity to strongly alter the genetic structure and mean fitness of local populations, as well as either enabling or suppressing adaptive evolution [6,8,27–32]. Much less explored are the effects of dispersal on rapid adaptation and temporal stability of populations experiencing persistent environmental fluctuations. Predictions from multi-species ecological models of stability in temporally varying environments provide some insight into this problem. For instance, in models of environmentally forced competition communities, the presence of phenotypic variation among species in environmental optima allows temporal variation to differentially select phenotypes over time. This can promote asynchronous responses in abundances of different phenotypes over time, reducing temporal variability in total abundance summed across phenotypes and promoting local phenotypic diversity [33–36]. Dispersal can enhance density compensation among phenotypes, promoting stability, if dispersal rates are low relative to demographic rates and if patches experience asynchronous environmental variation [37,38]. While these predictions focus on phenotypic variation among species, they also apply to dynamics of different genotypes or clones within asexual populations. For zooplankton species, such as *Daphnia pulex*, reproduction during a growing season is largely asexual and populations are often composed of obligate asexual clones [39,40]. Thus, we predict that *Daphnia* intraspecific phenotypic variation will promote asynchronous responses among clones, stabilizing short-term population dynamics.

We know of few experimental tests of the combined effects of dispersal on rapid adaptation and temporal stability of populations in fluctuating environments (though see [41]). We present results of a field experiment using artificial ponds in which we tested the effects of dispersal and spatial covariation in environmental fluctuations on clonal selection and temporal stability of *D. pulex* populations. We show that temporal asynchrony in *D. pulex* clonal dynamics enhances temporal stability of populations in fluctuating environments. Consistent with theoretical predictions, these effects are enhanced in the presence of dispersal when environmental fluctuations occur asynchronously among patches.

2. Material and methods

(a) Field experiment

The experiment was conducted outdoors at the Kellogg Biological Station (KBS), experimental pond facility (Hickory Corners, MI, USA). Artificial ponds consisted of polyethylene tanks containing 23 kg of silica sand as a bottom substrate and filled with 300 l of untreated well water. Tank tops were covered with 1 mm fibreglass screening to prevent invasion by macroinvertebrates. Because nitrogen and phosphorus levels were relatively low in the well water, we boosted initial levels by adding phosphorus and nitrogen as K_2HPO_4 and $NaNO_3$ to target concentrations of 150 µg P l and 2250 µg N l; concentrations were comparable to median levels found in natural ponds in the region [42,43]. We added 15 adult *Helisoma* sp. snails to reduce periphyton growth and promote nutrient recycling. All tanks were seeded with a diverse phytoplankton assemblage collected from 10 natural ponds in the area around KBS. Two litre water samples were collected from each pond, filtered through 30 µm mesh to remove zooplankton, mixed and then redistributed evenly among the experimental tanks. Phytoplankton were allowed to respond numerically for 5 days, at which time *D. pulex* individuals were added. The *D. pulex* assemblage consisted of 30 different clones collected from different ponds located in southern Michigan and included both obligate and cyclic parthenogenetic lines. Clones were chosen to represent a diversity of source pond conditions and were uniquely identifiable using four microsatellite markers. Clonal cultures were maintained in the laboratory under low density, high food conditions for several generations. At the start of the experiment, each tank received 18 individuals of each clone; we refer to this date as day 0 of the experiment. After one week of population growth, we redistributed *D. pulex* among the tanks to reduce variation in initial clonal composition owing to demographic stochasticity. To do this, we sampled 10% of each population (30 l) using a 10 l bucket, combined the individuals in a small volume of well water and then redistributed them evenly back into the tanks. The experiment was terminated on day 84.

