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Research article

Effects of intraspecific variation in a native species' phenology on its coexistence with non-native plants

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Intraspecific trait variation is ubiquitous and is likely to influence species coexistence. Despite theoretical progress, empirical work on the effects of intraspecific variation on the dynamics of competing species is rare. This is because of the formidable empirical requirements necessary to link intraspecific variation in species' functional traits with intraspecific variation in the demographic and competitive rates that mediate coexistence. Here we partially overcome these challenges to determine how intraspecific variation in reproductive phenology in a native Californian annual plant species *Lasthenia californica* affects its ability to coexist with two non-native species *Bromus madritensis* and *Lactuca serriola* that display contrasting phenological patterns. Using data from a field experiment, we empirically parameterize a model of competitive population dynamics, accounting for the effects of intraspecific phenological trait variation on the native species' response to both intra- and interspecific competition. We find that intraspecific variation in phenology drives differences in the native species' response to competition. Moreover, simulations of the parameterized model show that this variation improves the competitive performance of the native species. This occurs because of the effects of nonlinear averaging mediated by a nonlinear, concave-up competition function that is a general feature of competition across a wide range of taxa. While intraspecific variation improves competitive performance, we also find that the magnitude of the benefit is predicted to be insufficient to prevent competitive exclusion against the non-native species with early phenogy *Bromus*. Against the second non-native species with later phenology *Lactuca*, intraspecific variation is predicted to result in coexistence where competitive exclusion would otherwise occur, but we could not rule out alternative qualitative outcomes for this interaction.

Keywords: biological invasions, coexistence theory, competitive ability, intraspecific variation, Jensen's inequality, niche differences, nonlinear averaging, phenology, trait variation

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Introduction

Differences in trait values between individuals within species account for a large fraction of the total trait variation in ecological communities worldwide (Albert et al. 2010, Fajardo and Piper 2011, Siefert et al. 2015). Over the last decade there has been renewed interest in the consequences of this intraspecific variation for the dynamics of ecological communities (Bolnick et al. 2011, Violle et al. 2012, Des Roches et al. 2018). Intraspecific variation resulting from genetic differences between individuals or phenotypic plasticity results in differences in individual-level vital rates (Ortego et al. 2007, Lankau 2009), which are then expected to affect community dynamics (Crutsinger et al. 2006, Bolnick et al. 2011, Violle et al. 2012). There have been several conceptual and theoretical contributions that have identified different mechanisms by which intraspecific variation is expected to influence community dynamics (Bolnick et al. 2011, Violle et al. 2012, Hart et al. 2016, Uriarte and Menge 2018, Steinmetz et al. 2020). However, very few empirical studies have attempted to predict the effects of intraspecific variation on the outcome of interspecific competition in the field (Lankau 2009, Clark 2010), particularly in the context of recent developments in coexistence theory (HilleRisLambers et al. 2012).

Broadly considered, intraspecific variation can influence dynamics via evolutionary and/or ecological pathways (Bolnick et al. 2011). Recent theoretical work demonstrates that the purely ecological effects of intraspecific variation can increase the performance of competing species, but that on balance, intraspecific variation tends to reduce opportunities for species coexistence at local scales (Lichstein et al. 2007, Barabás and D'Andrea 2016, Hart et al. 2016). These effects occur because per capita offspring production in response to competition is commonly a nonlinear function of species-level competitive rates (i.e. competition coefficients; Bjørnstad and Hansen 1994, Hart et al. 2016). When there is intraspecific variation in competitive rates, these nonlinear relationships are subject to the often counter-intuitive effects of nonlinear averaging that apply as a consequence of Jensen's inequality (Jensen 1906, Bjørnstad and Hansen 1994, Ruel and Ayres 1999). By modifying offspring production in response to competition via the effects of nonlinear averaging, intraspecific variation influences the ability of species to coexist (Bjørnstad and Hansen 1994, Hart et al. 2016).

Importantly, in the vast majority of models of competitive population dynamics across a range of taxa, the relationship between competitive ability and offspring production is concave-up (i.e. the second derivative of the growth function with respect to the competition coefficients is positive; Ricker 1954, Beverton and Holt 1957, Leslie and Gower 1958, Law and Watkinson 1987, Pacala and Silander 1990, Inouye 2001, Melbourne and Hastings 2008, Levine and Hille Ris Lambers 2009, Hart and Marshall 2013). This does not preclude concave up (or more complex) functional forms describing components of ecological dynamics (e.g. type II and type III functional responses; Bjørnstad and Hansen 1994, Ruel and Ayres 1999), but such functional forms appear to be theoretically and empirically rare as descriptors of the effects of competitive ability on population growth. This consistency in the shape of common competition functions is important because a concave-up relationship means that variation in competitive ability within a population increases a species' mean per capita offspring production compared to populations with the same mean competitive ability but with no variation (for a thorough description of these effects, see Fig. 1 in Hart et al. 2016). Yet while these nonlinear averaging effects are theoretically well understood, there have been few attempts that we are aware of to empirically quantify how natural levels of intraspecific variation might mediate competitive outcomes via nonlinear averaging in the field (Hausch et al. (2018)

