OIKOS

Research

Competition as a demolition derby: why tolerating competitors is more important than suppressing them

Daniel Z. Atwater, Ragan M. Callaway and Sa Xiao

D. Z. Atwater (https://orcid.org/0000-0002-7166-3819) ✉ (danatwater@gmail.com), S. Xiao (https://orcid.org/0000-0002-8427-752X) and R. M. Callaway, Division of Biological Sciences and the Inst. on Ecosystems, The Univ. of Montana, Missoula, MT, USA. DZA also at: Biology Dept, Earlham College, Richmond, IN, USA. SX also at: School of Life Sciences, Lanzhou Univ., Lanzhou, PR China.

Oikos
130: 143–155, 2021
doi: 10.1111/oik.07634

Subject Editor: François Munoz
Editor-in-Chief: Dries Bonte
Accepted 27 September 2020

Tolerance and suppression are distinct components of competition among plants, and recognizing how they affect competitive outcomes is important for understanding the mechanisms and consequences of competition. We used simulations informed by experimental trials to ask whether tolerance or suppression of competitors was more important for the survival of native plants experiencing competition with an exotic invasive species. When competition was pairwise, tolerance and suppression contributed equally to competitive rank in simulations. However, when multiple native genotypes competed together against an invader, the ability to tolerate competition was up to 50 times more important than the ability to suppress the invader. In two-competitor communities the chief advantage of suppressing competitors was a global decrease in their abundance, but this advantage did not exist in communities of multiple competitors – which is more representative of natural conditions – because decreased competitor abundance benefited all plants regardless of their competitive ability. We suggest that this concept is analogous to a 'demolition derby,' an automotive contest where participants attempt to have the last functional vehicle on the playing field. Because strong suppressors share the benefits of eliminating competitors with other remaining competitors, we propose that tolerance of competitors is more beneficial than suppression when competition occurs in a multiplayer scenario – in a demolition derby and in nature. This finding has implications for our understanding of how competition influences plant species coexistence, plant community structure and invasion outcomes.

Keywords: competitive effect, competitive hierarchy, competitive response, invasion, pairwise competition

Introduction

Ecologists often evaluate the competitive ability of a plant species by comparing the size, survival or fitness of a target individual growing with a neighbor versus without a neighbor (Armas et al. 2004, Aschehoug et al. 2016). Two components of competitive ability determine the outcome of this interaction: suppression of competitors and tolerance of competitors (Miller and Werner 1987, Aarssen 1989, Goldberg 1990). Suppression is defined as the ability of a plant to reduce the growth of a neighbor

NORDIC SOCIETY OIKOS

www.oikosjournal.org

and tolerance is defined as the ability of a species to maintain growth under competition. Because tolerance and suppression are distinct components of competitive ability, they may respond differently to ecological and evolutionary processes (Uriarte et al. 2002, Golivets and Wallin 2018). Explicitly recognizing and testing this bipartite conceptual model of competition therefore has great value for understanding the properties and consequences of plant competition.

One way competition has been conceptualized is a comparison to a boxing match (Aarssen 1989) in which success is equally determined by knocking down one's opponent and by not being knocked down oneself (Fig. 1A–E). In this context, a focal plant may achieve success by simply being more tolerant of competition with an antagonist (Fig. 1C), or by suppressing its antagonist. In the latter scenario, the focal plant may experience a reciprocal benefit in the form of reduced resource preemption by the antagonist (Fig. 1B). Realistically, a plant may utilize some combination of both of these strategies. Suppression ability has been associated with fast growth and large size, and tolerance ability has been linked to altered root allocation, lower relative growth rate, more efficient nutrient uptake and higher tolerance to nutrient stress (reviewed by Goldberg 1996, but see Carlyle and Fraser 2006). Allelochemistry and indirect interactions mediated by effects on soil communities may also play a role in tolerance and suppression of neighbors (Aschehoug et al. 2016).

Suppression is usually thought to be roughly as important as tolerance in determining overall competitive ability, and it is thought that both strategies should contribute to the abundance of species and the fitness of genotypes (Goldberg and Werner 1983, Goldberg 1990, 1996). This conceptual model of a balance between suppression and tolerance works well when two individuals or two genotypes compete. However, in natural communities more than two individuals, genotypes or species compete. In such cases, we hypothesize that the relative benefits of suppressing neighbors may be considerably less important. Specifically, the benefits of suppressing neighbors are shared in communities of multiple competitors, as depicted in Fig. 1D. If a focal plant suppresses a competing neighbor (the 'antagonist,' in Fig. 1), the focal plant will benefit. However, other genotypes or species that also compete with that neighbor will also benefit even if they did not contribute to the suppression of the neighbor.

As a boxing match serves as a good example of pairwise competition, we point to a common carnival event in the United States of America as an example of multiplayer competition: the demolition derby. In a demolition derby, multiple cars on a dirt field crash into one another until only one car (the winner) remains drivable. If a driver suppresses a competitor by aggressively wrecking them, that driver's odds of winning improve. Crucially, all of the other drivers still on the track also benefit from another driver's aggression

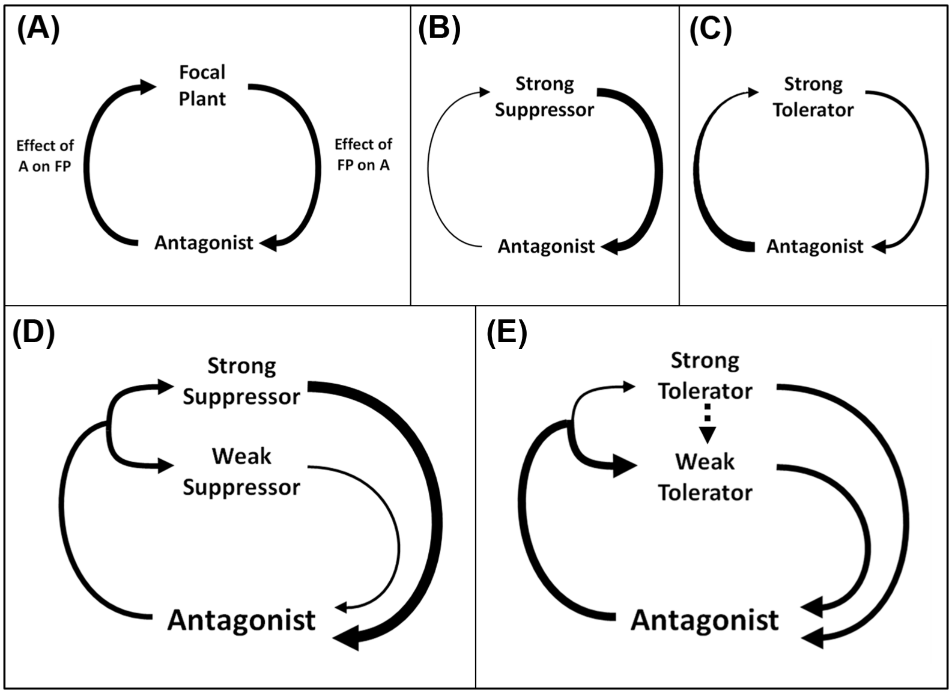

Figure 1. Boxing match and demolition derby models of competition. The thickness of the left arrow indicates the net competitive effect of the antagonist on the focal plant, and the thickness of the right arrow indicates the net competitive effect of the focal plant on the antagonist. The focal plant can reduce the net effect of the antagonist either by suppressing it, thereby weakening its reciprocal negative effects (B) or by tolerating its effects (C). When multiple plants compete with an antagonist, suppression no longer provides an advantage; if one plant suppresses the antagonist, the other plant benefits also (D). If focal plants vary in their tolerance ability, only the more tolerant plant will benefit, giving it an induced competitive advantage (E). The tapering arrow in (C) indicates that the antagonist can exert strong competitive effects, but that only weak effects are felt by a tolerant focal species.

regardless of whether they themselves ever cause any damage. Thus, in a demolition derby an offensive strategy improves the odds of winning for all remaining competitors. As a result, the best strategy, known as 'sandbagging,' is to avoid all contact with other cars. Sandbagging is in fact so effective that it is prohibited in demolition derby rules – but this rule of course cannot be enforced in plant communities.

