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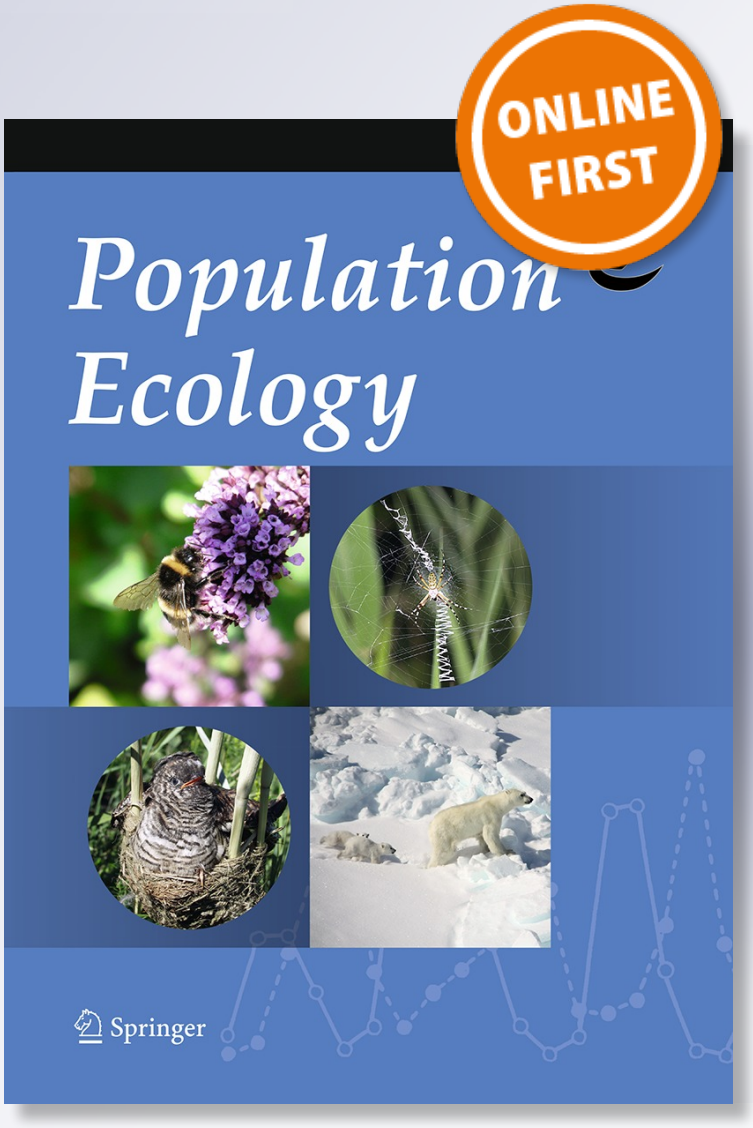

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ORIGINAL ARTICLE

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Abstract Controlling weed populations requires an understanding of their underlying population dynamics which can be achieved through a combination of model development and long-term studies. In this paper, we develop models based on long-term data from experimental populations of the weedy annual plant *Cardamine pensylvanica*. Four replicate populations of *C. pensylvanica* were grown in growth chambers under three different nutrient levels but with all other environmental conditions held constant. We analyze the resulting time series using generalized additive models and perform stability analyses using Lyapunov exponents. Further, we test whether the proposed mechanism, delayed density dependence caused by maternal effects, is operating in our system by experimentally manipulating maternal density and assessing the resulting offspring quality. Our results show that that increasing the frequency of nutrients causes plant population dynamics to shift from stable to damped 2-point oscillations to longer cycles. This shift in population dynamics is due to a shift at high nutrients from populations being regulated by first order density feedbacks to being regulated by both first order and second order density feedbacks. A consequence of these first order and second order feedbacks was an increase in cycle lengths as demonstrated by the presence of complex eigenvalues. A short-term experiment confirmed that when grown under high nutrients, the density of maternal plants strongly affected offspring size, providing a mechanism whereby these second order density feedbacks could operate. Our results demonstrate that increasing nutrient frequency results in a qualitative shift in dynamics from stable to longer cycles.

Keywords *Cardamine pensylvanica* · Complex cycles · Long-term experimental dynamics · Nutrients and plant dynamics · Plant population dynamics

Electronic supplementary material The online version of this article (doi:10.1007/s10144-013-0392-3) contains supplementary material, which is available to authorized users.

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Introduction

Models are important tools for analyzing and understanding the dynamics of weedy populations (Freckleton and Stephens 2009). Although an important tool for understanding and predicting population growth, there is a paucity of models that deal with the long-term predictions of population dynamics and very few models are fit to long-term empirical data (Holst et al. 2007; Freckleton and Stephens 2009). Furthermore, models of weed population dynamics are often fit for only one environmental condition (Freckleton et al. 2008). Yet, population dynamics and the generating mechanisms may vary greatly for different environmental conditions.