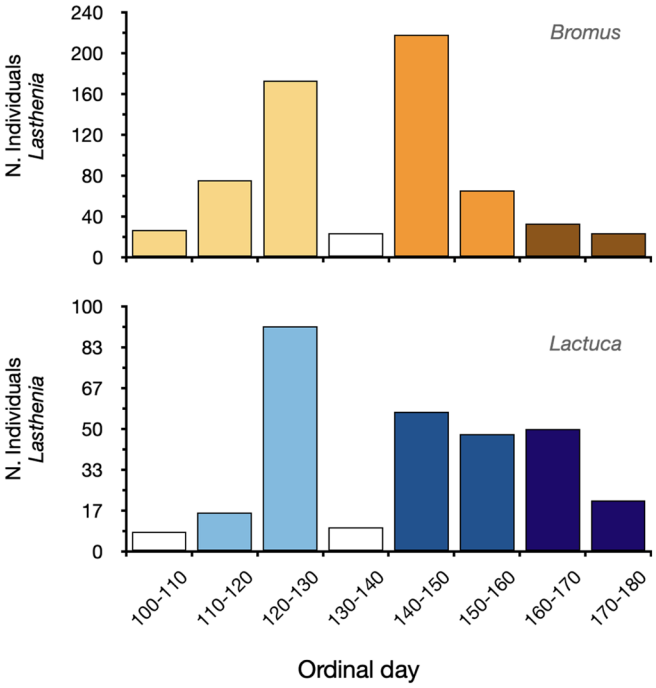


Figure 1. Histograms showing intraspecific variation in reproductive phenology in *Lasthenia californica* when competing against *Bromus madritensis* (a non-native species with similar average phenology to *Lasthenia*) and *L. serriola* (a non-native species with later average phenology than *Lasthenia*). Reproductive phenology was defined as the date when 50% of an individual's flowers were developing fruits. Histograms were created using data from 943 individuals (641 individuals competing against *Bromus* and 302 individuals competing against *Lactuca*). For each non-native species, we selected three phenotypic ranges of *Lasthenia* for which there were sufficient numbers of individuals to estimate competition-model parameters. There were 276, 284 and 57 individuals of *Lasthenia* in the early, middle, and late phenological ranges when in competition with *Bromus*, and there were 108, 105 and 71 individuals of *Lasthenia* in the early, middle and late phenological ranges when in competition with *Lactuca.* These three ranges account for more than 90% of observed individual phenologies in our experiment. Lighter colour represent earier phenological ranges, and no color represent individuals that were not included into a particular phenological range.

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for a laboratory test using one, three, and five genotypes of bean weevils).

There are two major challenges associated with quantifying how intraspecific variation affects competitive outcomes in the field. First, it has not always been straightforward to identify which species-level functional traits strongly mediate species coexistence. This is because functional traits have only rarely been linked to the demographic and competitive rates that mediate species coexistence (Angert et al. 2009). Recent empirical advances, however, have now identified that among a suite of candidate traits, reproductive phenology has consistently strong effects on species coexistence that occur as a consequence of complex combined effects on both niche and competitive differences (Godoy and Levine 2014, Kraft et al. 2015, Pérez-Ramos et al. 2019). Reproductive phenology is certainly not the only trait affecting coexistence, but it is a useful candidate trait with known strong effects on coexistence. At the species level, high phenological overlap is associated with strong plant competition for common resources such as light, water, nutrients and space (Craine and Dybzinksi 2013, DeMalach et al. 2017). Nevertheless, without linking individual-level phenological trait values to individual-level demographic or competitive rates it is difficult to predict how variation in phenology will affect coexistence – leading to a second challenge.

The second challenge arises because empirical and theoretical studies on the ecological effects of intraspecific variation have focused on different components of intraspecific variation. Most empirical studies tend to focus on intraspecific variation in functional traits (e.g. morphological, physiological, phenological or behavioural traits; Violle et al. 2012, Siefert et al. 2015, Fajardo and Siefert 2016), whereas theoretical studies tend to focus on intraspecific variation in competition coefficients (and other demographic rates) in models of competitive population dynamics (Lichstein et al. 2007, Barabás and D'Andrea 2016, Hart et al. 2016, Uriarte and Menge 2018). The challenge for empiricists is to bridge this empirical–theoretical divide by quantitatively linking empirically observed variation in functional traits with empirical estimates of the competition coefficients that determine competitive outcomes. Such a task remains difficult, however. This is because empirically estimating a single competition coefficient tends to require data-intensive regression approaches where focal individuals at low density compete against a gradient of densities of each competitor (Inouye 2001, Hart et al. 2018). The common approach of simply ignoring intraspecific variation requires only a single regression per competition coefficient per species (Inouye 2001, Hart et al. 2018). However, accounting for intraspecific variation significantly amplifies the empirical challenge because separate regressions (i.e. separate competitor density gradients) are required for each level of the functional trait of interest.

Here, we overcome these challenges by combining: 1) data on intraspecific variation in a trait known to influence species coexistence, with 2) empirical estimates of competition coefficients associated with different trait levels, to 3) predict the effects of intraspecific variation on species coexistence. We focus on intraspecific reproductive phenological variation (time of flowering/fruiting) in a native annual plant species *Lasthenia californica* competing against two competitively dominant annual non-native species with contrasted phenology, *Bromus madritensis* and *Lactuca serriola*, in a Californian grassland. We focus on intraspecific variation in phenology both because data are available from previous work, and because phenological traits are less well studied in work on intraspecific trait variation (Siefert et al. 2015, Fajardo and Siefert 2016) despite the fact that differences in phenology between species have been shown to mediate coexistence outcomes (Kraft et al. 2015, Pérez-Ramos et al. 2019). For example, a previous study predicted that average, species-level, differences in phenology would cause the non-native species to exclude the native *Lasthenia* (Godoy and Levine 2014). That study did not, however, account for any potential benefits of intraspecific variation on the persistence of the native species in the face of widespread success of non-native species (Strauss et al. 2006, Strauss 2014, Huang et al. 2018), which is the focus of the current study.