The advantages of a sandbagging strategy extend to any conflict between three or more competitors. Plants cannot simply avoid competitors the way drivers in a demolition derby can, but in plant communities there may be significant advantages to traits that improve tolerance rather than suppression ability, and ecological and evolutionary forces in plant communities may favor the ability to tolerate competitors more strongly than the ability to suppress competitors. Adaptations to accomplish this might include reducing growth and resource requirements (Goldberg 1996), avoiding root contact with competitors (Mahall and Callaway 1996), tolerating allelochemical secretions of neighbors (Callaway et al. 2005), and reducing sensitivity to competitor-caused changes in the soil community (Van der Putten et al. 2013). We note that this conceptual model does not distinguish between genotypes or species. Any time competition is multiplayer there is an opportunity for benefits of suppression to be shared among all participants, whether they are distinct individuals, genotypes or species.

Competitive suppression and tolerance both affect species abundances in the field (Growth et al. 1985, Mitchley and Grubb 1986, Keddy 1990, Howard 2001, Howard and Goldberg 2001), but only a few studies have explicitly compared the relative ecological importance of tolerance and suppression. For example, MacDougall and Turkington (2004) found that tolerance, but not suppression, predicted the abundance of two exotic invaders in competition trials in the field. More recently Willis et al. (2010) showed that both suppression and tolerance had important effects on the fitness of *Arabidopsis thaliana* competitors in two-genotype populations. Finally, in a complex model of tradeoffs for selection on herbivore defense versus competitive ability in *Solidago altissima* populations experiencing intraspecific competition, Uriarte et al. (2002) found that selection favored competitive tolerance and not suppression. In the context of exotic invasions, understanding the importance of suppression and tolerance-based competition may be a critical component of understanding the success of exotics and the survival of native plants following invasion. In a meta-analysis, Golivets and Wallin (2018) found that exotic plant species outperformed native species more often due to their ability to tolerate competition, rather than strong competitive suppression of natives. Several recent studies have also shown that invasive plants select for increased tolerance ability, but not increased suppression ability, in native plants (Leger 2008, Rowe and Leger 2011, Fletcher et al. 2016). While a consensus is emerging that tolerance is more important than suppression in determining competitive ability in the field, current models of plant competition are unable to explain the phenomenon.

Here we use simulation models to investigate how tolerance and suppression ability might affect the outcome of competition between native and invasive species in both pairwise and multiplayer scenarios. These models were informed by experimental competition trials with 23 different accessions of *Pseudoroegneria spicata* (bluebunch wheatgrass), a bunchgrass native to the western United States, and one accession of *Centaurea stoebe* ssp. *micranthos* (spotted knapweed), a Eurasian species which commonly invades *Pseudoroegneria*-dominated grasslands. We measured the average competitive ability of each accession in single-pot competition experiments, then simulated invasion of populations containing a single accession of *Pseudoroegneria*, as well as models in which we invaded mixed populations of multiple *Pseudoroegneria* accessions, conforming, respectively to a pairwise scenario (i.e. boxing match) and a multiplayer scenario (i.e. demolition derby). *Centaurea* and *Pseudoroegneria* were chosen as representative native and invasive species with the ultimate goal of generalizing our results. To do so, we generated artificial plant communities with greater variation in tolerance and suppression ability, where we also altered the life expectancy and mode of dispersal of both species. We note that competition between two populations can be considered as pairwise – just as competition between two individuals can – provided that each population contains only a single genotype, because reciprocal benefits of competitor suppression benefit only the focal genotype when that is the only genotype present in the population.

We conducted our study in the context of exotic invasion because competition often plays an important role in invasions in general (Vila and Weiner 2004) and for *Centaurea* and *Pseudoroegneria* specifically (Maron and Marler 2008, Callaway et al. 2011), and because invasions have been at the center of a bulk of studies investigating the ecological importance of tolerance and suppression (Golivets and Wallin 2018); however the interactions observed in this study were not particular to invasive plants and may be extended to include competition between sessile organisms in general. We hypothesized that 1) in pairwise models suppression and tolerance would have similar effects on the ability of accessions to survive invasion, and 2) in the multiplayer models tolerance will be a more important determinant of survival and abundance than suppression. We note that the models presented here were designed to isolate effects of variation in tolerance and suppression ability on competitive outcomes, and they are not intended to simulate any mechanistic processes or to specifically forecast invasion outcomes. Rather, we ask how variance in plant tolerance and suppression may influence competition outcomes generally, and whether competition might select for plants that are strong tolerators or strong suppressors.

Methods

Study species

Pseudoroegneria spicata is a large, perennial, cool-season, drought-tolerant bunchgrass and a dominant member of native grasslands throughout the western United States. *Centaurea stoebe* is a short-lived perennial forb that is native to Eurasia and that has become invasive in the USA since its introduction at the beginning of the 20th century (Roche Jr. and Talbott 1986). These species are often found together in the grasslands of the Mountain West (Strang et al. 1979), but *Centaurea* can also form mono-dominant stands that exclude most natives (Maddox 1979), due in part to its ability to outcompete native plants (Herron et al. 2001, Maron and Marler 2008, Aschehoug et al. 2014).

Experimental protocol

We acquired seeds of 23 *Pseudoroegneria* accessions from the Plant Germplasm Introduction and Testing Research Station in Pullman, Washington, USA (Supplementary information). Accessions from different populations were chosen rather than harvesting from a single population because they were known to be true-breeding and to vary in competitive ability. These seeds were from true-bred lines collected from populations in eight states and British Columbia. *Centaurea* seeds were field-collected from a single site near Missoula, Montana, USA to minimize variation in competitive ability. We germinated seeds of each *Pseudoroegneria* accession into 24 500 ml pots containing a 50/50 v/v mix of sand and native soil from a grassland near Missoula. After four weeks we thinned seedlings to one per pot, and added seeds of *Centaurea* to half of the pots (twelve for each accession), which were in turn thinned to one seed per pot so that one individual *Pseudoroegneria* competed with one individual *Centaurea* in each pot. *Pseudoroegneria* was given this head start because we knew from prior experience that this would put both species at equal footing in a pot experiment. We also planted *Centaurea* alone. After 20 weeks, all above and belowground biomass of both *Pseudoroegneria* and *Centaurea* was harvested, dried in a drying oven and weighed.

We estimated competitive tolerance and suppression ability using the relative interaction intensity (RII) index (Armas et al. 2004):

$$\mathrm{RII} = \frac{\text{biomass alone} - \text{biomass in competition}}{\text{biomass alone} + \text{biomass in competition}}$$

Values of this metric range from 1 to −1. A negative value indicates inhibition and a positive value indicates facilitation. The RII for each *Pseudoroegneria* accession can be interpreted as the tolerance of that accession to competition with *Centaurea*, with less negative values indicating better tolerance ability. Likewise, we calculated RIIs for *Centaurea* representing the suppression ability of each *Pseudoroegneria* accession, with more negative values indicating stronger ability of *Pseudoroegneria* to suppress *Centaurea*. We used the RIIs to calculate tolerance ability (T) and suppression ability (S) for each *Pseudoroegneria* accession i, as follows:

$$T_i = 1 + \mathrm{RII}_{\textit{Pseudoroegneria } i}$$

$$S_i = -1 \times \mathrm{RII}_{\textit{Centaurea } i}$$

We also created 256 ‘artificial accessions’ that possessed each combination of 16 evenly spaced levels of T and S, in order to provide a more general test of the importance of tolerance and suppression. The artificial accessions possessed every possible combination of 16 evenly spaced values of tolerance and suppression ability. This number was chosen to provide high resolution of how competitive ability in a population might vary as a function of tolerance and suppression ability.

To simulate the long term effects of competition and to compare pairwise boxing match scenarios to multiplayer demolition derby scenarios, we simulated invasion of native populations using individual-based spatially explicit dual-lattice simulation models (Doebeli and Knowlton 1998, Yamamura et al. 2004, Supplementary information) performed in R (<www.r-project.org>). The goal of these models was to investigate the relative importance of tolerance and suppression in determining fitness, not to predict realistic outcomes of invasion or specific consequences of interaction between *Centaurea* and *Pseudoroegneria* in a natural setting. A brief description of these models follows, description according to the ODD protocol (Grimm et al. 2010) available in the Supplementary information.