Ultimately, understanding the population dynamics of plants is fundamental to our ability to manage and predict

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ecosystem response, especially in light of human alteration of climate and nutrient cycles (Cao and Woodward 1998; Luo 2007). The continued enrichment of ecosystems by agricultural runoff can cause profound changes in plant community composition, but less well-known is whether these enriched systems will also have altered population dynamics. If nutrient enrichment induces higher population growth rates, populations grown under nutrient enriched conditions may overshoot environmental carrying capacity, leading to population cycles. A well-developed theoretical literature posits that increased population growth rates causes populations to be stable, undergo cycles of increasing length, and eventually exhibit deterministic chaotic fluctuations (May 1974, 1975). Weedy plant populations incorporate many of the traits known to induce cycles, such as high per capita seed production, changes in individual growth, and reproduction in response to changes in resource availability (Baker 1965; Westoby et al. 2002; Reich et al. 2003; Moles and Westoby 2004, 2006; Sutherland 2004; Deegan et al. 2007). However, there has been considerable skepticism about whether cyclical and/or complex chaotic dynamics can occur in plant populations (Freckleton and Watkinson 2002). The rationale behind these arguments rests largely on the idea that plant growth is highly plastic, so effects of crowding are less drastic than assumed by simple models. Yet, cyclical dynamics have been documented in several short-lived weed populations (Gonzalez-Andujar et al. 2006; Pardini et al. 2009), and chaotic dynamics have been predicted for a perennial grass species subject to high nutrient enrichment (Tilman and Wedin 1991). In a Minnesota old field, increased nitrogen caused the perennial grass, *Agrostis scabra* to have a steep decline in biomass triggered by increased litter production at high nutrients, thus setting up a delayed feedback that simple difference delayed models indicate would produce chaotic dynamics (Tilman and Wedin 1991). Such delayed feedback relationships may also occur in weedy annuals, primarily through maternal effects, giving these systems the potential to cause complex and even chaotic dynamics (Crone 1997a). However, conclusions about plant population dynamics depend on the models used to interpret them (Turchin and Taylor 1992; Crone and Taylor 1996).

In this study, we make use of a model experimental system of weedy annual plant populations to determine how increased nutrient inputs affects their population dynamics, and whether increased nutrients destabilizes the dynamics in accordance with population dynamics theory. Our approach is to experimentally alter nutrients to create conditions under which cyclical dynamics are more likely, primarily because a broad range of population models predict less stable dynamics in more enriched systems (Rosenzweig 1971; May 1974). Thus, instead of directly manipulating individual vital rates to fit the functional form of a predetermined specific model, we carefully control environmental variation, but allow plant reproduction and dispersal to occur naturally. The resulting time series are analyzed using tools from dynamical systems theory, rather than fitting a particular model to the time series data. The use of a flexible model structure combined with stability analysis using Lyapunov exponents allows us to more accurately determine dynamics from experimental data. Further, we test whether the proposed mechanism, delayed density dependence caused by maternal effects, is operating in our system by experimentally manipulating maternal density and assessing the resulting offspring quality.

Methods

Experimental populations were taken from more than 100 individuals from each of three long-established greenhouse populations of *Cardamine pensylvanica* (Brassicaceae), an ephemeral weed of damp habitats (Al-Shehbaz 1988), and established in growth chambers at the University of Vermont in November 1996. We used greenhouse populations as seed sources because plants in these populations are self-fertile and have no specific germination or flowering requirements, and had spent many generations in environments similar to our experimental conditions (see Crone and Taylor (1996) for a more complete description). Four replicate populations were grown at three different nutrient treatments for 18 generations under constant conditions in environmental growth chambers. Although 18 generations is a short time series for dynamical system theory, it represents a long time series for studying weed dynamics where data is typically on the order of 3–5 years (Holst et al. 2007). We varied the frequency of nutrient addition to our experimental populations to simulate different levels of nutrient enrichment. We changed the frequency of application of the nutrients (rather than the level); this may more accurately simulate agricultural runoff that enters a field after a rainfall event. Half-strength Hoagland's solution was applied to the experimental populations on the following schedule: once (a), three times (b), and seven times per week (c) via an aqueous nutrient medium in the morning It was inappropriate for us to include a control treatment of no nutrients because we used a non-nutritive media and plants needed at least some nutrients to survive. In the afternoon, plants were given pure water, preventing toxic nutrient concentrations developing within the experimental populations.

Each replicate population consisted of a set of 16 pots arranged in a long narrow array (Crone and Taylor 1996) (2 pots × 8 pots) (Fig. 1). Pots were 2.5 cm diameter by 10 cm deep tubular pots (RL 200 Conetainers, Stuewe and Sons, Corvallis, OR, USA). The populations were watered

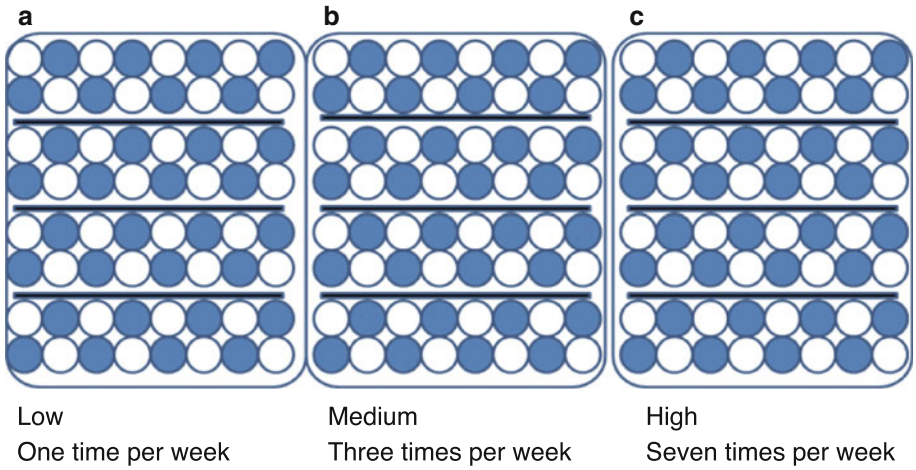

Fig. 1 Set up of experimental populations. Four replicate populations were grown at three different nutrient treatments for 18 generations under constant conditions in environmental growth chambers. Nutrient treatment consisted of nutrients applied once **a** three times **b** and seven times per week **c** via an aqueous nutrient medium in the morning. Plants occupied the shaded and white cells in alternating generations (see "Methods")

from the bottom by filling a system of interconnected tanks until the pots were saturated and then draining the system. Populations were isolated from each other by clear plexiglass barriers.