Our treatment design consisted of a manipulation of nutrient input (pulsed or continuous) crossed with dispersal presence/absence (1% twice weekly). Populations that experienced no dispersal were single tanks that experienced either continuous or pulsed nutrient input, in which pulsed treatments corresponded to pattern P1 (figure 1). Metapopulations in which dispersal occurred were composed of two tanks that experienced either (i) continuous nutrient input for both tanks, (ii) synchronously pulsed nutrient input in which both tanks experienced pulse pattern P1, or (iii) asynchronously pulsed nutrient input in which one tank experienced pulse pattern P1 and the other experienced pulse pattern P2. Nutrient pulses in pattern P2 occurred two weeks out of phase of P1 (figure 1). All metapopulations (dispersal present treatments) and dispersal absent tanks that experienced continuous nutrient input were replicated four times. The dispersal absent treatments that experienced pulsed nutrient input were replicated eight times.

The tanks experienced semi-continuous replacements of water, but the timing and amount of nutrients added depended on the nutrient input treatment. Every 2–3 days (on Mondays and Thursdays), tanks were gently mixed and 30.5 l of water (containing plankton) was removed using a 10 l bucket (care was taken to not disturb bottom sediments). Water was then replaced with

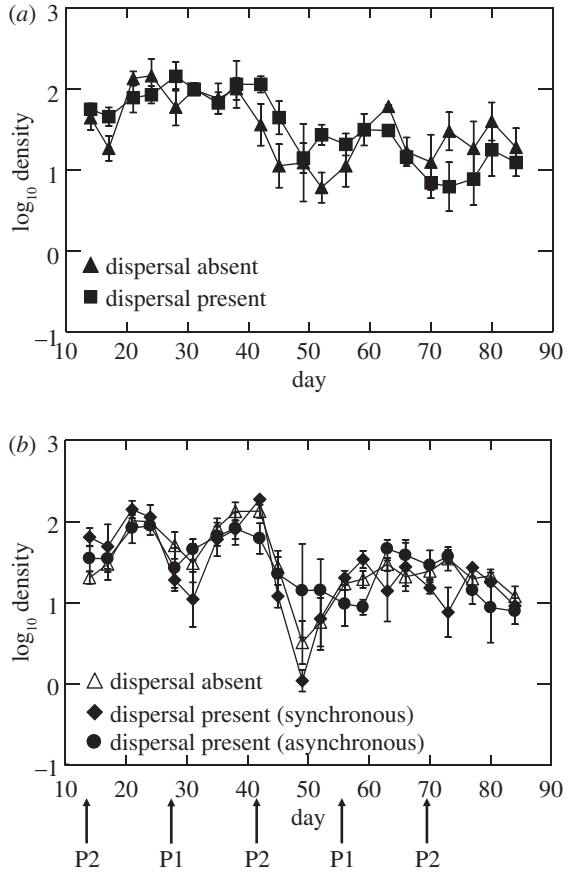

Figure 1. *Daphnia pulex* mean log density (±s.e.) over time in target tanks. Shown separately are dynamics in the presence/absence of dispersal and in (*a*) treatments that experienced continuous nutrient inputs, or (*b*) treatments that experienced pulsed nutrient inputs. Shown in panel (*b*) are the dates on which nutrient pulses occurred (arrows). Synchronously pulsed metapopulations experienced pulse pattern P1 in both patches; asynchronously pulsed metapopulations contained one patch that experienced pulse pattern P1, while the other experienced pulse pattern P2. Dispersal absent populations experienced pulse pattern P1.

fresh well water. For tanks that did not experience nutrient perturbations, the replacement water contained dissolved phosphorus and nitrogen at target levels (described above). Tanks that experienced nutrient perturbations received their nutrients as pulses at four week intervals; this frequency was long enough to permit numerical responses by *D. pulex* which has a maximum population growth rate of 0.2–0.4 d^{-1}. For a pulse event, replacement medium contained amounts of nitrogen and phosphorus equivalent to four weeks of replacements. Following a pulse, water replacements were performed using well water without added nutrients until the next pulse event. The unenriched well water contained 22 times less phosphorus than the water added to the continuous nutrient treatments. Hence, nutrient perturbation treatments consisted of both a pulse of potential productivity followed by a prolonged period of nutrient dilution and reduced potential productivity. Tanks that experienced pulse pattern P1 received their first pulse on day 0 of the experiment; P2 tanks received their first pulse on day 14. Water removed for replacements was used as a plankton sample.