Material and methods

Summary of approach

To determine how intraspecific variation affects the coexistence of native and non-native species we used a combined empirical-modeling approach. In experimental field plots we quantified intraspecific variation in flowering/fruiting time – the reproductive phenological trait we focus on – of the native annual Californian species *L. californica* competing separately against a gradient of densities of the two annual non-native European species, *B. madritensis* (early phenology and similar to *Lasthenia*) and *L. serriola* (late phenology). We note that we did not collect data on the timing of other life-history traits for our species. We simultaneously measured the fecundity of a set of target individuals with different phenological trait values of the native species in these plots. We then fit a model of competitive population dynamics to the fecundity data associated with the different phenological trait values. This procedure allowed us to estimate competition model parameters separately for different phenological trait values of the native species. Using the same approach (but ignoring intraspecific variation) we also estimated flowering/fruiting times and competition model parameters for each non-native species. Finally, using numerical simulations of the parameterized model, we predicted coexistence outcomes between the native and each non-native species, with and without intraspecific variation in the phenological trait of the native species.

Competition experiments

We used data from field competition experiments to parameterize a competition model following methods described

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in Hart et al. (2018). The experimental design consisted of planting *Lasthenia* together with either *Bromus* or *Lactuca* in nine randomly-selected plots assigned to each species pair (i.e. 18 competition plots in total). Plots were circular 0.5 m^2 areas cleared of existing plants and separated by landscape fabric to control weeds. In five of the nine plots assigned to each species pair, 10 g of viable seed was sown per m^2, but with the proportions of each species differing between plots according to a replacement series design (Supporting information). Specifically, these plots were sown with 1.2, 3.2, 7.6, 8.7 and 9.8 g m^{-2} of viable seeds of the non-native species, with seeds of the native *Lasthenia* making up the remaining portion of the 10 g of total viable seed sown. In the remaining four of the nine competition plots for each species pair, viable seeds were sown at either 2 g m^{-2} (in two plots) or 4 g m^{-2} (in two plots). In these plots, we varied seed relative abundance so that both *Lasthenia* and its non-native competitor were sown at either high (0.8) or low (0.2) relative abundance in one of the two plots per density. In addition to the 18 competition plots, to quantify how individuals perform in the absence of competitors we established ten additional plots in which we grew individual plants of each of the three species with no neighboring individuals (i.e. no competition). We achieved this by thinning these ten plots after germination to obtain replicate individuals of each species that were isolated from any neighboring individuals by at least 15 cm, which assumes that the majority of an individual's response to competition is driven by processes occurring within 15 cm of an individual plant. This competitor-free radius has been commonly used in studies of annual plant competition (Levine and Hille Ris Lambers 2009, Kraft et al. 2015, Mayfield and Stouffer 2017), and has been shown to be appropriate for predicting competitive outcomes via parameterized models for several annual plant species (Levine and Hille Ris Lambers 2009).

Overall, our experimental design incorporating a total of 18 competition plots and ten plots where individuals grew alone generated a gradient of competitor densities for each native-non-native pair, as is required to estimate parameters in a competition model (Hart et al. 2018). We note that because our analyses rely on fitting regression models (i.e. our independent variable, density, is continuous), it is more efficient to have more levels of the independent variable (density) than it is to replicate within levels (Cottingham et al. 2005). However, all treatments (species and densities) were randomly assigned to plots to remove effects of confounding variables. Moreover, we did have replicate plants growing in the absence of competitors because this allows us to more accurately estimate the intercept in our regression models, which is important for providing good estimates of a key demographic rate (lambda, λ) in our competition model (Eq. 2).

Experiments were done at the University of California Sedgwick Reserve, California, USA (34°40′ N, 120°00′ W). Plots were established and seeds were sown in October 2010, and trait and demographic data were collected (as described below) between February and August 2011.

Measurements of phenological traits

Reproductive phenology of each species was assessed by recording fruiting and flowering dates of target individuals of all species twice a week from April to August 2011. An individual's reproductive phenological trait was recorded as the date on which 50% of the individual's flowers were developing fruits. For the native *Lasthenia*, we measured fruiting and flowering dates for all individuals (943 individuals in total) across all experimental plots planted with different competitor densities. Most of these measurements (905 individuals) were taken in plots where an exotic species was present, the rest belong to individuals that did not experience competition (38 individuals). In these plots, we measured 641 *Lasthenia* individuals competing against *Bromus*, and 264 individuals competing against *Lactuca*. For the non-native species, we measured fruiting and flowering dates on eight haphazardly-chosen individuals per plot.

We used linear mixed effects models to estimate mean phenological trait values for *Lasthenia* in competition with each non-native species. We included competitor species (*Bromus*, *Lactuca*) as a fixed effect and plot as a random effect in these analyses, and we used a likelihood ratio test to compare differences in phenological timing in *Lasthenia* when in competition with the different competitors. We used Levene's test to compare the variance in phenology for *Lasthenia* when in competition with each of the non-native species. Finally, we compared linear models with and without the effects of species' relative abundance to determine if relative abundance influenced phenology.

Demographic measurements

Demographic measurements were required to parameterize the competition model in order to determine competitive outcomes. To assess fecundity, at the end of the growing season we measured seed production of a haphazardly selected subset of target individuals with different phenological trait values. Estimates of fecundity were corrected for seed viability using established methods (Godoy and Levine 2014). To assess species-level emergence rates we recorded the number of emergent individuals from seeds of all species in repeated censuses of a subset of 14 plots sown with known densities of viable seeds. To assess seed survival rates of each species in the seedbank, we measured the viability of seeds before (October 2010) and after (September 2011) a growing season of burial in ten nylon mesh-bags per species (Godoy and Levine (2014) for methodological details). With this approach, we estimated an average rate per species of seed survival and emergence, but we did not estimate its spatial variation across the experimental area.

Competition model and model parameterization

Using our demographic data, we parameterized a model commonly used to describe the population dynamics of competing annual plant species in the field (Beverton and

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Holt 1957, Leslie and Gower 1958, Law and Watkinson 1987, Pacala and Silander 1990, Levine and Hille Ris Lambers 2009):

$$N_{i,t+1} = (1 - g_i)\, s_i N_{i,t} + \frac{\lambda_i g_i}{1 + \alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}} N_{i,t} \quad (1)$$

In this model, $N_{i,t}$ is the number of seeds of species i in year t, g_i is the germination rate, s_i is the seed survival rate, λ_i is the number of viable seeds produced per individual in the absence of neighbors, and α_{ij} is the per capita effect of a germinant of species j on the seed production of a germinant of species i. We note that α_{ij} can also be described in terms of the sensitivity of species i to competition from species j. The first term in this equation describes the dynamics of the seedbank, while the second term describes production of new seeds after accounting for the negative effects of both intra- and interspecific competition. A second equation with subscripts reversed describes the dynamics of the second species in a pairwise competitive interaction.