Replicate populations were initialized with seedlings of *C. pensylvanica* taken from stock populations grown under constant (growth chamber) conditions. Details of the seed source can be found in Crone and Taylor (1996). The original seed source was taken from greenhouse populations of *C. pensylvanica* because these populations did not exhibit dormancy (Crone and Taylor 1996). Dormancy would have complicated both the experimental protocol and the models we were testing. We considered that any ungerminated seeds were dead but we cannot rule out that some small fraction of our assumed dead seeds were dormant. Seeds from these populations can germinate within a week of reaching a suitably moist environment and individuals begin to set seed about 2 months after germination. One seedling was placed in each of eight pots in a zig-zag pattern (shaded circles in Fig. 1). The remaining pots contained vermiculite but no plants (white circles in Fig. 1). Seedlings that died were replaced in order to keep the initial starting conditions constant. Thus, the starting conditions for our experimental populations consisted of one plant per pot and eight plants per population and four replicate populations per treatment. The plants then went through their entire life-cycle (growth, flowering, seed set, dispersal) without further experimental interference. Seeds dispersed throughout the experimental populations through explosive dehiscence of individual seed pods at maturity (see Crone and Taylor (1996)). Since there was temporal variation in when siliques dispersed their seeds, we had to choose a time in which to stop one generation and initiate a new generation; we set this time at when 80 % of siliques had dispersed their seed because this captured the majority of the seeds and prevented generations from becoming asynchronous. Thus, we initiated a new generation when we determined that 80 % of the siliques had dispersed their seeds. Once dispersal was 80 % complete, the original pots (shaded in Fig. 1) were removed, and replaced with pots containing fresh vermiculite; meanwhile, the remaining pots (white in Fig. 1) contained the seeds for the subsequent generation. Each generation ran for approximately 45 days. This procedure was continued for 18 generations. Nutrients were changed once per week and the system was cleaned to keep conditions as constant as possible. Growth chambers were maintained at constant temperature, humidity and light level (550 umol m^{-2} s^{-1}, 18 °C, 18 h daylight, watered 4 × per day) to ensure that fluctuations in population size reflected endogenous population feedback, as opposed to changes in environmental conditions.

We tested whether nutrient enrichment altered population dynamics in two ways. First, we compared qualitative patterns of population dynamics using MANOVAs. These analyses excluded the transient period during the first five generations. We compared autocorrelation functions (ACFs) among treatments. In general, ACFs indicate cyclical or chaotic dynamics if there is a negative correlation at a low lag, followed by positive correlations at higher lags. We compared ACF patterns across treatments using MANOVAs in which point estimates of the ACF at lags 1–6 were entered for each population. Following significant overall differences among treatments, we tested which lags had correlations different from 0 in each treatment. For medium nutrient populations, ACFs were clearly heterogeneous across treatments. As a result we analyzed three cyclical populations separately from the acyclical population. We also used a MANOVA to test for overall differences in qualitative descriptors of dynamics (average population size, standard deviation of population size and cycle period, calculated as two-times the first local minimum in the ACF). Differences in dynamics among treatments likely affect the variance, as well as the mean of these derived statistics across treatments. For example, populations characterized by white noise might have less

structured ACFs than strongly cyclical populations. Therefore, we verified analytical test statistics (Wilks' λ and Pillai Trace) by randomizing data vectors among treatments, and comparing test statistics for actual data sets to 10,000 bootstrapped replicates.

Second, we used generalized additive models (GAMS) (Hastie and Tibshirani 1990; Wood 2006) to estimate relationships between population growth rate and population size. Specifically, we modeled population growth rates $[\ln(N_t/N_{t-1})]$, as a function of direct density dependence, $[\ln(N_t/N_{t-1})] = f(N_t)$, i.e., first order dynamics, and/or delayed density dependence $[\ln(N_t/N_{t-1})] = f(N_{t-2})$, i.e., second order dynamics. We fit different density feedback terms, $f(N_t)$ and $f(N_{t-2})$, to pooled observations from each nutrient treatment (thin plate regression splines, estimated using the mgcv package in R). In keeping with our empirical approach of not specifically manipulating experimental parameters such as growth rate, r, or density dependent terms, we used GAM's rather than fit specific models (i.e., logistic, Ricker, Gompertz) because GAM's do not assume any specific model a priori. However, maximum likelihood methods were used to fit logistic and Ricker first order and second order density dependent models and these models did not adequately fit the data (E. Crone, unpublished data).

In addition to testing statistical significance of GAM terms, we used fitted GAMs to evaluate dynamical stability. We simulated stochastic population trajectories using the predict.gam function to calculate population growth rate as a function of N_{t-2} and N_{t-1}, then adding stochastic variance estimated from the mean squared error around fitted GAMs (See Electronic Supplementary Material, ESM). We used the resulting time series from these simulations to test for chaotic population dynamics using Lyapunov exponents (LEs), a tool from dynamical systems theory, which measures how rapidly small deviations in initial conditions grow with time (Alligood et al. 1996). Negative LEs indicate that dynamics eventually converge to equilibria or stable cycles, while positive LEs signify chaotic dynamics. LEs close to zero suggest "quasi-chaotic" dynamics (Turchin and Ellner 2000) and indicate conditions in which stochastic fluctuations can push populations into the chaotic regime. In addition, LEs can also be calculated directly from measured data using the method of Rosenstein et al. (1993). Using the model free method of Rosenstein et al. (1993), the three treatments were all found to result in slightly positive LEs, but the results were deemed inconclusive given the small sample size (4 replicates of 18 generations) and the sensitivity of the method to any kind of stochastic noise (demographic or environmental). Thus, we only interpreted the LE's calculated from synthetic data created by simulation models fit to the measured data.