Dispersal treatments consisted of density-independent dispersal events performed every 2–3 days on the day following samplings. Dispersal was imposed by gently mixing each source tank in a metapopulation and removing 3 l of water (1% of total volume) from each using a bucket. Samples were filtered using an 80 µm sieve and the water was returned to its source tank. Isolated zooplankton were then transferred to their target tank in a small volume of untreated well water. For dispersal absent treatments, tanks were gently mixed but no samples were taken. The dispersal rate we used was chosen to match prior experiments that showed it to be adequate for sustaining *D. pulex* populations under strong environmental forcing of similar periodicity [38]. How this rate compares to natural dispersal rates is unknown. Although prior studies have quantified zooplankton immigration rates into water bodies [44–46], we know of none that have estimated emigration rates from natural ponds.

Water removed for replacements served as plankton samples. A 500 ml sample was stored on ice and a sub-sample was later filtered onto GF/F filters for analysis of chlorophyll *a* as a measure of total algal biomass. A second chlorophyll *a* sub-sample was first filtered through a 35 µm mesh then filtered onto GF/F filters to measure algal biomass within the edible size range of *Daphnia*. Results for the total and less than 35 µm size fractions of chlorophyll *a* were qualitatively similar; thus, we present results for the latter. Zooplankton samples were concentrated in the field using an 80 µm sieve, preserved in 70% ethanol and later enumerated using a stereomicroscope. Temperature was measured weekly at mid-depth in each tank with a Hydrolab MS5 multiprobe (Hach Environmental, Loveland, CO, USA). To determine clonal composition of *D. pulex* populations, microsatellite analyses were performed on a sub-sample of 48 haphazardly chosen individuals taken from the ethanol-preserved samples. Analyses were performed every two weeks beginning on day 14 of the experiment and ending on day 84 (see the electronic supplementary material for additional molecular methods). Clones were identified as multi-locus genotypes based on unique combinations of alleles for four microsatellite loci. Frequencies (relative abundances) of clones were then estimated for each sub-sample.

(b) Laboratory experiments

Our results showed that *D. pulex* populations were dominated by three clones (clones 18, 29 and 33). To investigate functional trait variation among these clones, we used laboratory-based, short-term juvenile growth assays to measure performance under different environmental conditions [47]. Clonal lines were established from laboratory cultures and maintained under high food, low density conditions at 25°C, for three generations to remove effects of prior culture conditions. The experiments were performed using offspring of the F_3 generation. We measured juvenile growth rates of each clone in monoculture under two different food concentrations (5×10^3 versus 5×10^4 cells of *Ankistrodesmus falcatus* per millilitre at 25°C). Because temperatures also varied over time in our experiment (range = 16.7–28.9°C), we performed a second set of growth experiments measuring responses of the three clones at a non-limiting food level (5×10^4 cells of *A. falcatus* per millilitre) and at two different temperatures (15°C versus 30°C) that encompassed the range observed in the experiment. Experiments were performed under 24 h light in temperature-controlled environmental chambers using 200 ml beakers filled with 150 ml of aged tap water (the same medium used to culture the zooplankton). At the start of each assay, neonates of each clone (less than 18 h old) were isolated from their stock cultures and five individuals were then haphazardly chosen and placed into each experimental beaker. At least 15 neonates of each clone were retained for measures of initial biomass (as dry weight). Replication varied depending on availability of neonates and ranged from 5 to 12 replicate beakers for each treatment combination. After 24 h, juveniles were transferred to new beakers with fresh medium and food. After 48 h, juveniles were isolated and dried for more than 48 h at 50°C and then weighed individually on a microbalance. For each individual, somatic growth rate was calculated as [ln(final dry weight/mean

initial dry weight)]/(2 days). Individual growth rates were averaged to obtain a mean growth rate for each replicate beaker.