We empirically estimated all of the demographic rates and competition coefficients in this model for the native and both non-native species. Because of the very large data requirements for estimating parameters for each level of our phenological trait, it was not feasible to estimate intraspecific variation in the model parameters for the non-native species. Therefore, we focused on the effects of intraspecific variation in the native species, only. We describe the limitations of this necessarily pragmatic approach in the discussion. For all species, germination (g_i) and seed survival (s_i) rates were estimated directly from our field measurements of germination and seed survival, noting that these parameters were estimated at the species level (i.e. we did not estimate intraspecific variation in g_i or s_i even in the native species). In this context, it is more important to note that even if intraspecific variation in g_i or s_i is present, this variation cannot affect the outcome of competition via nonlinear averaging. This is because the relationship between population growth and g_i and s_i in Eq. 1 is linear, thus providing no opportunity for the effects of nonlinear averaging to emerge (Hart et al. 2016). While this is also true of λ_i, estimates of λ_i can influence estimates of the competition coefficients, and so our parameter estimation methods do allow for intraspecific variation in λ_i in the native species.

To estimate λ_i and the competition coefficients, we used maximum-likelihood methods in R (www.r-project.org, function 'optim', method L-BFGS-B and log-normal error structure) to fit our fecundity data, F_i, to the following function:

$$F_i = \frac{\lambda_i}{1 + \alpha_{ii} G_{i,t} + \alpha_{ij} G_{j,t}} \quad (2)$$

where the parameters are as previously described, and $G_{i,t}$ is the number of successfully germinating neighbouring individuals ($=g_i N_{i,t}$) in the plot of each target native and non-native species. Because we ignored the effects of intraspecific variation in the non-native species, for the non-native species we fit the model Eq. 2 with per germinant fecundity (F_i) calculated as the average viable seed production across all the target individuals of each non-native species within each plot. Separate models were fit for each non-native species as the focal species i in Eq. 2.

For *Lasthenia*, ideally we would have estimated competition coefficients for each separate flowering date (i.e. for each level of the phenological-trait value). The difficulty, however, is that a single estimate of each competition coefficient requires a regression approach (Inouye 2001, Hart et al. 2018), which would require several individuals with exactly the same flowering date experiencing different competitor densities (which is the independent variable in the regression). This was not feasible in our study and is unlikely to be feasible more generally given that even clones will vary in trait values as a consequence of phenotypic plasticity. Therefore, we pooled individual-level phenological-trait values into three ranges , which accounted for the most frequent phenological-trait values in the population (Supporting information). This allowed us to use fecundity data from several individuals within each phenological trait range but exposed to different densities of intra- and interspecific competitors to estimate trait-specific competition model parameters for *Lasthenia*.

We used different phenological trait ranges for estimating the competition coefficients when *Lasthenia* was interacting with the different non-native species because the most frequent phenological traits differed depending on competitor identity (Supporting information). There were three phenological trait ranges for *Lasthenia* competing with each of the two non-native species, noting that one trait range was the same when in competition with both competitors giving five different phenological trait ranges in total. Equation 2 was fitted separately to the fecundity data (F_i) from each of these five phenological trait ranges, providing trait-specific estimates of λ_i, and the intra- and interspecific competition coefficients when in competition with the two non-native species. Ultimately, this empirical-analytical method enabled some of the first empirical estimates of intraspecific variation in competition model parameters as they relate to intraspecific variation in a species' trait values.

Numerical simulations of the ecological effects of intraspecific variation

We used numerical simulations of the parameterized competition model to predict the outcome of competitive population dynamics with and without intraspecific variation in *Lasthenia*. Intraspecific variation can be incorporated into model simulations by describing competition coefficients as distributions (Melbourne and Hastings 2008, Hart et al. 2016). In our case, we derived a distribution for each of *Lasthenia*'s competition coefficients based on our estimates of these coefficients for each phenological trait value, weighted by the proportion of observed individuals having each specific phenological trait. These distributions of competition coefficients were based on 548 *Lasthenia* individuals in competition with *Bromus*, and 238 *Lasthenia* individuals in

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competition with *Lactuca*. The competition coefficients that we associated with each of these individuals according to our trait-specific model parameterization are provided in the Supporting Information.

For simulations excluding intraspecific variation, we simulated dynamics using the competition model Eq. 1 parameterized with the point estimates of g_i, s_i and λ_i for all species, the point estimates of each competition coefficient for the non-native species, and the mean of the distributions of the intra- and interspecific competition coefficients for *Lasthenia*. For simulations including intraspecific variation, the only difference was that we simulated dynamics using the empirically-derived distributions of both the intra- and interspecific competition coefficients for *Lasthenia* (i.e. the distributions of α_{ii} and α_{ij} when *Lasthenia* is species *i*). Allowing intraspecific variation in *Lasthenia*'s competition coefficients to be described according to distributions, we simulated dynamics using the following modification of Eq. 1 (Hart et al. 2016):

$$N_{i,t+1} = (1-g_i)s_i N_{i,t} + \mathbb{E}\left[\frac{\lambda_i g_i}{1+\alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}}\right] N_{i,t} \quad (3)$$

where α_{ii} and α_{ij} are now each described by distributions, and $\mathbb{E}$ denotes the expected value. The distributions for α_{ii} and α_{ij} in our simulations were derived by sampling with replacement 10^6 values of these individual competition coefficients estimated from our experimental populations. Note that including or excluding the covariance between α_{ii} and α_{ij} had negligible effects on our results (see the Supporting information for all data and code showing how our simulations were implemented, and to allow readers to repeat these simulations with and without including intraspecific variation in the competition coefficients, and with and without covariance between the intra- and interspecific competition coefficients).