We also characterized dynamical stability by recording the proportion of negative leading eigenvalues of the Jacobian stability matrix (indicative of 2-point cycles or damped 2-point cycles), and the proportion for which the leading eigenvalue was complex (indicative of longer period cycles, e.g., Hopf bifurcations; see, e.g., Crone (1997b)). We evaluated model selection uncertainty in these simulations by fitting models to 10,000 bootstrapped data sets, created by sampling N_t, N_{t-1}, N_{t-2} triplets from data in each treatment, with replacement. For each bootstrapped data set, we retained only statistically-supported smoothed functions ($P < 0.10$ or $P < 0.05$). Results did not change as a function of significance threshold, so we present results for $P < 0.10$. We then simulated a stochastic time series for each bootstrapped model (10,000 total simulated time series for each nutrient treatment).

We also tested whether delayed density dependence occurs via maternal effects; plants in crowded conditions produce smaller seeds that grow into smaller plants in the next generation (Crone 1997a). We sowed *C. pensylvanica* seeds at 5 densities: 10, 50, 100, 250, 500, and 800 seeds per pot. Each density was planted in 6 pots at each of the three nutrient treatments (6 pots $\times$ 5 densities = 30 pots per nutrient treatment). In the parental generation, we recorded the number of plants that survived from each sowing density. Sowing density treatments successfully produced a range of adult plant densities: low: 1–13 adult plants/pot, medium: 1–16 adult plants/pot; high: 1–28 adult plants/pot. We harvested seeds from these parents, and grew three seeds from each parent pot at low density. Following germination, we weeded seedlings to one plant per pot. Offspring plants were allowed to grow to maturity, harvested, and oven-dried at 58 °C for biomass measurement.

We tested for the significance of maternal effects by fitting GAMs to offspring size as a function of sowing density and adult plant density in each nutrient treatment.

Results

All populations in all treatments fluctuated over time, in spite of the relatively constant environmental conditions (Fig. 2), with an initial peak in population size, followed by a decline to steady state fluctuations starting in about the fifth generation. Increasing frequency of nutrients altered patterns of population dynamics over time, as measured by average population size, standard deviation and autocorrelation function (Table 1; Fig. 2). Increasing nutrients elevated both average and variance in plant abundance (Table 1). Under low nutrients, ACFs of all four replicate populations were consistent with the expectations of what one would observe when there is no structure to the ACFs

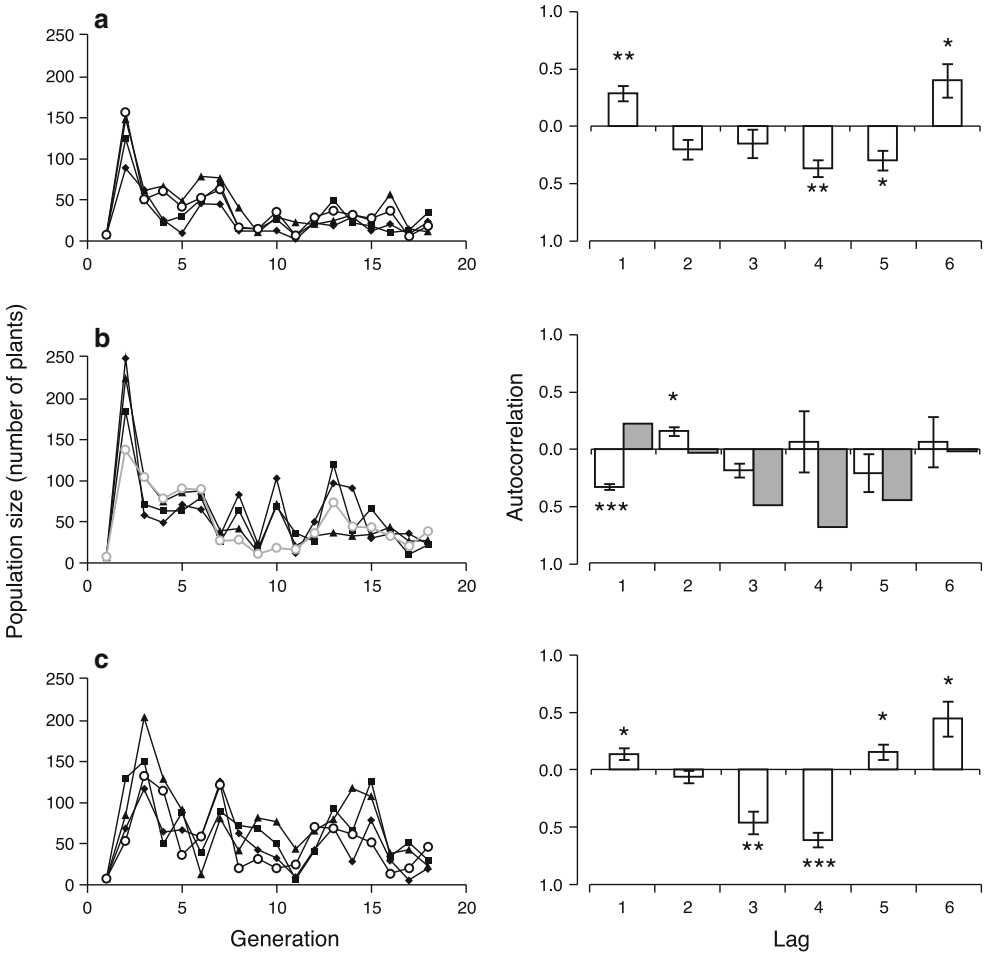

Fig. 2 Population size (*left*) and autocorrelation function (*right*) of *C. pensylvanica* populations in **a** low nutrient, **b** medium nutrient, and **c** high nutrient treatments. Population size is the number of plants in each of four replicate populations. ACFs are averages across the four populations ±1 SE in high and low nutrients. In medium nutrients, three populations displayed 2-point cycles, but one did not. The outlier population is identified by gray lines and separate gray ACF bars. Deviations from 0 for autocorrelations were identified using 1-sample *t* tests ($0.15 > P \geq 0.10$; *$0.10 > P \geq 0.05$; **$0.05 > P \geq 0.01$; ***$0.01 > P$)