Simulations: environment

The models consisted of two overlapping ‘lattices’, each consisting of a 100 × 100 cell grid (10 000 cells per lattice). *Pseudoroegneria* occupied one lattice, and *Centaurea* occupied the other. These lattices ‘wrapped’ so that the cell on one edge of the lattice was treated as adjacent to the cell on the opposite edge (Yamamura et al. 2004). Thus all cells were identical in the topology of the matrix.

Every cell in a lattice could either be empty or contain a single adult individual of the species occupying that lattice. Because the *Pseudoroegneria* and *Centaurea* lattices perfectly overlapped, each filled-or-empty *Pseudoroegneria* cell exactly overlapped a single filled-or-empty *Centaurea* cell.

State of individual cells

In the greenhouse trials we competed various *Pseudoroegneria* accessions against a single accession of *Centaurea*. Consequently, in the models we specified *Centaurea* to be monotypic, with no intraspecific variation, meaning that the only relevant information about a *Centaurea* cell was whether or not it was filled. Individuals in the population did not vary, e.g. in size, age or competitive ability. However, for each *Pseudoroegneria* accession we had information about its tolerance ability (T) and suppression ability (S).

Passage of time

Initially, the *Pseudoroegneria* lattice was completely filled, and 1% of the *Centaurea* lattice was filled with randomly-dispersed individuals (100 out of 10 000 cells). Time passed in discrete steps. First, the survival of each individual was assessed according to its innate survival probability, modified by competition with an overlapping cell. Surviving individuals then reproduced, sending propagules into their own lattice. Among all propagules landing in a cell, one was randomly chosen to establish. That individual would become a reproductive adult in its established cell in the next time step. The cycle of death, reproduction and establishment continued for 2000 or 5000 time steps, conceptually equivalent to the same number of years, which was sufficient to allow stabilization of all models. We note however that the models are not intended to be 'realistic' with respect to the passage of time, and both the rate of change in the community and the final outcome of competition should be interpreted with caution. Instead, we recommend readers interpret general trends in the relative importance of tolerance and suppression in determining the fitness of each accession.

Survival and competition

When a filled *Pseudoroegneria* cell overlapped a filled *Centaurea* cell, the individuals in those two cells were considered to be in direct competition. Otherwise (i.e. when a filled cell of one species overlapped an unfilled cell of the other species), no direct competition occurred. The instantaneous survival probability of an individual not experiencing competition (i.e. whose overlapping cell in the other lattice was empty), defined as P_{max}, was independent of its age or competitive ability. All individuals of a species had the same value of P_{max} in a given simulation, but P_{max} could differ between species.

When filled cells overlapped, a *Pseudoroegneria* individual '*i*' and *Centaurea* individual '*j*' were in competition. In that case, the survival probability of the *Pseudoroegneria* was influenced by its tolerance ability, T and the survival probability of *Centaurea* was influenced by the suppression ability, S, of its competitor, in a linear fashion:

$$\text{for } Pseudoroegneria \text{ individual '}i\text{': } P_i = P_{\max,P} \times T_i$$

$$\text{for } Centaurea \text{ individual '}j\text{': } P_j = P_{\max,C} \times \left(1 - S_i\right)$$

where $P_{\max,P}$ was the maximum survival probability of *Pseudoroegneria* and $P_{\max,C}$ was the maximum survival probability of *Centaurea*. Survival was assessed by checking whether a randomly generated number exceeded P. There was no direct inter- or intra-specific interaction among non-overlapping cells. Survival was assessed instantaneously. Therefore, it was possible for two competing individuals to die in the same time step due to competition with one another.

Reproduction and establishment

Every surviving individual produced a single propagule identical to itself. For *Pseudoroegneria* this meant that a propagule inherited its sole parent's T and S values. Propagules were dispersed either randomly (any propagule could land anywhere in the lattice) or to the eight cells adjacent to the parent. Propagules never dispersed into the parent cell. If a propagule arrived in an occupied cell, it immediately died. If it arrived in an empty cell, it was guaranteed to establish provided it was the only propagule arriving in that cell. Otherwise, one propagule was randomly chosen from all arriving propagules. Thus, a form of intraspecific competition existed among *Pseudoroegneria* accessions, because they competed for limited space during reproduction. This was the only direct intraspecific competition in our models.

A surviving propagule became a fully-established adult in the next time-step. Establishment in one lattice did not depend on conditions in the other lattice; for example, a *Centaurea* plant had an equal chance to establish overlapping an empty cell as to establish overlapping a *Pseudoroegneria* competitor. As a result, priority effects were weak especially in models with global dispersal. Because establishment was scheduled after adult mortality, is was possible for an individual to establish in a cell that had been vacated by a dying adult in the same time step.

Variation among models

Several parameters varied among simulations: 1) the P_{max} for either species; 2) whether dispersal was global or limited for either or both species; 3) whether the *Pseudoroegneria* represented 23 'real' or 256 'artificial' accessions; and 4) whether the models were 'pairwise' models in which all *Pseudoroegneria* individuals were identical, each having the same T and S, or whether the models were 'multiplayer', in which the *Pseudoroegneria* population initially contained all accessions. Table 2 serves as a list of all model variants that were run. Multiple replicates were run for each combination of parameters.

Variation in P_{max} served to vary the life-expectancy of a competition-free individual. With $P_{max} = 0.800$, the competition-free life expectancy was approximately 3.1 time-steps. With $P_{max} = 0.975$, the competition-free life expectancy was approximately 27.4 time-steps. These two values were chosen because the corresponded to roughly an order-of-magnitude variation in life expectancy, and were roughly equivalent to the life-expectancies of *Centaurea* (a short-lived perennial forb) and *Pseudoroegneria* (a long-lived bunchgrass) in years. In pairwise models we only used $P_{\max,P} = 0.975$ or 0.800, and $P_{\max,C} = 0.800$. In multiplayer models either species could have either value of P_{max} in a fully-factorial fashion.

As described above, dispersal could be either global, in which propagules randomly distributed throughout the entire lattice, or local, in which propagules only distributed to the eight cells adjacent or diagonal to the parent cell. Dispersal could be global for both species, local for both species or global for one and local for the other. For the multiplayer models, dispersal mode varied in a fully-factorial manner with P_{max}. For the pairwise models, dispersal was either all-local or all-global (Table 2).

Table 1. Competitive ranks of accessions in the pairwise and multiplayer models involving *Pseudoroegneria* accessions with measured RIIs.

Accession	Rank pairwise	Rank multiplayer	RII *Pseudoroegneria*	RII *Centaurea*	*T*	*S*
12	3.0	1.8	−0.540	−0.344	0.460	0.344
19	1.0	2.0	−0.484	−0.218	0.516	0.218
11	2.0	2.1	−0.433	−0.248	0.567	0.248
5	15.6	4.8	−0.424	−0.378	0.576	0.378
10	5.0	6.0	−0.364	−0.257	0.636	0.257
3	4.5	6.2	−0.334	−0.224	0.666	0.224
21	15.8	10.1	−0.331	−0.349	0.669	0.349
13	9.8	9.5	−0.304	−0.276	0.696	0.276
15	8.1	9.6	−0.300	−0.254	0.700	0.254
17	7.0	9.2	−0.292	−0.219	0.708	0.219
20	5.6	8.6	−0.289	−0.175	0.711	0.175
18	12.9	12.4	−0.284	−0.310	0.716	0.310
16	9.1	11.0	−0.274	−0.239	0.726	0.239
14	18.2	14.7	−0.272	−0.370	0.728	0.370
23	11.1	13.2	−0.260	−0.268	0.740	0.268
2	22.0	17.7	−0.255	−0.536	0.745	0.536
9	12.0	14.9	−0.248	−0.270	0.752	0.27
1	14.7	16.3	−0.230	−0.291	0.770	0.291
7	22.1	21.0	−0.187	−0.453	0.813	0.453
6	19.0	20.0	−0.179	−0.343	0.821	0.343
8	19.9	21.4	−0.162	−0.346	0.838	0.346
22	15.9	19.7	−0.144	−0.183	0.856	0.183
4	21.9	23.0	−0.142	−0.392	0.858	0.392

Competitive ranks of real *Pseudoroegneria* accessions (arbitrarily numbered from 1 to 23) from the pairwise and multiplayer models are shown, along with the RII values, *T* and *S* for each accession. The table is sorted according to *T*. Rank corresponds to mean final abundance, averaged across all replicates or time-to-extirpation for accessions that were extirpated. A higher rank is better. Ranks are averages of models with global dispersal and a longer life-expectancy for *Pseudoroegneria* than for *Centaurea*.