To predict competitive outcomes between the native and the non-native species we applied the mutual-invasibility coexistence criterion (Chesson 2000). We simulated the ability of each non-native species to grow from low density (10^{-8} individuals/plot; Ellner et al. 2016) in the presence of *Lasthenia* at its predicted single-species equilibrium abundance, and for *Lasthenia* to similarly invade each non-native species. We repeated the simulations with and without intraspecific variation in *Lasthenia* as described above. All data and the annotated R code (www.r-project.org) for understanding and running these simulations is provided in the Supporting Information. Further justification for our simulation approach incorporating intraspecific variation can be found in Hart et al. (2016).

Results

Intraspecific variation in phenology and competition model parameters in Lasthenia

Our measurements of reproductive phenology in 943 *Lasthenia* individuals allowed us to generate empirical distributions describing intraspecific variation in phenology in this species (Fig. 1). We found that the distributions of flowering/fruiting time differed as a function of competitor identity. Specifically, mean time of flowering/fruiting of *Lasthenia* occurred earlier when in competition with *Bromus* (Julian day 137.1, 95% CI: 132.6–141.6) than when in competition with *Lactuca* (Julian day 144.8, 95% CI: 140.2–149.5; LRT: $\chi^2_{df=1} = 5.4$, $p = 0.02$). This means that *Lasthenia* tended to reproduce slightly earlier in the season when competing against *Bromus*, which is the non-native species with more similar phenology to the native. We also found that variance in the timing of flowering in *Lasthenia* was higher when competing against *Lactuca* (variance = 303.1) than against *Bromus* (variance = 375.0, Levene's test for equal variances: $F_{1,941} = 10.5$, $p = 0.0013$). Finally, we note that there was no evidence for a relationship between reproductive phenology and species' relative abundance in our experiment ($\chi^2_{df=1} = 0.115$, $p = 0.702$).

From the distributions of flowering phenology, we subjectively identified three intraspecific phenological ranges of *Lasthenia* competing against *Bromus* as 110–130, 140–150 and 165–175 ordinal days (mean phenological trait value = 140; Fig. 1). For *Lasthenia* competing against *Lactuca*, these ranges were 120–130, 145–160 and 165–175 ordinal days (mean phenological trait value = 150; Fig. 1). As described in the methods, we estimated competition coefficients for each of these phenological trait ranges, noting again that this approach was required because of the need for replicate individuals with similar flowering phenology to estimate competition coefficients as a function of flowering phenology. Results show that intraspecific variation in flowering/fruiting phenology was associated with intraspecific variation in competition model parameters (Table 1). Estimates of the competition coefficients indicate that *Lasthenia* was, in general, more sensitive to interspecific competition from *Bromus* than *Lactuca* (Table 1). When in competition with *Bromus*, individuals with relatively early or late phenology tended to be more sensitive to interspecific competition (i.e. had higher values of the interspecific competition coefficient, α_{ij}, when *Lasthenia* is species *i*), while when in competition with *Lactuca*, individuals with early or mid-range phenological values were less sensitive to competition than individuals with late phenology (Table 1; we note that the value of α_{ij} is a function of the traits of both species in a competing pair).

Ecological effects of intraspecific variation on coexistence

Our simulations show that intraspecific variation in flowering/fruiting phenology increases *Lasthenia*'s invasion growth rate when in competition with both *Bromus* (log invasion growth rates: −0.77 without variation versus −0.65 with variation) and *Lactuca* (−1.51 without variation versus 2.11 with variation). Because *Lasthenia* experiences no intraspecific competition when it is invading a resident species, the increase in invasion growth rates occurs because of intraspecific variation in *Lasthenia*'s response to interspecific competition (i.e. variation in α_{ij} when *Lasthenia* is species *i* in Eq. 3). By contrast, variation in *Lasthenia*'s response to intraspecific competition (α_{ii}) increased its single-species equilibrium density (Fig. 2).

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Table 1. Intraspecific variation in reproductive phenology in *Lasthenia californica* was associated with intraspecific variation in *Lasthenia*'s maximum finite rate of increase (λ_i), and response to intra- and interspecific competition when competing against (a) *Bromus* and (b) *Lactuca*. Parameter values are means ± SE. Lambda for *Bromus* and *Lactuca* were 1710.2 ± 524.1 and 23316.1 ± 6255.9, respectively. Competitive effects of *Lasthenia* on *Bromus* and *Bromus* against itself were 0.0096 ± 0.033 and 0.122 ± 0.073, respectively. Competitive effects of *Lasthenia* on *Lactuca* and *Lactuca* against itself were 0.021 ± 0.009 × 10^{-3} and 0.049 ± 0.018, respectively. *Lasthenia*, *Bromus*, and *Lactuca* germination rates were 0.07 ± 0.03, 0.35 ± 0.11 and 0.12 ± 0.05, respectively, and seed survival rates were 0.20 ± 0.08, 0.02 ± 0.01 and 0.43 ± 0.17, respectively.