Table 1 Comparison of descriptors of population dynamics across nutrient treatments

		Wilks λ		Pillai trace		Boot-strap	Nutrient treatment averages*		
	df	*F*	*P*	*F*	*P*	*P*	Low	Med	High
A. MANOVA									
ACF	2, 9	3.9	0.031	4.0	0.01	0.014	N/A	N/A	N/A
Statistics	6, 14	4.9	0.007	4.8	0.005	0.004	N/A	N/A	N/A
Pillai trace	6, 16						N/A	N/A	N/A
B. Individual statistics									
Number of plants	2, 9	12.5	0.003				25.6^{a}	41.2^{b}	55.1^{b}
SD	2, 9	7.2	0.014				16.0^{a}	$23.6^{a,b}$	31.7^{b}
CV	2, 9	0.4	0.700				0.6^{a}	0.6^{a}	0.6^{a}
Cycle period	2, 9	5.0	0.034				7.0^{a}	3.5^{b}	7.5^{a}

* Means with the same letter do not differ significantly

^{a,b} Denotes whether or not the means were statistically different from each other for the different treatment averages

(Fig. 2). Three of four medium-nutrient nutrient populations demonstrated two-point cycles, with ACFs alternating between positive and negative correlation ACF's at even and odd lags; the fourth resembled low nutrient populations (Fig. 2). Under high nutrients, ACF patterns tended to alternate between positive and negative, but at longer intervals. Across populations, autocorrelations were significantly negative at lags 3 and 4 and tended to return to positive at lags 5 and 6 (Fig. 2).

Table 2 GAM analysis of plant density vs. population growth rate

Treatment	Coefficient			SE
A. Parametric coefficients (mean $\ln[N_t/N_{t-1}]$)				
Low nutrients	−0.30			0.10
Medium nutrients	−0.06			0.08
High nutrients	0.15			NA
	Estimate	*df*	*F*	*P*
B. Smoothed terms (direct and delayed density-dependence)				
Low N_{t-1}	3.7	8	6.1	<0.001
Medium N_{t-1}	3.1	7	7.4	<0.001
High N_{t-1}	4.7	9	4.8	<0.001
Low N_{t-2}	1.0	3	1.3	0.293
Medium N_{t-2}	1.3	3	2.1	0.096
High N_{t-2}	5.7	9	2.2	0.024

Fitted GAMs indicated that nutrient enrichment qualitatively changed density dependence. Direct density dependence influenced population growth rates in all three nutrient treatments, with effects of similar magnitude across treatments (Table 2; Fig. 3). The main difference between the low and medium nutrients was in the average abundance of the populations and the wider confidence limits associated with the low nutrient populations compared to the medium nutrient populations. Delayed density dependence was not significant in low-nutrient populations, and marginally statistically significant but very weak in medium-nutrient populations (Fig. 3). High nutrient population dynamics were driven by both direct and delayed density dependence, and the effects of direct and delayed density dependence were of similar magnitude (Table 2; Fig. 3).

These differences in the amount of direct and delayed density dependence altered population dynamics. Mean LE's became less negative with increased nutrients: $\bar{x} = -2.6$, SE $= 0.0281$, $\bar{x} = -2.4$, SE $= 0.025$, and $\bar{x} = -1.8$, SE $= 0.021$ in low, medium and high treatments, respectively (Fig. 4). Although the overall dynamics predicted by the simulations was stable, a small percentage of stochastic simulations led to positive LE's in each treatment: ($\sim$0.5 % were positive in low nutrients, <0.01 % were positive in medium nutrients, and $\sim$1 % were positive in high nutrient populations). Medium-nutrient populations