In multiplayer models, the *Pseudoroegneria* lattice initially contained equal numbers of each accession – either the 23 experimentally observed accessions, or on the 256 artificial accessions. No model contained a mix of real and artificial accessions. Because neither 23 or 256 is a factor of 10 000, some accessions were randomly chosen to have one extra individual in order to fill the entire lattice. Multiplayer models were run for 5000 time steps with 50 replicates per parameter set.

In pairwise models, all *Pseudoroegneria* individuals were identical. Models for each accession (either real or artificial) were run separately and then compared. Pairwise models were run for only 2000 time steps, in part to save computational time and in part because they tended to stabilize more quickly than multiplayer models. Pairwise models based on real accessions had 100 replicates, but models based on artificial accessions had only 18 replicates due to computational limitations. Likewise, pairwise models were practically limited to only a few parameter combinations (Table 2).

Data analyses

All accessions were ranked in ascending order of final abundance, followed by time of extirpation for accessions that were extirpated. Accessions with numerically higher ranks survived longer or had higher final abundance than accessions with numerically lower ranks. For both pairwise and multiplayer models ranks were calculated within a replicate and then averaged across replicates. The relative importance of *T* and *S* in each model was calculated by fitting linear models with rank as a response variable and *T* and *S* as predictors. We then calculated dominance weights from these models (*D*; Azen and Budescu 2003). For our models, which had only two predictors, these were simply calculated as:

$$D_T = \left(R_{\mathrm{ts}}^2 + R_{\mathrm{t}}^2 - R_{\mathrm{s}}^2\right) \div R_{\mathrm{ts}}^2$$

$$D_S = \left(R_{\mathrm{ts}}^2 + R_{\mathrm{s}}^2 - R_{\mathrm{t}}^2\right) \div R_{\mathrm{ts}}^2$$

where R_{ts}^2 is the R^2 value of the model containing both tolerance and suppression as predictors, where R_{t}^2 is the R^2 value of the model containing only tolerance, and R_{s}^2 is the R^2 value of the model containing only suppression.

For ease of comparison, these were also standardized by dividing *D* for each predictor by the coefficient of determination (R^2). This was done 1) because we were more interested in the relative contribution of *T* and *S* to explained variance in rank than the absolute contribution of each variable to total variance in rank, and 2) to facilitate comparison of models that varied in their coefficient of determination. Both standardized and unstandardized weights are reported. We note that the accuracy of these estimates depend on linear relationships between *T*, *S* and rank – an assumption that was not always met in our simulations. In the multiplayer models, we also calculated the relative effect of tolerance and

Table 2. Results of linear regressions of accession competitive rank against tolerance and suppression.

		Dispersal		Life expect.		B ± SE		D			D/R^2	
		C.	*P.*	*C.*	*P.*	T	S	T	S	R^2	T	S
Multiplayer models	Artificial accessions	local	local	3.1	3.1	250.19 ± 7.00***	103.21 ± 7.00***	0.731	0.124	0.86	85.5%	14.5%
		local	local	27.4	3.1	361.85 ± 7.29***	87.43 ± 7.29***	0.861	0.050	0.91	94.5%	5.5%
		local	local	3.1	27.4	175.15 ± 6.80***	85.01 ± 6.80***	0.619	0.146	0.76	80.9%	19.1%
		local	local	27.4	27.4	375.84 ± 6.57***	156.67 ± 6.57***	0.799	0.139	0.94	85.2%	14.8%
		local	global	3.1	3.1	230.61 ± 5.30***	42.39 ± 5.30***	0.857	0.029	0.89	96.7%	3.3%
		local	global	27.4	3.1	372.31 ± 5.79***	52.86 ± 5.79***	0.925	0.019	0.94	98.0%	2.0%
		local	global	3.1	27.4	36.77 ± 4.20***	12.01 ± 4.20*	0.226	0.025	0.25	90.2%	9.8%
		local	global	27.4	27.4	380.15 ± 6.87***	113.61 ± 6.87***	0.853	0.076	0.93	91.8%	8.2%
		global	local	3.1	3.1	393.26 ± 4.79***	64.6 ± 4.79***	0.939	0.025	0.96	97.4%	2.6%
		global	local	27.4	3.1	420.27 ± 4.17***	64.02 ± 4.17***	0.954	0.022	0.98	97.7%	2.3%
		global	local	3.1	27.4	408.51 ± 4.32***	113.67 ± 4.32***	0.904	0.070	0.97	92.8%	7.2%
		global	local	27.4	27.4	431.82 ± 4.06***	117.68 ± 4.06***	0.912	0.068	0.98	93.1%	6.9%
		global	global	3.1	3.1	373.68 ± 4.90***	52.96 ± 4.90***	0.940	0.019	0.96	98.0%	2.0%
		global	global	27.4	3.1	414.33 ± 4.43***	57.77 ± 4.43***	0.954	0.019	0.97	98.1%	1.9%
		global	global	3.1	27.4	399.81 ± 4.25***	104.54 ± 4.25***	0.912	0.062	0.97	93.6%	6.4%
		global	global	27.4	27.4	428.54 ± 4.00***	109.93 ± 4.00***	0.919	0.060	0.98	93.8%	6.2%
	Real accessions	local	local	3.1	3.1	48.64 ± 3.02***	28.25 ± 3.60***	0.722	0.227	0.95	76.1%	23.9%
		local	local	27.4	3.1	56.57 ± 3.49***	16.67 ± 4.16**	0.841	0.099	0.94	89.5%	10.5%
		local	local	3.1	27.4	41.98 ± 4.46***	25.31 ± 4.46**	0.651	0.217	0.87	75.0%	25.0%
		local	local	27.4	27.4	54.28 ± 3.07***	23.33 ± 3.66***	0.795	0.159	0.95	83.4%	16.6%
		local	global	3.1	3.1	56.15 ± 3.17***	14.66 ± 3.78**	0.861	0.087	0.95	90.8%	9.2%
		local	global	27.4	3.1	57.52 ± 3.28***	11.78 ± 3.90*	0.880	0.066	0.95	93.0%	7.0%
		local	global	3.1	27.4	38.20 ± 3.49***	15.28 ± 4.16*	0.750	0.135	0.88	84.8%	15.2%
		local	global	27.4	27.4	55.41 ± 3.03***	19.96 ± 3.61***	0.826	0.128	0.95	86.6%	13.4%
		global	local	3.1	3.1	57.21 ± 3.14***	14.96 ± 3.14**	0.864	0.087	0.95	90.8%	9.2%
		global	local	27.4	3.1	58.23 ± 3.43***	13.28 ± 4.08*	0.869	0.074	0.94	92.1%	7.9%
		global	local	3.1	27.4	56.03 ± 3.07***	20.16 ± 3.66***	0.826	0.128	0.95	86.6%	13.4%
		global	local	27.4	27.4	57.00 ± 3.12***	18.64 ± 3.71***	0.839	0.114	0.95	88.1%	11.9%
		global	global	3.1	3.1	56.46 ± 3.15***	14.56 ± 3.75**	0.863	0.086	0.95	91.0%	9.0%
		global	global	27.4	3.1	57.93 ± 3.34***	12.95 ± 3.98*	0.872	0.073	0.94	92.3%	7.7%
		global	global	3.1	27.4	55.57 ± 2.80***	20.01 ± 3.33***	0.832	0.129	0.96	86.6%	13.4%
		global	global	27.4	27.4	56.89 ± 2.94***	18.32 ± 3.50***	0.846	0.112	0.96	88.3%	11.7%
Pairwise models	Artificial	local	local	3.1	3.1	282.08 ± 12.05***	323.78 ± 12.05***	0.360	0.474	0.83	43.2%	56.8%
		local	local	3.1	27.4	124.06 ± 12.94***	376.50 ± 12.94***	0.077	0.711	0.79	9.8%	90.2%
		global	global	3.1	3.1	300.30 ± 13.09***	304.32 ± 13.09***	0.399	0.409	0.81	49.3%	50.7%
		global	global	3.1	27.4	152.73 ± 11.45***	400.93 ± 11.45***	0.107	0.740	0.85	12.7%	87.3%
	Real	local	local	3.1	3.1	53.06 ± 2.98***	32.01 ± 3.55***	0.719	0.240	0.96	75.0%	25.0%
		local	local	3.1	27.4	30.48 ± 6.69**	50.45 ± 7.97***	0.290	0.496	0.79	36.9%	63.1%
		global	global	3.1	3.1	53.12 ± 3.18***	31.62 ± 3.78***	0.719	0.235	0.95	75.4%	24.6%
		global	global	3.1	27.4	41.09 ± 4.22***	47.38 ± 5.02***	0.471	0.447	0.92	51.3%	48.7%