Phenological range (ordinal days)	*Lasthenia* Lambda (λ_i)	*Lasthenia* response to intraspecific competition ($\alpha_{ii} \times 10^{-3}$)	*Lasthenia* response to interspecific competition ($\alpha_{ij} \times 10^{-3}$)
(a) *Lasthenia* in competition with *Bromus*			
110–130	470.6 ± 99.5	3.48 ± 0.81	17.56 ± 5.17
140–150	359.5 ± 67.9	1.99 ± 0.45	6.88 ± 2.39
165–175	430.0 ± 72.3	0.75 ± 0.14	23.75 ± 0.66
(b) *Lasthenia* in competition with *Lactuca*			
120–130	395.0 ± 89.1	2.32 ± 0.62	2.12 ± 0.83
145–160	407.7 ± 53.4	0.95 ± 0.25	1.94 ± 0.77
165–175	430.0 ± 72.3	0.75 ± 0.20	7.31 ± 2.73

Both effects occur because population growth rates are non-linear concave-up functions of both α_{ij} and α_{ii} (as per Eq. 1; Hart et al. 2016). Although intraspecific variation caused an increase in *Lasthenia*'s invasion growth rate when in competition with *Bromus*, this increase was not sufficient to allow *Lasthenia* to invade *Bromus* because the invasion growth rate remained negative (Fig. 2). Therefore, any benefits of intraspecific variation for *Lasthenia* are insufficient to prevent its predicted competitive exclusion by *Bromus* and this is the case even without accounting for any potential positive effects of intraspecific variation on *Bromus* dynamics, which were not quantified in our study. By contrast, when in competition with *Lactuca*, intraspecific variation in *Lasthenia* caused invasion growth rates to shift from negative to positive, allowing the species to coexist (Fig. 2).

Discussion

While ecologists have been increasing their efforts to quantify the magnitude of intraspecific variation in ecological communities (Laughlin et al. 2012, Jung et al. 2014, Valladares et al. 2014, Siefert et al. 2016), very few empirical studies have been able to relate this variation to the outcome of species interactions (Clark 2010). This is because while it is relatively straightforward to measure functional traits on different individuals to estimate intraspecific trait variation, it is much more difficult to empirically relate these functional trait values to the demographic and competitive rates that can be used to make predictions about competition outcomes. Here, we have shown that by estimating trait differences between individuals, and quantitatively linking these trait differences to both intra- and interspecific competition coefficients using field experiments, one can make predictions about the ecological effects of intraspecific trait variation on species coexistence.

Intraspecific variation in reproductive phenology can be beneficial for native species. In our study, against one non-native species *Bromus*, these benefits are insufficient to allow the persistence of the native species (Fig. 2b). While the effects of intraspecific variation are predicted to increase the single-species equilibrium population size of *Lasthenia,* these

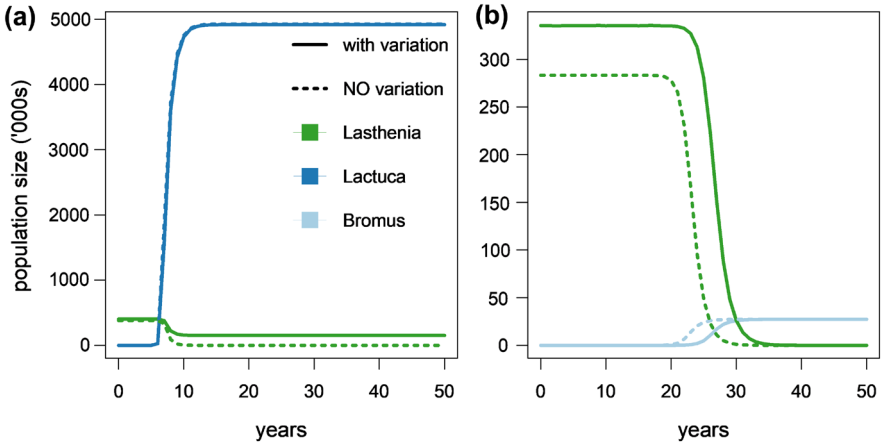


Figure 2. Numerical simulations of competitive population dynamics with (solid lines) and without (dashed lines) intraspecific variation in *Lasthenia.* (a) *Lasthenia* in competition with *Lactuca.* (*b) Lasthenia* in competition with *Bromus.* In each panel an invasion scenario is simulated, where *Lasthenia* is initialized at its predicted single-species equilibrium density, and each non-native species is initialized at very low density (10^{-8} individuals; Ellner et al. 2016).

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benefits only serve to delay but not prevent competitive exclusion against *Bromus* (Fig. 2b). Because the non-native species, *Bromus*, should also benefit from intraspecific variation but this benefit was not quantified in our study, our conclusion that intraspecific variation in *Lasthenia* is likely to be insufficient to allow *Lasthenia* to coexist with *Bromus* is conservative. In contrast, against a second non-native species *Lactuca*, intraspecific variation in the native species *Lasthenia* was predicted to allow the native and non-native species to coexist, where they would not be predicted to coexist when only considering the mean phenological trait values. However, for this interaction we cannot rule out the possibility of a different qualitative outcome if the unmeasured benefits of intraspecific variation in non-native *Lactuca* overwhelm the benefits of intraspecific variation in *Lasthenia.* Indeed, the major conclusion of previous theoretical work demonstrates that for a given level of intraspecific variation, dominant competitors will, in fact, always benefit more from the effects of nonlinear averaging than inferior competitors (Barabás et al. 2016, Hart et al. 2016). Thus not accounting for these effects effectively disadvantages the dominant competitors in our study such that the interaction outcome between *Lasthenia* and *Lactuca* remains uncertain.

Intraspecific phenological variation and the role of competitor identity

Our study focused on the consequences for coexistence of intraspecific variation in phenology. This was because previous work has shown that interspecific differences in phenology can be important determinants of competitive outcomes when annual plant compete for common resources such as water and space (Godoy and Levine 2014, Kraft et al. 2015, Alexander and Levine 2019, Pérez-Ramos et al. 2019). Despite the general importance of phenology for the outcome of species interactions, there has been relatively less attention – particularly when compared with other functional traits – on the magnitude and consequences of intraspecific differences in phenology (Miller-Rushing et al. 2010, Siefert et al. 2016, Carter and Rudolf 2019). Together with other recent studies (Siefert et al. 2015, Fajardo and Siefert 2016), our results demonstrate that intraspecific phenological variation can be large, spanning more than two months in our strongly seasonal system (Fig. 1). Given the focus on phenological changes in response to changing climate, and the potential for large consequences of intraspecific phenological variation on species interactions, more work on the causes and consequences of intraspecific variation in phenology is likely warranted (CaraDonna et al. 2014, Carter and Rudolf 2019).