(c) Statistical methods

For statistical analyses of the field experiment, we used a target-neighbour approach in which responses from a single tank from each metapopulation was used for comparisons among treatments. For metapopulations that experienced pulsed nutrient input, we used the tanks that experienced the P1 pulse pattern facilitating comparisons with the dispersal absent treatments that also experienced pattern P1. Note that P1 tanks received the same total amount of nutrients over the course of the experiment as tanks that experienced continuous nutrient inputs. In order to analyse main effects and interactions of dispersal and nutrient input on responses, four replicates of the dispersal absent, pulsed nutrient treatment were randomly assigned as controls for the dispersal present, synchronously pulsed treatment; the remaining four replicates of the dispersal absent, pulsed nutrient treatment were used as controls for the dispersal present, asynchronously pulsed treatment. To quantify the degree of temporal synchrony among different clones within a population, abundances of each clone on each sample date were determined by multiplying clone frequencies by total *D. pulex* population density. Synchrony of clones over time was then quantified using the synchrony index of [48]. While this index was originally formulated as a measure of synchrony among different populations within communities, it can also be applied to asexually reproducing clones within populations. The index scales between 1 (complete synchrony) and 0 (complete asynchrony). Unlike other metrics such as correlation coefficients or covariances, it is not sensitive to differences in the number of clones or total population densities among populations. Thus, it is a robust comparative measure of synchrony [48]. To quantify temporal variability of *D. pulex* populations, the coefficient of variation (CV) of population densities over time was used as an inverse measure of temporal stability; CVs were calculated using sample dates on which clonal composition was determined. To estimate clonal diversity, we used the inverse Simpson's index which puts greater weight on abundant clones and is less sensitive to limited sample size compared with other metrics [49].

Treatment effects on temporal variability, clonal synchrony and time-averaged chlorophyll *a* measures were analysed using ANOVA. Clonal diversity responses through time were analysed using repeated measures ANOVA; time-averaged clonal diversity responses were analysed using ANOVA. Based on prior theory, we predicted that in the presence of nutrient pulses dispersal would decrease synchrony and temporal variability when pulses were spatially asynchronous; we predicted no effect of dispersal in the absence of pulses. Thus, following detection of significant interactions in ANOVA, we performed planned comparisons on subsets of our data. We tested the effect of dispersal on synchrony and temporal variability in the presence of nutrient pulses using ANOVA followed by pairwise comparisons using Tukey's HSD. A separate planned comparison was made testing the effect of dispersal in the absence of nutrient pulses using ANOVA. Treatment effects on clonal composition over time were analysed using repeated measures PERMANOVA based on Bray–Curtis distances of square root transformed clone abundances. Three replicates were excluded owing to population extinctions (see Results) resulting in an unbalanced design. Thus, we used type III sums of squares for all ANOVA and PERMANOVA analyses. For results of the juvenile growth assays, effects of environment (food level or temperature) and clone identity were analysed using ANOVA with type III sums of squares. For the ANOVA tests, all response variables met assumptions of normality and homogeneity of variances tested using Lilliefor's and Levene's tests, respectively. All statistics were performed using R v. 3.0.2 [50], with the exception of repeated measures PERMANOVA, which was performed in PRIMER v. 6.1 [51], and repeated measures ANOVA, which was performed in SYSTAT v. 13 (Systat Software, Inc., San Jose, CA, USA).

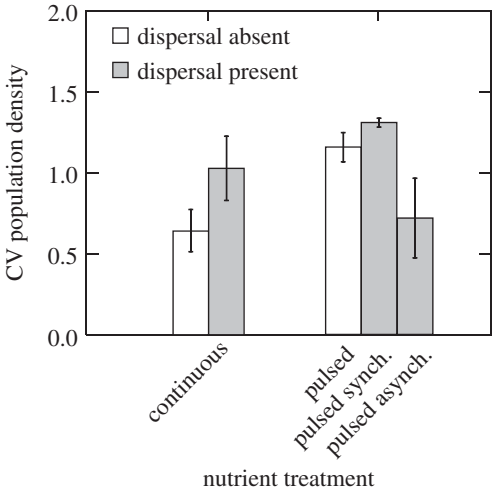

Figure 2. *Daphnia pulex* temporal population variability measured as the coefficient of variation (CV) of total density over time. Shown are mean responses (± s.e.) in the presence/absence of dispersal and in the different nutrient treatments.