Regressions were performed on both the multiplayer and pairwise models, using tolerance (T) and suppression (S) abilities of 23 real *Pseudoroegneria* accessions and of 256 simulated accessions. For each model, the regression coefficient (B ± SE), adjusted dominance weight (D/R^2), dominance weight (D) and determination coefficient (R^2) are shown. Results of models with dispersal limitation for one species, both species or neither species are shown. Life expectancy of each species in time-steps is also shown. Significance of each predictor (T or S) is shown by an asterisk next to the parameter estimate (^{a} $p=0.647$, * $p < 0.05$, ** $p< 0.001$, *** $p < 0.0001$).

suppression on fitness at each recorded time-step, by calculating unstandardized regression coefficients of change in abundance against tolerance and suppression ability.

Results

Our greenhouse experiment revealed that the ability to tolerate competition from *Centaurea* (*T*) and the ability to suppress *Centaurea* (*S*) varied substantially among the 23 accessions of *Pseudoroegneria*. RIIs for suppression ranged from −0.54 to −0.17 and RIIs for tolerance ranged from −0.54 to −0.14. Importantly, *T* and *S* were not significantly correlated ($r=0.281$, $p=0.195$, $n=23$, Table 1, Fig. 2). *Centaurea* and *Pseudoroegneria* were roughly equivalent competitors in our experimental conditions.

In the pairwise models based on the 23 real *Pseudoroegneria* accessions, three accessions competitively excluded *Centaurea* (2, 4 and 7; Table 1), and three did not survive invasion when dispersal was limiting (11, 12 and 19; Table 1). The other 17 accessions coexisted with *Centaurea* but varied in final abundance. When dispersal was global and life expectancies were short only one *Pseudoroegneria* accession excluded *Centaurea* and only one was extirpated. Dominance weight analyses indicated that ability to tolerate competition accounted for ~24% of the total variance and ~25% of the explained variance in final rank (Table 1, Fig. 2). In contrast, suppression accounted for 72% of the total variance and 75% of the explained variance in rank. The relative benefits of suppression were qualitatively similar when dispersal was random versus limited in pairwise models based on real accessions. In the pairwise models based on 256 artificial genotypes, suppression was less important overall and essentially equal to tolerance in importance when life expectancies were short (Table 2). However, a long life expectancy of *Pseudoroegneria* increased the importance of suppression in all models, dramatically so in a few cases.

In the 256-accession models *Centaurea* was usually excluded by *Pseudoroegneria* with $T > 0.5$, so there was little variation in competitive rank among strong tolerators. Among less tolerant genotypes, final abundance was primarily affected by suppression ability, to the extent that accessions with $S < 0.5$ usually were extirpated. This was especially pronounced when dispersal was global for both species (Supplementary information). In the pairwise models this resulted in a curious outcome: the ability of *Pseudoroegneria* to persist depended on the tolerance ability of its competitor.

The performance of *Pseudoroegneria* accessions in pairwise models was a poor predictor of their success in the multiplayer models. When dispersal was global for both *Pseudoroegneria* and *Centaurea* and both species were short-lived, 91% of the explained variance in the overall competitive rank of natural accessions was determined by tolerance, with just 9% determined by suppression (Table 2, Supplementary information). Suppression was more beneficial in models with dispersal limitation, although it was still three times less important than tolerance in determining rank. In models containing 256 artificial genotypes the variance explained by suppression was between 1.9% and 19.1%, although in most cases it was less than 10% (Table 2). Suppression tended to be more beneficial in models with dispersal limitation in both species and long life expectancy of *Pseudoroegneria*. Our estimates of the effects of *T* and *S* on rank were influenced by the fact that the true effects of *T* and *S* were not strictly linear. This is apparent in Fig. 3, which depicts competitive rank for each

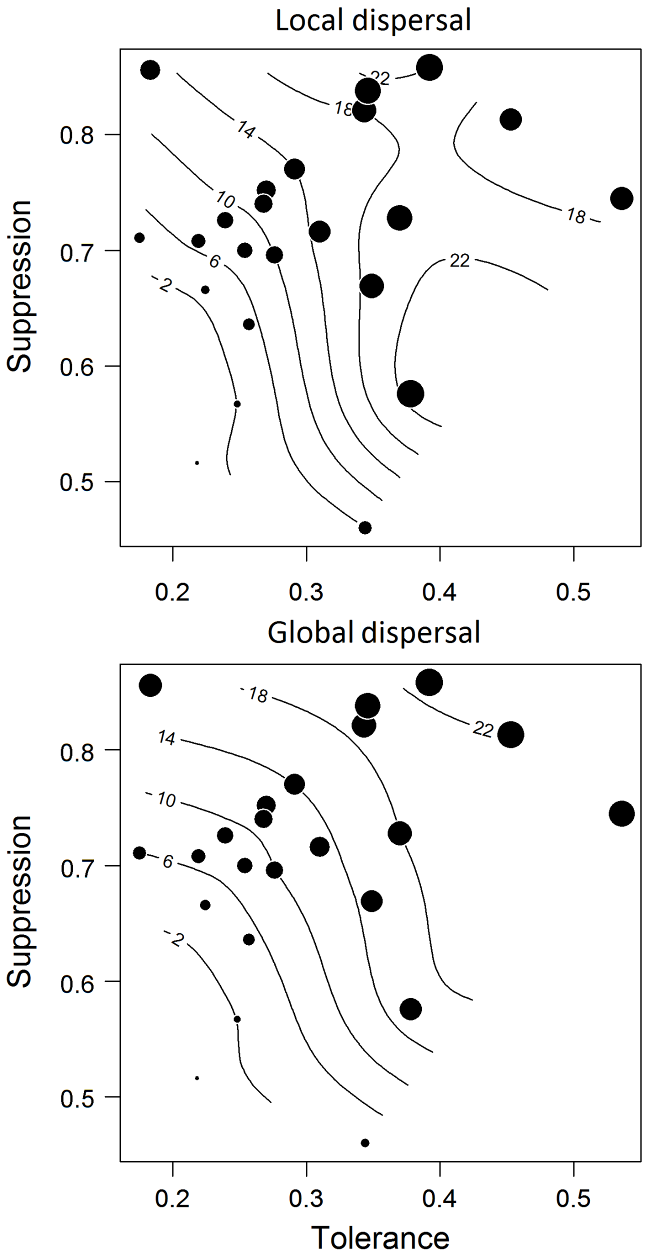

Figure 2. Tolerance and suppression abilities of the 23 accessions of *Pseudoroegneria*, and their effects on competitive rank. Dot area equals simulated competitive rank. Contours also show how simulated competitive rank varies depending upon tolerance and suppression ability. Contour plots can be read like a topographic map; with rising contours indicating rising competitive rank. Models with and without dispersal limitation are shown.

combination of *T* and *S*. Linear effects would produce parallel contour lines. Instead, the lines sometimes diverged, meaning that the effects of tolerance and suppression varied as time passed and as the relative abundance of strong tolerators and strong suppressors changed.

In all multiplayer models, tolerance was favored and mean *T* (averaged across all individuals in the model) increased rapidly as time passed (Fig. 3, 4). Suppression ability was weakly favored and mean *S* increased slowly. This process continued until the genetic diversity of *T* became zero, at which point selection acted only on suppression ability, which would gradually increase until the invader was eventually extirpated.