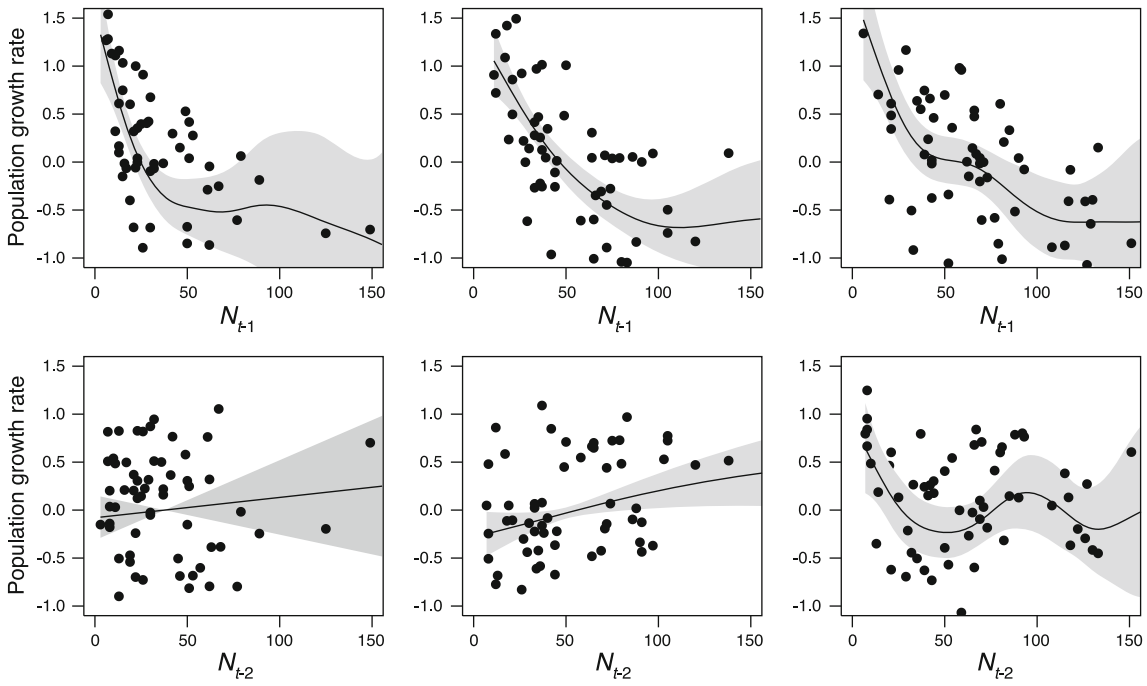

Fig. 3 Partial regression plots for GAM functions for direct (N_{t-1}) and delayed density (N_{t-2}) dependence in each treatment. The *x*-axis is the prior density (N_{t-1}) for direct density dependence and for delayed density dependence (N_{t-2}) and the *y*-axis is the population growth rate ($\ln N_t/N_{t-1}$). The *line* is the fitted GAM function, the *shaded area* is the 95 % confidence limits and the *black dots* are the actual points

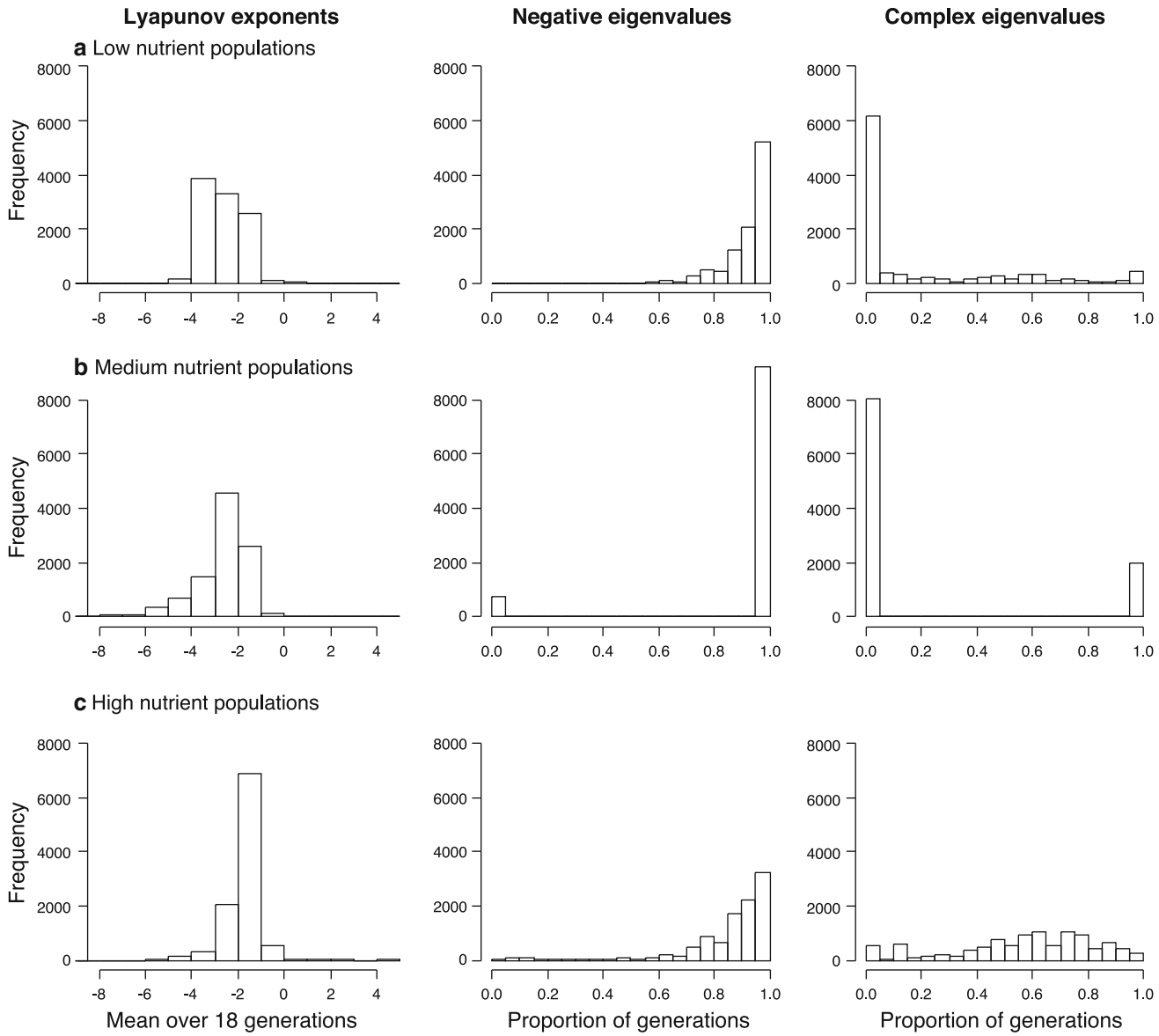

Fig. 4 The dynamics properties of GAMS fitted to data from the three different nutrient treatments. Lyapunov exponents characterize the tendency for population trajectories to be chaotic i.e., divergence over 18 generations. Negative leading eigenvalues characterize the tendency for populations to have two-point cycles or damped two-point cycles; this was evaluated at every generation during the simulation. Complex leading eigenvalues characterize the tendency for populations to undergo longer cycles or damped cycles; these were also calculated during each generation during the simulation

were consistently characterized by damped 2-point oscillations (negative, real leading eigenvalues); high nutrient populations were characterized by longer-period oscillations (complex leading eigenvalues). Dynamics differed most among replicate simulations for low nutrient populations (Fig. 4). Visual inspection of bootstrapped data sets suggested this variation is due to the broad confidence limits around the direct density feedback term (see Fig. 3).