3. Results

(a) Field experiment

Three populations went extinct during the course of the experiment and have been excluded from all analyses. This included one replicate of the continuous nutrient, dispersal absent treatment; one replicate of the pulsed nutrient, dispersal absent treatment; and one replicate of the synchronously pulsed, dispersal present treatment. Temporal variability of the less than 35 µm size fraction of chlorophyll *a* increased in the presence of pulsed nutrient inputs (electronic supplementary material, figures S1 and S2; $F_{2,15} = 9.54$, $p < 0.01$, ANOVA) but was unaffected by dispersal ($p > 0.18$, ANOVA). Chlorophyll *a* concentrations averaged over time did not vary among treatments (electronic supplementary material, figure S3; all $p > 0.17$, ANOVA). Time-averaged relative abundance of less than 35 µm chlorophyll *a* (calculated as less than 35 µm chlorophyll *a*/total chlorophyll *a* concentration) also did not vary among treatments (electronic supplementary material, figure S3; all $p > 0.14$, ANOVA). *Daphnia pulex* population dynamics showed a similar pattern, tending to exhibit greater temporal variability in the presence of nutrient pulses (figure 1*a* versus *b*). Analysis of CVs of population densities revealed a weak effect of nutrient treatment (figure 2; $F_{2,15} = 3.36$, $p = 0.062$, ANOVA). However, dispersal moderated the destabilizing effects of nutrient perturbations when pulses occurred asynchronously among patches (figure 2); a significant interaction between dispersal and nutrient treatment was detected ($F_{2,15} = 4.37$, $p = 0.032$, ANOVA). Planned contrasts revealed that dispersal had no effect on temporal population variability in the absence of nutrient pulses ($F_{1,5} = 3.13$, $p = 0.13$, ANOVA). However, an effect of dispersal was detected when examining pulsed nutrient treatments (figure 2; $F_{2,11} = 4.97$, $p = 0.03$, ANOVA); dispersal reduced temporal variability in the presence of spatially asynchronous nutrient pulses

when compared with synchronously pulsed metapopulations ($p = 0.04$, Tukey's HSD) and treatments without dispersal ($p = 0.06$, Tukey's HSD). No differences were detected between the latter two treatments ($p = 0.70$, Tukey's HSD).

When examining clonal composition and dynamics, initial clonal sorting occurred rapidly; the majority of populations were dominated by three clones (clones 18, 29 and 33) by the first sample date (electronic supplementary material, figure S4). These clones were known from prior laboratory assays to reproduce via obligate parthenogenesis. Repeated measures ANOVA of clonal diversity revealed a significant effect of time ($F_{5,75} = 12.17$, $p < 0.001$) but no interactions between time and treatments (all $p > 0.35$). Thus, diversity varied among sample dates, tending to decline over time across all treatments (electronic supplementary material, figure S5). When analysing time-averaged diversity, effects of dispersal appeared to vary with nutrient treatment, reducing diversity in the asynchronously pulsed nutrient treatment relative to the continuous and synchronously pulsed treatments (electronic supplementary material, figure S6). However, the interaction was not statistically significant ($p = 0.08$, ANOVA). Repeated measures PERMANOVA of clone abundances revealed a significant interaction of time, dispersal and nutrient perturbations ($p = 0.04$). Thus, clonal composition varied over time with responses dependent on dispersal level and the form of nutrient perturbation imposed. Populations that experienced dispersal and asynchronous nutrient pulses showed more rapid increases and sustained dominance by clone 29 over time when compared with the other treatments (electronic supplementary material, figure S4). Interactive effects of dispersal and nutrient treatments on clonal dynamics were reflected in measures of clonal synchrony over time. Treatment effects on synchrony paralleled temporal stability responses (figure 3); nutrient perturbations increased synchrony among clones in the absence of dispersal and in the presence of dispersal when patches experienced synchronous perturbations. However, dispersal enhanced asynchrony among clones when perturbations occurred asynchronously among patches (figure 3); a significant interaction between dispersal and nutrient perturbations was detected ($F_{2,15} = 14.93$, $p < 0.001$, ANOVA). Planned contrasts revealed that dispersal had a weak positive effect on clonal synchrony in the absence of nutrient pulses ($F_{1,5} = 5.35$, $p = 0.07$, ANOVA). An effect of dispersal was detected when examining pulsed nutrient treatments (figure 3; $F_{2,11} = 21.87$, $p < 0.001$, ANOVA); dispersal reduced synchrony in the presence of spatially asynchronous nutrient pulses when compared with synchronously pulsed metapopulations ($p < 0.01$, Tukey's HSD) and in the absence of dispersal ($p < 0.01$, Tukey's HSD). No differences were detected between the latter two treatments ($p = 0.55$, Tukey's HSD). Population temporal variability was strongly and positively associated with temporal synchrony of clonal dynamics when examining responses across treatments (figure 4; $R = 0.87$, $p < 0.001$, Pearson correlation). Thus, populations whose clonal dynamics were more asynchronous over time were more stable.