Our results suggest that the phenology of the native species was influenced by the identity of the non-native competitor in the competition plots (Fig. 1). This suggests that different competitors may elicit different responses in *Lasthenia* phenology. Similar, competitor-dependent shifts in phenology have been found in laboratory *Arabidopsis* populations (Taylor et al. 2019) and under field conditions in annual plant communities (Pérez-Ramos et al. 2019) as a consequence of phenotypic plasticity. While we do not know what mechanisms may have underpinned neighbor-dependent phenological shifts in our study, recent evidence suggests that changes in the composition of interacting species can influence phenology by influencing the local soil micro-environment (Wolf et al. 2017). As noted by Pérez-Ramos et al. (2019), the fitness consequences of neighbour-dependent phenotypic changes have rarely been explored empirically (see Vasseur et al. 2011 for a theoretical viewpoint). In our study, the different phenological responses were associated with differences in the response of *Lasthenia* to competition (Table 1). Notably, the identity of the heterospecific competitor in the competition plots also influenced *Lasthenia*'s response to intraspecific competition (Table 1), perhaps suggesting a higher-order interaction (Levine et al. 2017, Letten and Stouffer 2019). While interesting, these results are problematic for developing a general understanding of the effects of intraspecific trait variation because they suggest that these effects may depend strongly on the nature of the competitive environment.

Ecological effects of intraspecific variation on the dynamics of native versus non-native species

In general, intraspecific variation in phenology was predicted to improve the performance of *Lasthenia* in competition with both non-native species, which is the theoretical expectation (Fig. 2; Bjørnstad and Hansen 1994, Barabás et al. 2016, Hart et al. 2016). The ability to produce offspring is a nonlinear function of the competition coefficients in the annual plant model (Eq. 1, Hart et al. 2016). Therefore species-level performance is a nonlinear average of this function when the experience of competition varies between individuals. As with most competition models, the function relating offspring production to the competition coefficients is concave-up for the annual plant model (i.e. Eq. 1 has positive second derivative with respect to the competition coefficients). This causes variation between individuals in their competition coefficients to increase species-level offspring production according to Jensen's inequality (Jensen 1906, Bjørnstad and Hansen 1994, Hart et al. 2016). Biologically this occurs because individuals that are stronger competitors than average produce more seeds than are lost by individuals that are weaker competitors than average, resulting in a net increase in seed production at the species level. Together with the laboratory study of Hausch et al. (2018), our study is one of very few to empirically quantify the potential magnitude of these effects in the field, rather than use arbitrary levels of intraspecific variation in theoretical models (Lichstein et al. 2007, Barabás et al. 2016, Hart et al. 2016). Our ability to empirically quantify these effects highlights the importance of defining a model that describes competitive population dynamics to make predictions about the effects of intraspecific variation on competitive coexistence via nonlinear averaging.

Given the dependence of our result on the shape of the competition function, it may be tempting to dismiss our result as

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being model-specific. However, as noted in the Introduction, the vast majority of models of competition that have been proposed to describe dynamics across a range of taxa share the feature of a concave-up competition function (Ricker 1954, Beverton and Holt 1957, Leslie and Gower 1958, Hassell and Comins 1976, Law and Watkinson 1987, Pacala and Silander 1990, Inouye 2001, Melbourne and Hastings 2008, Levine and Hille Ris Lambers 2009, Hart and Marshall 2013). This suggests that our general results showing a positive effect of individual variation on population abundance are unlikely to be model or system-specific, although the magnitude of this positive effect might be model-specific. What is truly specific to our study is that the empirically-estimated benefits of intraspecific variation for *Lasthenia* were insufficient to overcome its on-average competitive disadvantage in at least one of the interactions studied (Fig. 2b). Similar empical studies in other systems are now required to determine how common this particular result may be.

More generally, our results further demonstrate that accounting for the ecological effects of intraspecific variation can be important. In particular, our results show that nonlinear averaging allows realized levels of intraspecific variation to cause large deviations in community dynamics and population sizes than those predicted based on average trait values (Fig. 2). Given the ubiquity of empirically-supported, concave-up competition functions it is likely that intraspecific variation will have similarly strong effects on dynamics in other systems. This means that the common approach in empirical studies of coexistence of ignoring intraspecific variation (Levine and Hille Ris Lambers 2009, Adler et al. 2013, Kraft et al. 2015, Pérez-Ramos et al. 2019) is likely to misrepresent the dynamics, if not the outcome, of competition in nature. This is also true of studies that focus on the coexistence of native and non-native species (Richards et al. 2006, Keller and Taylor 2008, Van Kleunen et al. 2010, Godoy et al. 2012, Matesanz and Sultan 2013). Our results suggest that linking trait variation to population dynamic models is one approach that may be used to begin to quantify the magnitude of the effects of intraspecific variation in nature.

Previous work has shown that differences in mean phenological timing can influence coexistence via complex combined effects on both niche and competitive differences between species (Godoy and Levine 2014, Kraft et al. 2015). These conclusions were based on estimates of niche and competitive differences calculated using single estimates of each of the demographic and competitive rates in Eq. 1 for each species. In our study, the demographic and competitive rates varied with phenological traits within species and it would be tempting to recalculate niche and fitness differences based on the consequences of this variation. This would seem to be a simple exercise but is difficult and of questionable use in practice. This is because niche and competitive differences are calculated based on the values of the competition coefficients (and other demographic rates) but the 'realized' values of these coefficients in a model that includes intraspecific variation are not simply the mean of the coefficients. Instead, the realized values of the coefficients in a model with intraspecific variation need to inferred based on realized population growth rates after accounting for the effects of nonlinear averaging. This is not only a trivial exercise, but we believe it would be of questionable inferential use. Instead, we think it more important to emphasize the simple fact that empirical estimates of variation in competitive rates can alter the predicted outcome of competitive interactions.