Our maternal density experiment supports the results from our long-term data (Table 3). Under low nutrient conditions, parent density did not affect offspring size (GAM of adult plant density vs. offspring size: $F = 0.4$, $P = 0.53$, Pearson correlation: $r = 0.10$). Under medium nutrient conditions, parent density weakly affected offspring size, closely mirroring the marginally significant, positive delayed feedback we observed in analysis of population dynamics (GAM of adult plant density vs. offspring size: $F = 2.5$, $P = 0.12$, Pearson correlation: $r = 0.05$). Under high nutrient conditions, crowded parents produced smaller offspring (GAM of adult plant density vs. offspring size: $F = 3.4$, $P < 0.01$, Pearson correlation: $r = -0.03$). GAM models confirm that nutrient enrichment

of parental plants results in smaller offspring size (Fig. 5). Such a change in the quality of the offspring at high density results in a qualitative shift in population regulation for this species, from a first order density feedback to being regulated by both a first order and second order density feedback.

Discussion

Here we demonstrate that increasing nutrients changes how population regulation occurs in this experimental weedy system. As expected, enhanced nutrients increased the maximum population growth rate but more interestingly, at higher nutrients populations switch from being regulated only by first order density dependent feedbacks to being regulated by both first order and second order density feedbacks (Ehrlen 2000). Delayed feedback mechanisms have been found in other experimental plant populations (Gonzalez-Andujar et al. 2006) and can be associated with maternal environmental effects that affect offspring quality (Crone 1997a; Beckerman et al. 2002; Plaistow et al. 2006). Maternal plants grown at high density produce smaller offspring, which can result in fewer viable seeds the next generation producing a delayed density feedback (Beckerman et al. 2002; Plaistow and Benton 2009).

Table 3 Effects of maternal density on offspring biomass

	Estimated *df*	*F*	*P*
A. Full models (maternal seed and adult density vs. offspring size)			
Low nutrients			
Seed density	1.0	0.23	0.633
Adult density	1.0	0.16	0.689
Medium nutrients			
Seed density	1.0	0.61	0.441
Adult density	1.0	2.97	0.089
High nutrients			
Seed density	1.0	5.05	0.038
Adult density	7.2	4.41	<0.001
B. Univariate models (maternal adult density vs. offspring size)			
Low nutrients	1.0	0.40	0.527
Medium nutrients	1.0	2.49	0.118
High nutrients	7.9	4.34	0.002

The alteration in density feedbacks at higher nutrient levels causes populations to undergo longer cycles as demonstrated by the complex eigenvalues in the high nutrient treatment. This switch to longer cycles denotes less predictable dynamics at higher nutrient levels providing the first empirical documentation in plants that enriching systems lead to loss of stability as predicted by paradox of enrichment (Rosenzweig 1971; Scheffer et al. 2009).

Chaotic dynamics are predicted to occur in models that include a delayed feedback term (Crone 1997b). Yet, despite the significance of the delayed feedback term in the GAMS models, the stochastic simulations of these parameters indicated only a small percent ($\sim$1 %) of parameter combinations would result in chaotic dynamics. Nevertheless, the longer cycles present under the high nutrient treatment suggest that understanding and predicting weedy populations under enriched conditions may prove more challenging given the inherently longer cycles. More importantly, our approach of combining long-term experiments under controlled conditions and analyzing the resulting time series with flexible semi-parametric models such as GAMS (Wood 2006) as opposed to preselecting the model structure revealed a fundamentally new mechanism by which plant regulation can occur in the face of increasing nutrient enrichment and, one that could not have been anticipated prior to conducting the experiment. Our approach provides an alternative way to analyze and predict population dynamics that does not rely on detailed demographic submodels. Our hope is that this approach can be profitably applied to any plant population for which a moderate size time series is available.

We based our analyses of dynamical properties on fitted GAMs, which, like all models, have particular strengths and limitations. GAMs are a flexible way to model the deterministic component of population dynamics, and were

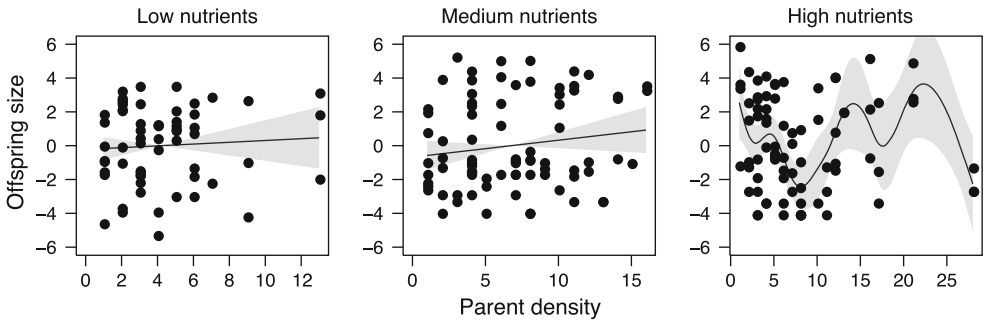

Fig. 5 Offspring size [ln(g)] as a function of parental density for the low, medium and high nutrient treatment. The grey area is the 95 % confidence limits. The scales of the horizontal axis label differ