When dispersal was global for either or both species, *Pseudoroegneria* accessions with strong tolerance abilities had a strong competitive advantage and mean *T* increased rapidly. In comparison, the fitness benefits of suppression were much lower, and increases in mean *S* were negligible (Supplementary information). Both species benefitted from having a longer life-expectancy and were more abundant when they were long-lived versus short-lived. When *Centaurea* was long-lived, it invaded rapidly and selection on the native was intense. This resulted in strong selection for improved competitive ability in *Pseudoroegneria*, but the long life expectancy of *Centaurea* forestalled its eventual extirpation. When the *Pseudoroegneria* was long-lived, but *Centaurea* was not, selection was weak and the invader persisted at low abundance until it was eventually extirpated by *Pseudoroegneria* as it evolved to become a better competitor. Dispersal limitation was disadvantageous for both species, as it reduced the number of available sites for propagules, increasing intraspecific competition for recruitment sites and limiting population growth. As a result, it tended to have a stabilizing effect and promoted coexistence. Dispersal limitation in both species caused aggregation of *Centaurea* and weak suppressors in long-lasting patches (Supplementary information).

Discussion

Two components determine the outcome of competition: suppression of competitors and tolerance of competitors (Miller and Werner 1987, Aarssen 1989, Goldberg 1990). Traits that improve competitor tolerance allow plants to grow and reproduce despite competition, and traits that improve competitor suppression allow plants to remove their competitors, thereby gaining a greater share of resources. In this way, competition between two plants can be described as a boxing match (Aarssen 1989), in which plants can achieve success

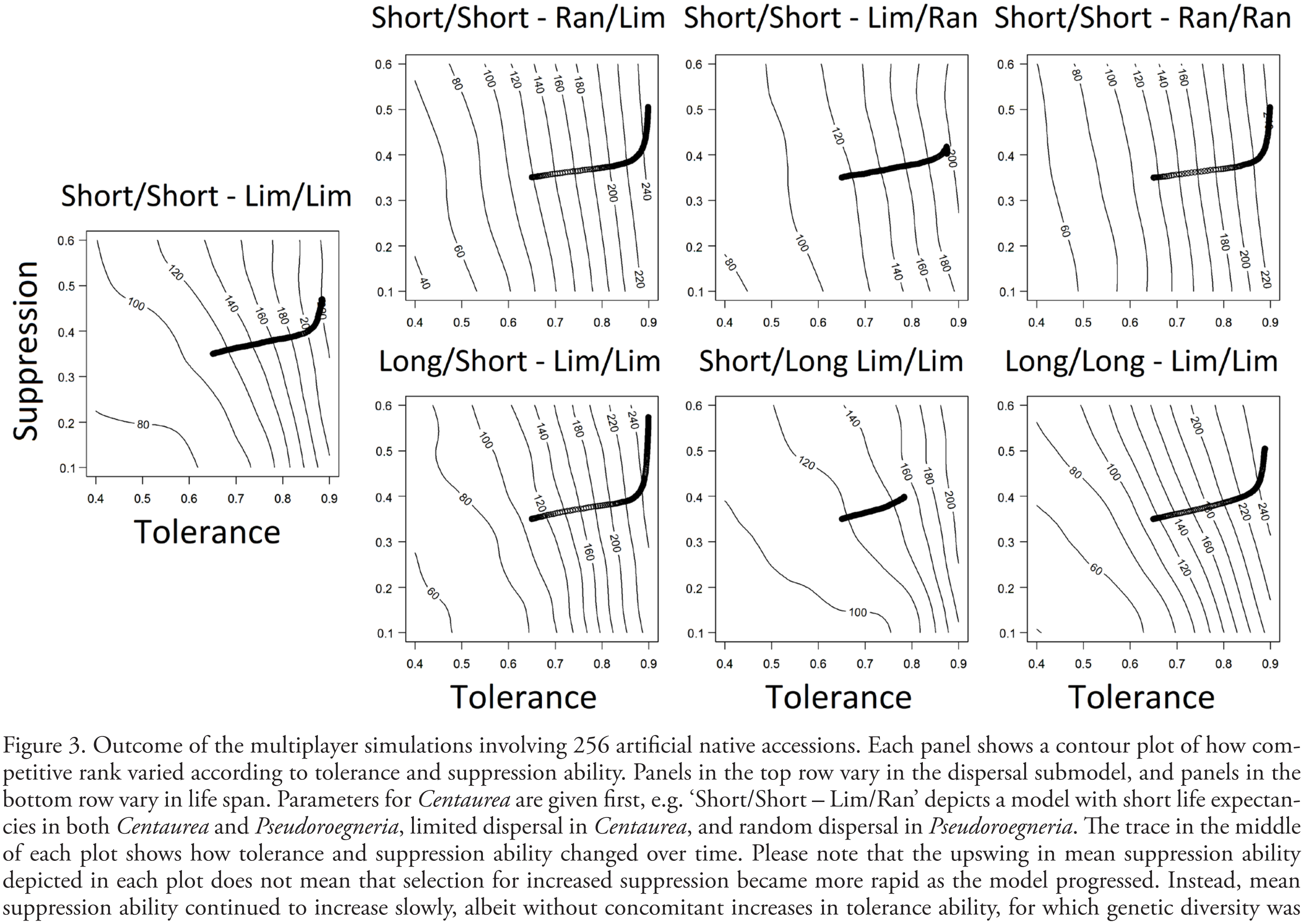

Figure 3. Outcome of the multiplayer simulations involving 256 artificial native accessions. Each panel shows a contour plot of how competitive rank varied according to tolerance and suppression ability. Panels in the top row vary in the dispersal submodel, and panels in the bottom row vary in life span. Parameters for *Centaurea* are given first, e.g. 'Short/Short – Lim/Ran' depicts a model with short life expectancies in both *Centaurea* and *Pseudoroegneria*, limited dispersal in *Centaurea*, and random dispersal in *Pseudoroegneria*. The trace in the middle of each plot shows how tolerance and suppression ability changed over time. Please note that the upswing in mean suppression ability depicted in each plot does not mean that selection for increased suppression became more rapid as the model progressed. Instead, mean suppression ability continued to increase slowly, albeit without concomitant increases in tolerance ability, for which genetic diversity was soon exhausted.

via some combination of neighbor suppression and neighbor tolerance (Fig. 1A–C). Our results suggest that this model of competition holds true when competition is pairwise, occurring either between two competing individuals or two genetically homogenous populations. However, when competition is multiplayer, as in virtually all natural circumstances, we found that indirect interactions caused a dramatic reduction in the benefits of neighbor suppression. This occurred because, in multiplayer competition, plants that suppress their neighbors indirectly benefit the other competitors in the community (Fig. 1D).

In our models, the indirect benefit of neighbor suppression was produced by two complementary processes. One process occurred at the local, or per plant, scale, whereby any native plant that killed a competing invader experienced reduced competition from the invader. We term this the 'neighbor effect of suppression' because the benefit of suppressing a neighbor was mediated by reducing competition from that neighbor. This was the intended, explicitly-modeled benefit of suppression in our models. The other process occurred at the population scale, whereby suppression of invaders resulted in lower invader abundance, reducing the chance of a focal native plant or its offspring encountering competition in the future. We call this the 'abundance effect of suppression', because the indirect benefit of suppression was mediated by changes in competitor abundance. The abundance effect was an emergent, population-level consequence of individual competitive interactions in our models. It modified the strength of the neighbor effect by altering the probability that a plant which excluded its neighbor would experience competition in the future – the higher the abundance of *Centaurea*, the more quickly competitively excluded *Centaurea* individuals would be replaced. Thus, neighbor suppression by one individual reduced competition for the community as a whole by reducing the population size of the competing species.