(b) Laboratory experiments

Juvenile growth experiments revealed a significant clone by environment interaction in response to resource concentration (electronic supplementary material, figure S7; $F_{2,47} = 7.81$, $p < 0.01$, ANOVA). No differences in growth rates were detected among clones at the high resource level, but clone 18 had a significantly lower growth rate at the low resource level when compared with clones 29 and 33 (electronic supplementary material, figure S7; $p < 0.05$, Tukey's HSD). A clone by environment interaction was also present in the temperature assay ($F_{2,42} = 5.34$, $p < 0.01$, ANOVA). Clone 29 had a significantly lower growth rate compared with clones 18 and 33 at 15°C (electronic supplementary material, figure S7; $p < 0.05$, Tukey's HSD), but no differences in growth rate were detected among clones at 30°C (all $p > 0.10$, Tukey's HSD).

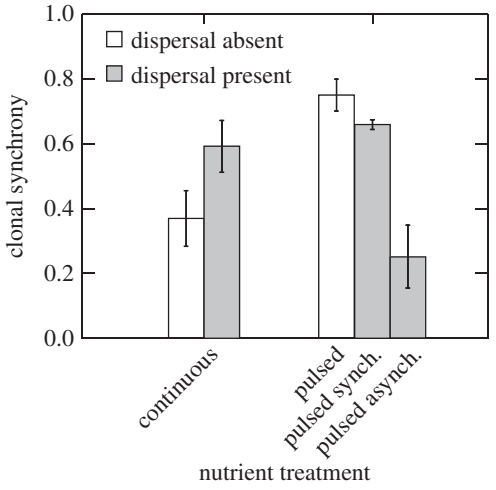

Figure 3. Synchrony of *Daphnia pulex* clones over time measured using the synchrony index of [48]. Shown are mean responses (± s.e.) in the presence/absence of dispersal and in the different nutrient treatments.

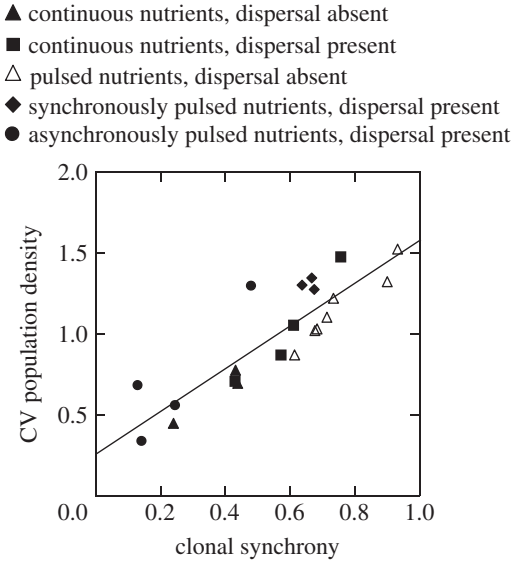

Figure 4. The relationship between *Daphnia pulex* temporal population variability and synchrony of *D. pulex* clones over time. Symbols display different treatment combinations. Shown also is the linear regression line.