very effective at capturing the signal of increased delayed feedback at higher nutrient levels. However, GAMs are not as flexible as some other methods for modeling the stochastic component of population dynamics. Our simulation results include two kinds of variance. First, we estimated model selection and parameter estimation uncertainty by bootstrapping data. Visual inspection of results indicates that this uncertainty is responsible for most of the scatter in dynamical statistics (histograms in Fig. 4). Second, we added a stochastic term at each generation in simulations, based on residual variance around fitted models. This step is a simple phenomenological way to include both demographic and environmental stochasticity, because it includes all variance around expected growth rates. Visual inspection of simulated time series indicates that this form of stochasticity did not fundamentally alter stability properties, e.g., the Jacobian matrix was relatively insensitive to the magnitude of the stochastic term. In addition, a third kind of variance in which the functional form of density dependence varies stochastically over time (Turchin 2003; Freckleton and Stephens 2009) can lead to shifts between stable and unstable parameter regimes (quasi-chaos sensu Turchin and Ellner 2000). One limitation of the GAM method is that, because smoothed functions are nonparametric, it is not mathematically natural to explicitly model stochastic variation in model parameters per se. Our bootstrapping procedure provides an absolute *minimum* estimate of the amount of variation that we would observe in parameter values, analogous to the relationship between standard error and standard deviation. A more sophisticated treatment of both deterministic and stochastic dynamics is a key area of population ecology that requires further analytical and empirical work (Turchin 2003).

Given these limitations of model-fitting, what can we conclude from the time series themselves? First, populations started with a strongly synchronous rise, then fell in population size. Over time, fluctuations dampened than became less synchronous. Initial synchrony makes sense because populations started with identical starting conditions, and 18 generations is probably not long enough for populations to desynchronize. We also observed a surprisingly large amount of stochastic variation around deterministic dynamics, given that populations were grown under constant environmental conditions. We cannot rule out the possibility that populations were influenced by some, unmeasured, driving variables but it is unlikely that the subtle differences in temperature, humidity or light conditions present in the growth chambers were sufficient to cause changes in plant productivity (J. Molofsky, personal observation). However, a more likely possibility is that populations developed spatial structure over time (Molofsky and Ferdy 2005). Initially, plants were distributed evenly among pots, which would minimize competition. Over time, variance in plant density increased, leading to among-pot heterogeneity in plant density, and, at high nutrients, within-pot variation in plant quality (plants dispersed from sites with different maternal densities). In contrast to this hypothesis, dispersal among pots could homogenize the density among pots within a population (Pacala and Silander 1985) so that spatial ACFs fitted to our populations may not differ significantly from those expected from a single large population. Therefore, we are not sure if spatial heterogeneity actually contributed to noise in the demographic data.

Our results strongly echo predictions from simple deterministic models, i.e., longer and unstable cycles under higher conditions that would lead to higher growth rates (May 1974, 1975). However, we found that fitting these simple deterministic models—which do not include delayed density dependence—directly to our time series provided a poor fit to our population data. The simple models that motivated our experiments included only first-order feedbacks, i.e., greater ability to overshoot carrying capacity at high plant densities. In our populations, increasing the population growth rate also increased the importance of second order feedbacks. At high nutrients, maternal effects became more important. As delayed density dependence becomes more important, dynamics become unstable (Beckerman et al. 2002). Thus, the reason for the change in dynamics is fundamentally different than the explanation provided by earlier models (May 1974, 1975), even though the qualitative predictions of these models are the same.

Effects of nutrients on plants are widely studied at the individual level and at the community level but less well studied at the population level. At the individual level, plants have been shown to grow larger at increased nutrient concentration (Taiz and Zeiger 2002). In our study, plants were larger at the higher nutrient levels initially; however, because of the delayed feedback term, plants grown at higher nutrients produced plants in the second generation that were smaller than would be predicted from single generation studies. These second generation effects of nutrients on plant growth destabilize populations, pushing them into an unstable regime where slight instances of demographic stochasticity can destabilize the dynamics. Plant community studies indicate that intermediate levels of nutrients produce more diverse plant communities (Rajaniemi 2003). In our single species study, the most stable populations were found at the intermediate nutrient level with populations less stable at both lower and higher nutrient levels. In addition, populations subject to intermediate levels of nutrients were stable but cycled. Theoretical and empirical studies have shown that fluctuating populations can enhance diversity (Huisman and Weissing 1999; Chesson 2000; Dakos et al. 2009). However, it is not clear if the kinds of patterns shown here within species are responsible for the relationship at the community level.

In agricultural cropping systems, the dynamics of weed populations are often unpredictable and thus hard to control (Freckleton et al. 2008). Our results highlight the difficulty of managing fast-growing weeds in agricultural and natural systems; if weed populations have long cycles, future population sizes are inherently difficult to control, even if population biology is well understood. Furthermore, in the presence of strong density dependence, control measures can have unexpected effects; if increasing population growth rates at low density can shift populations from cyclical to longer cyclical dynamics, then reducing low-density population growth rates, even by directly killing plants, could reduce extinction risk (see Pardini et al. 2009). Finally, if agricultural systems are subject to increased fertilization, and runoff increasingly impacts ecosystems, dynamics may become increasingly unpredictable, increasing the likelihood of unexpected outbreaks of weedy plant populations. Overall, the world-wide increase of weedy species (Lodge et al. 2006) demonstrates the need for predictive models to manage these populations (Hulme 2006). Yet few predictive models of weed populations exist (Freckleton and Stephens 2009). Our results show that strong delayed density dependence should be considered in these models, a radical change from most approaches now used to guide weed management (Holst et al. 2007). Our approach of combining GAMS on time series data, simulating the resulting models with some stochastic variation and analyzing the results using tools from complex systems theory can provide an alternative modeling approach to understanding the dynamics of weeds.

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