In pairwise models, in which a genetically homogenous native population competed against a genetically homogenous invader population, both the neighbor effect and abundance effect provided unshared benefits to a competitor – in other words, both the neighbor and abundance affects worked to benefit accessions able to suppress their neighbors. However, during multiplayer competition the abundance effect did not provide a unique fitness advantage. Instead, the benefits of the abundance effect were shared by all *Pseudoroegneria* accessions, because a decrease in *Centaurea* abundance benefitted all *Pseudoroegneria* in the community regardless of their suppression ability (Fig. 1D). If the abundance effect was weak, a switch from pairwise to multiplayer competition would not result in a large decline in the importance of suppression, because the neighbor effect continued to provide exclusive benefits to neighbor suppression when competition was multiplayer, but the abundance effect did not. However, we saw that suppression was much less beneficial in the multiplayer models than in the pairwise models, meaning that the abundance effect dominated in our models. This finding is significant because it suggests that competition goes beyond a local interaction

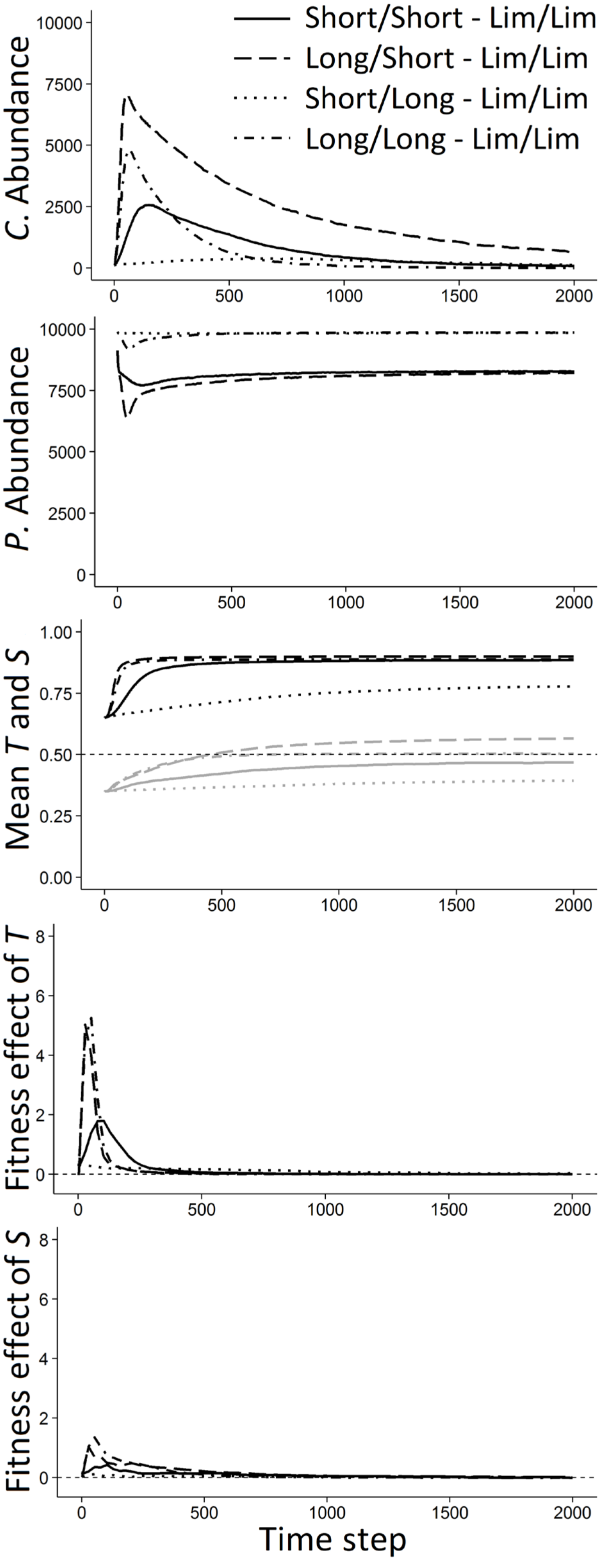

Figure 4. Changes in native and invader abundance, mean native tolerance ability (*T*: black) and native suppression ability (*S*: grey), the fitness benefit of tolerance, and the fitness benefit of suppression as multiplayer models progressed. Results from dispersal-limited models with varying life expectancy of artificial native and invasive genotypes are shown.

between two neighboring individuals, instead involving indirect interactions that propagate throughout the entire community with potentially dramatic consequences (Aschehoug and Callaway 2015). We suggest that it may be crucial to consider the community-level consequences of competition in addition to the local-level consequences, as we find that the outcomes of local processes may not necessarily scale up to influence community level outcomes in straightforward or intuitive ways.

Neighbor suppression by *Pseudoroegneria* was more beneficial when *Pseudoroegneria* was long-lived, *Centaurea* was short-lived and dispersal was local. Each of these conditions allowed *Pseudoroegneria* accessions to exert more local control of their competitive environment and lessened the tendency of the abundance effect to distribute benefits of suppression among accessions. Our models indicate that priority effects and dispersal limitation might act to increase the fitness benefit of neighbor suppression. The only competitive asymmetry in our models was variation in life expectancy between competitors, but in that case selection favored suppression when *Pseudoroegneria* was longer-lived than its competitor and tolerance when it was shorter-lived. If this is a general pattern, we hypothesize that selection will favor suppression in larger, longer-lived species and tolerance in smaller, shorter-lived species.

Adaptation by native plants has been hypothesized to improve resistance of native communities to invasion (Simberloff and Gibbons 2004, Callaway et al. 2005, Strauss et al. 2006, Lau 2008, Fletcher et al. 2016), and understanding the relative importance of tolerance and its potential fitness benefits sheds new light on how this process may occur. For example, if invaders select for native genotypes with superior tolerance ability, and if tolerance ability is heritable, invasions may lead to evolutionary increases in competitive tolerance and shifts in the composition of the plant communities towards more tolerant species (Aarssen 1983, Strauss et al. 2006, Lau 2008, Thorpe et al. 2011). Depending upon the mechanism that promotes tolerance, this could hasten competitive exclusion of either competitor (e.g. if tolerance involves changes in R*; Chesson 2000) or stabilize coexistence of native and invasive species (e.g. if tolerance involves adaptation to exotic allelochemistry), gradually attenuating invasions over time. Interestingly, exotic species appear to demonstrate stronger competitive tolerance than native species they interact with, rather than exerting different suppressive effects (Golivets and Wallin 2018).

Perhaps counterintuitively, the results of our simulations suggest that the evolution of competitor tolerance might destabilize plant interactions, as the invader was more likely to be extirpated when it competed with strong tolerators relative to strong suppressors. We believe this happened because monotypic populations with high tolerance ability were able to maintain a very high abundance regardless of the invader abundance. Thus, the invader was never able to gain a foothold when competing with strong tolerators because it was never able to escape competition. In contrast, populations of strong suppressors could not extirpate invaders unless they were also strongly tolerant of the presence of the invader. Otherwise, they would eventually yield ground to the invader.

Our models were built around certain assumptions and simplifications. There was no within-species variation in the competitive ability of *Centaurea*, there was no direct intraspecific competition, there was no direct interaction between adjacent cells, only a few dispersal modes and life expectancies were modeled, and we did not model age, growth, resource uptake or priority effects. Many of these assumptions were guided by parsimony, ensuring that our model was as simple as possible as informed by our experimental competition trials. These assumptions also enabled us to focus on the process of interest – how the relative importance of tolerance and suppression varied between pairwise and multiplayer competition – while also limiting our ability to accurately model population dynamics and long-term consequences of invasion. In the case of intraspecific competition, the abundance effect should occur just as it did in the models presented here, weakening benefits of neighbor suppression. Furthermore, if intraspecific competition is strong, there could be a particular disadvantage to suppressing a neighbor of a different species, if it meant replacement by a more competitive conspecific. We saw an element of that process when dispersal was limited for both species: *Pseudoroegneria* accessions that were tolerant of *Centaurea*, but that were also poor suppressors, maintained patches of *Centaurea* that excluded less-tolerant *Pseudoroegneria* accessions, creating a form of mutual facilitation. This process is visible in Supplementary information, where patches of *Centaurea* overlap accessions with poor suppression ability (blue) and strong tolerance ability (red) for much of the model duration.

The limited life-history parameters allowed us to see that life history variation might influence the relative importance of tolerance and suppression competition, without providing a detailed picture of exactly how. Likewise, further study is needed to determine how variation in other parameters, or in the model environment, might influence our results. Nonetheless, our data provide evidence that in genetically-diverse plant populations suppression might be a much less important component of competitive ability than can be inferred from a pairwise paradigm of competition.