4. Discussion

Our work demonstrates the influence of contemporary evolution on the dynamic stability of populations in ecological time. Relative to controls, nutrient perturbations increased the synchrony of *Daphnia* clonal dynamics and destabilized populations in the absence of dispersal. Dispersal mediated these

responses but the strength of the effect depended on its interplay with spatial covariation in fluctuations. Among populations that experienced pulsed nutrients, asynchrony in clonal dynamics was strengthened and populations stabilized when dispersal occurred among patches that experienced spatially asynchronous perturbations, consistent with general theoretical predictions. No effects were apparent when dispersal took place between synchronously pulsed patches. Interestingly, dispersal appeared to have a weak destabilizing effect on populations that experienced continuous nutrient inputs. Both temporal variability and clonal synchrony tended to increase in the presence of dispersal in this treatment, though the effects were not statistically significant at the 0.05 level.

Theory predicts that dispersal can stabilize population dynamics through both ecological and evolutionary mechanisms. Source–sink dynamics have been shown theoretically and empirically to be a process that can enhance the persistence and temporal stability of populations in the absence of intraspecific phenotypic variation [22,23,25,26]. However, this mechanism cannot completely account for our findings. First, if the clones in our experiment lacked relevant phenotypic variation and source–sink dynamics acted alone to influence stability, then clone abundances should have varied randomly over time. Consequently, asynchrony and clonal composition would show no pattern among treatments. This was clearly not the case in our study; composition and asynchrony varied among treatments with the latter being strongly related to temporal stability. Our laboratory-based experiments also revealed significant variation among the three dominant clones in ecologically relevant traits, further supporting the role of dispersal-driven clonal selection as a stabilizer in perturbed *Daphnia* populations. Finally, if clones exhibited neutral dynamics in our experiment, then clone growth rates over time should have varied as a function of total *D. pulex* abundance but shown no relationship with their relative frequencies. Examining growth rates of the dominant three clones across sample dates and treatments, all three showed statistically significant negative frequency dependence, though patterns were only strong for clone 18 (electronic supplementary material, figure S8). Thus, clones were able to increase in abundance when rare, consistent with the operation of fluctuation-dependent stabilizing mechanisms [52].

While our results demonstrate that dispersal can promote differential clonal responses and population stability, the form of clonal dynamics in our experiment deviated from standard patterns of compensatory fluctuations predicted by models. Instead, clonal asynchrony in the asynchronously pulsed, dispersal present treatment was driven by an early directional increase in the relative frequency of clone 29 followed by sustained numerical dominance. This was qualitatively reflected in measures of clonal diversity in which dispersal appeared to reduce diversity in the asynchronously pulsed treatment relative to the synchronously pulsed treatment, though the effect was not statistically significant. Our laboratory trait assays provide a potential explanation for this. Theory predicts compensatory dynamics among phenotypes in fluctuating environments when phenotypes exhibit trade-offs in their environmental optima—this allows phenotypes to increase when rare and temporally partition environmental variation [33,34,37]. While our assays uncovered significant clone by environment interactions in response to food quantity, it did not reveal reversals in performance ranking. Clone 29 showed a growth advantage under low food availability, but all three clones exhibited comparable performance when resources were non-limiting. Thus, in our experiment, nutrient pulses probably created short periods of near neutral dynamics among clones (as algal abundance peaked and clones exhibited comparable fitnesses) followed by extended periods of positive selection for clone 29 (as tanks experienced increasing nutrient dilution and depressed algal abundance). In this scenario, dispersal among asynchronously fluctuating patches could enhance dominance of clone 29 by providing an influx of clone 29 individuals from source patches into target patches experiencing periods of neutral dynamics.