Relationship between mathematical theory and empirical results

Our study was in part motivated by recent theoretical work that showed how intraspecific variation can influence species coexistence (Hart et al. 2016). In this context it is worthwhile briefly discussing how our empirical results relate to this theory. In Hart et al. (2016), we explored how intraspecific variation influenced species coexistence via four pathways: 1) intraspecific variation in species' competitive ability; 2) intraspecific variation in species' competition coefficients; 3) intraspecific variation in niche differences and 4) effects of intraspecific variation that arise because of the discreteness of individuals. We do not explore the fourth pathway in the current paper, but see Schreiber et al. (2023) for further recent work on these effects in an empirical context. With respect to the first three pathways, in the theoretical work of Hart et al. (2016), we were able to construct models to isolate the influence of intraspecific variation in competitive ability (by removing niche differences) and to isolate the effects of variation in competition coefficients (by removing competitive differences) and niche differences (by ensuring that trait variation mapped perfectly to niche differentiation following a classic evolutionary model). In nature, however, species have non-zero competitive and niche differences, and traits do not map perfectly to either niche and competitive differences (Kraft et al. 2015, Pérez-Ramos et al. 2019). That phenology does not map perfectly to competitive differences confounds easy predictions or conclusions about how intraspecific variation in phenology influences niche or competitive differences between species. Nevertheless, niche and competitive differences are simple functions of the competition coefficients themselves (Chesson 2012, Kraft et al. 2015, Hart et al. 2018). Therefore, in the current study, while we do not isolate the independent effects of variation in competitive and niche differences on dynamics, our empirical estimates of intraspecific variation in the competition coefficients implicitly incorporate intraspecific variation in competitive and niche differences. Moreover, as noted in Hart et al. (2016), variation in the competition coefficients themselves that is likely to be most empirically relevant for assessing effects of intraspecific variation on coexistence, which is what we focus on in the current study.

Limitations

Because we were unable to relate individual-level trait values to individual-level competition coefficients, our study

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potentially underestimated the magnitude of intraspecific variation in *Lasthenia*. Similarly, we were unable to measure intraspecific variation in the non-native species *Bromus* and *Lactuca*, and so the effects of variation in each of these three species on pairwise and multispecies dynamics are not accounted for in our study. As indicated in the Introduction, accounting for the effects of intraspecific trait variation on multiple competition coefficients in each of the competing species would require experiments that are orders of magnitude larger than the one we have achieved, for which we believe there is no precedent in the literature. This limitation, which we believe is worth highlighting for studies seeking to understand how intraspecific variation influences species interactions, has different consequences for predictions about the outcome of interactions in our study. When the native *Lasthenia* competes with the non-native *Bromus*, our qualitative conclusions are unlikely to change. This is because *Bromus* will also benefit from intraspecific variation via nonlinear averaging, which would only increase the predicted rate of competitive exclusion in Fig. 2b. However, and as noted earlier in the discussion, accounting for any benefit of intraspecific varation in the non-native *Lactuca* could result in competitive exclusion even though we predict that intraspecific variation in *Lasthenia* promotes coexistence (Fig. 2a). For a more complete understanding of these dynamics future work should attempt to quantify intraspecific variation in all competition coefficients as a function of multiple trait values in all interacting species, noting the formidable empirical challenges required to do so.

We did not consider intraspecific variation in g_i, s_i because variance (or higher moments) in these parameters can not effect dynamics when growth is linear in these parameters (as for Eq. 1, and for most other models of competitive population dynamics that we are aware of). Nevertheless, covariance between any of these parameters and the competition coefficients may affect dynamics. While studies of intraspecific variation on ecological dynamics have not generally considered the influence of covariance between demographic rates, it is likely to be a fruitful avenue for future work given the possibility of tradeoffs between different demographic and competitive rates (Villellas et al. 2015, Laughlin et al. 2020).

Our conclusions are based on simulations run over multiple generations of a model parameterized using data collected over a single generation. While our approach is one of very few studies to provide some realistic bounds on the otherwise arbitrary parameterizations of mathematical models in theoretical studies of intraspecific variation, we emphasise that our study does not account for any effects of temporal environmental variation or inter-annual variation in the levels of intraspecific variation, on coexistence outcomes. More generally, we are unaware of any attempts to understand how temporal (phenological) variation interacts with intraspecific variation in phenology to affect coexistence outcomes, and we do not currently know how such dynamics might influence our conclusions.

Conclusions

Intraspecific variation has the potential to alter expectations for species coexistence compared with predictions based only on estimates of average differences between species (Lichstein et al. 2007, Barabás et al. 2016, Hart et al. 2016, Uriarte and Menge 2018). Our approach demonstrates how empiricists can link trait variation to variation in the demographic and competitive rates that determine coexistence outcomes. Future research would benefit from using similar approaches to explore how intraspecific variation in other phenotypic traits influence coexistence. Our results suggest that the consequences of intraspecific variation may be particularly important for understanding the persistence of native species threatened by non-native species. Our study suggests that while native species can benefit from the ecological effects of intraspecific variation, these benefits will not always be sufficient to allow the persistence of native species competing against dominant non-native competitors. More generally, our results suggest that understanding the dynamics of species interactions may benefit from incorporating the dynamical effects of intraspecific variation.

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Author contributions

Oscar Godoy: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Noelia Gonzalez-Muñoz**: Formal analysis (equal); Visualization (equal); Writing – original draft (equal). **Simon P. Hart**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data and code are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.8300659 (Godoy et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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