An unanswered question is what facilitated persistence of clones other than 29, most notably clone 18 which frequently showed periods of numerical dominance over the course of the experiment and negative frequency-dependent growth rates. One possibility was the presence of natural temperature fluctuations in our experiment, which ranged between 16.7°C and 28.9°C over the experimental period (electronic supplementary material, figure S9). Our laboratory experiments revealed significant clone by environment interactions in response to temperature, with clone 18 exhibiting a performance advantage over clone 29 at low temperature (15°C). Thus, periods of sufficiently low temperatures could have differentially selected for clone 18. Interestingly, peaks in clone 18 relative frequencies tended to follow sample dates with low temperatures (e.g. days 42 and 70; electronic supplementary material, figure S9). To more formally analyse differential responses to temperature, we first quantified changes in relative frequencies of the dominant clones from sample date to sample date using the selection coefficient $s = [\ln(1 - p_t)/p_t - \ln(1 - p_t')/p_t']/(t - t')$ [53], where p_t' is the relative frequency of the clone at time t' and p_t is its relative frequency at time t in the future. Negative s values indicate selection against the clone over the time interval (i.e. a decline in its relative frequency); positive values indicate positive selection. When analysing s values across treatments and sample dates for each clone, we found a significant negative relationship with temperature for clone 18 ($R = -0.478$, Bonferroni adjusted $p < 0.001$, Pearson correlation). Selection coefficients for clone 18 shifted from positive to negative with increasing mean temperature, indicative of a relative fitness advantage under low temperatures (electronic supplementary material, figure S10). No relationship with temperature was detected for clones 29 or 33 ($p > 0.86$; electronic supplementary material, figure S10).

While prior studies have demonstrated the effects of rapid microevolutionary responses on population dynamics and stability [13,15,16,54,55], there are remarkably few experimental tests of the effects of dispersal on eco-evolutionary dynamics in fluctuating environments. In a study of experimental yeast populations experiencing directional environmental change, Bell & Gonzalez [41] demonstrated that dispersal can facilitate the evolutionary rescue and persistence of populations. Our work complements this finding by highlighting the interplay of dispersal, rapid evolution and stability in systems experiencing spatially and temporally varying environmental conditions. How our results apply to natural populations is unknown. While dispersal of zooplankton is known to readily occur among lakes and ponds [45,46,56–58], rates of movement can vary greatly depending on the proximity of waterbodies and degree of connectivity via in- and outflows [44,46,57]. Furthermore, our study focused on short-term selection and sorting among asexually reproducing clones. Thus, we consider

a form of evolutionary response that does not encompass the effects of mutation and recombination and whose mechanisms are primarily ecological—an approach that has been taken in prior studies of rapid adaptation [9,13]. While our results are more relevant for understanding intra-annual clonal dynamics in *Daphnia* populations, sexual reproduction in *Daphnia* results in the production of dormant eggs that commonly emerge annually in the spring. This form of temporal dispersal from the egg bank is probably a major source of genetic and phenotypic variation for many natural zooplankton populations [59]—one that could either impede rapid adaptation and reduce stability (through the introduction of maladaptive phenotypes) or act as a source of novel phenotypes, enhancing adaptive capacity and stability in the presence of environmental change [59,60]. Our experiment is one small clue to the manner in which gene flow may influence short-term eco-evolutionary dynamics in fluctuating environments. Much more work is required to understand how spatial and temporal dispersal influence adaptive evolution and stability of *Daphnia* populations at intra- and inter-annual scales.

Data accessibility. Data is available in the Dryad database http://dx.doi.org/10.5061/dryad.jr5fd.

Authors' contributions. C.F.S. conceived the study, designed and carried out the field experiment, designed the laboratory experiments, performed data analyses and wrote the manuscript; R.D.S. participated in the field experiment; M.T. participated in the field experiment; L.S., K.P. and L.K. carried out the laboratory experiments. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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