By modeling competition as a phenomenological process rather than a mechanistic process – e.g. *Pseudoroegneria* and *Centaurea* did not contest for a resource in our models – we were able to draw general conclusions irrespective of the mechanism underlying an interaction. For example, in some mechanisms of competition, such as shading, competition is asymmetric and tolerance and suppression are correlated, making them difficult to distinguish. A phenomenological perspective provides clarity; even when tolerance and suppression are mechanistically correlated, our conceptual model predicts that neighbor suppression is incidental to the benefits of tolerance (in this example, increased light capture). Also, tolerance and suppression precede community assembly processes because they are not extrinsic measurements of ecological outcomes. Instead, they are intrinsic traits of individual plants that describe how plants engage in competitive interactions. For example, a strong tolerator is a species that has a higher instantaneous survival or reproductive output in competition than a weak tolerator. Likewise, a strong suppressor is a plant that tends to have stronger negative effects on the instantaneous survival and reproductive output of competitors than a weak suppressor. This is an important distinction because, first, it does not presuppose any particular outcome of the interaction between two competitors. Thus, it is not a tautology that tolerance is a stronger determinant of fitness than suppression. Second, tolerance and suppression as measured in one system can be used to predict ecological outcomes in other systems. Third, the fitness consequences of tolerance and suppression are easily analyzed because tolerance and suppression are, by their definition, traits that can be directly acted on by selection. Our finding that tolerance may be much more important than suppression in plant communities has important implications for our understanding of the selective forces that competing plants experience, how ecological conditions alter those forces, how competitive interactions between plants affect their distribution and abundance in nature, and it highlights a need for further field studies of the importance of tolerance and suppression competition in natural communities with multiple competing plants.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sf7m0cg4c> (Atwater et al. 2020).

Funding – This research was supported by the Project of the National Natural Science Foundation of China (41830321, 31870412, 32071532, 31670435, 31670437) We thank the NSF Graduate Research Fellowship Program for funding. We are grateful for funding from the U.S. National Science Foundation DEB 0614406 and NSF EPSCoR Track-1 EPS-1101342 (INSTEP 3) to RMC. We thank the Plant Germplasm Introduction and Testing Research Station, and Curator Vicki Bradley, in Pullman, WA, for supplying *Pseudoroegneria* seeds.

Author contributions

Daniel Atwater: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Validation (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Ragan M. Callaway**: Conceptualization (supporting); Data curation (equal); Investigation (supporting); Project administration (supporting); Resources (lead); Software (lead); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Sa Xiao**: Conceptualization (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Software (supporting); Validation (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

References

Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. – Am. Nat. 122: 707–731.

Aarssen, L. W. 1989. Competitive ability and species coexistence: a 'plant's-eye' view. – Oikos 56: 386–401.

Armas, C. et al. 2004. Measuring plant interactions: a new comarative index. – Ecology 85: 2682–2686.

Aschehoug, E. T. and Callaway, R. M. 2015. Diversity increases indirect interactions, attenuates the intensity of competition and promotes coexistence. – Am. Nat. 186: 452–459.

Aschehoug, E. T. et al. 2014. Fungal endophyte increases the allelopathic effects of an invasive forb. – Oecologia 175: 285–291.

Aschehoug, E. T. et al. 2016. The mechanisms and consequences of interspecific competition among plants. – Annu. Rev. Ecol. Evol. Syst. 47: 263–281.

Atwater, D. Z. et al. 2020. Data from: Competition as a demolition derby: why tolerating competitors is more important than suppressing them. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.sf7m0cg4c>.

Azen, R. and Budescu, D. V. 2003. The dominance analysis approach for comparing predictors in multiple regression. – Psychol. Methods 8: 129–148.

Callaway, R. M. et al. 2005. Natural selection for resistance to the allelopathic effects of invasive plants. – J. Ecol. 93: 576–583.

Callaway, R. M. et al. 2011. Escape from competition: neighbors reduce *Centaurea stoebe* performance at home but not away. – Ecology 92: 2208–2213.

Carlyle, C. N. and Fraser, L. H. 2006. A test of three juvenile plant competitive response strategies. – J. Veg. Sci. 17: 11–18.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. – Annu. Rev. Ecol. Syst. 31: 343–366.

Doebeli, M. and Knowlton, N. 1998. The evolution of interspecific mutualisms. – Proc. Natl Acad. Sci. USA 95: 8676–8680.

Fletcher, R. A. R. A. et al. 2016. An exotic invasive plant selects for increased competitive tolerance, but not competitive suppression, in a native grass. – Oecologia 181: 499–505.

Goldberg, D. E. 1990. Components of resource competition in plant communities. – In: Grace, J. B. and Tilman, D. (eds), Perspectives on plant competition. Blackburn Press, pp. 27–49.

Goldberg, D. E. 1996. Competitive ability: definitions, contingency and correlated traits. – Phil. Trans. R. Soc. B 351: 1377–1385.

Goldberg, D. E. and Werner, P. A. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. – Am. J. Bot. 70: 1098–1104.

Golivets, M. and Wallin, K. F. 2018. Neighbour tolerance, not suppression, provides competitive advantage to non-native plants. – Ecol. Lett. 21: 745–759.

Grimm, V. et al. 2010. The ODD protocol: a review and first update. – Ecol. Model. 221: 2760–2768.

Growth, R. B. et al. 1985. Relationships between growth and competitiveness of four annual weeds. – J. Appl. Ecol. 22: 895–905.

Herron, G. J. et al. 2001. Influence of nutrient availability on the interaction between spotted knapweed and bluebunch wheatgrass. – Restor. Ecol. 9: 326–331.

Howard, T. G. 2001. The relationship of total and per-gram rankings in competitive effect to the natural abundance of herbaceous perennials. – J. Ecol. 89: 110–117.

Howard, T. G. and Goldberg, D. E. 2001. Competitive response hierarchies for germination, growth and survival and their influence on abundance. – Ecology 82: 979–990.

Keddy, P. A. 1990. Competitive hierarchies and centrifugal organization in plant communities. – In: Grace, J. B. and Tilman, D. (eds), Perspectives in plant competition. Academic Press, pp. 265–290

Lau, J. a. 2008. Beyond the ecological: biological invasions alter natural selection on a native plant species. – Ecology 89: 1023–1031.

Leger, E. A. 2008. The adaptive value of remnant native plants in invaded communities: an example from the great basin. – Ecol. Appl. 18: 1226–1235.

MacDougall, A. S. and Turkington, R. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. – J. Ecol. 92: 422–434.

Maddox, D. M. 1979. The knapweeds: their economics and biological control in the Western States, USA. – Rangelands 1: 139–141.

Mahall, B. E. and Callaway, R. M. 1996. Effects of regional origin and genotype on intraspecific root communication in the desert shrub *Ambrosia dumosa* (Asteraceae). – Am. J. Bot. 83: 93–98.

Maron, J. L. and Marler, M. 2008. Field-based competitive impacts between invaders and natives at varying resource supply. – J. Ecol. 96: 1187–1197.

Miller, T. E. and Werner, P. A. 1987. Competitive effects and responses between plant species in a first-year old-field community. – Ecology 68: 1201–1210.

Mitchley, J. and Grubb, P. J. 1986. Control of relative abundance of perennials in chalkgrassland in southern England. I. Constancy of rank order and results of pot- and field-experiments on the role of interference. – J. Ecol. 74: 1139–1166.

Roche Jr., B. and Talbott, C. 1986. The collection history of Centaureas found in Washington State. – Res. Bull. Agric. Res. Center, Washington State Univ. No. XB 0978.

Rowe, C. L. J. and Leger, E. A. 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. – Evol. Appl. 4: 485–498.

Simberloff, D. and Gibbons, L. 2004. Now you see them, now you don't! – population crashes of established introduced species. – Biol. Invas. 6: 161–172.

Strang, R. et al. 1979. Knapweeds: British Columbia's undesirable aliens. – Rangelands 1: 141–143.

Strauss, S. Y. et al. 2006. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? – Ecol. Lett. 9: 357–374.

Thorpe, A. S. et al. 2011. Interactions among plants and evolution. – J. Ecol. 99: 729–740.

Uriarte, M. et al. 2002. A model of simultaneous evolution of competitive ability and herbivore resistance in a perennial plant. – Ecology 83: 2649–2663.

Van der Putten, W. H. et al. 2013. Plant–soil feedbacks: the past, the present and future challenges. – J. Ecol. 101: 265–276.

Vila, M. and Weiner, J. 2004. Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. – Oikos 105: 229–238.

Willis, C. G. et al. 2010. Genetic variation in tolerance of competition and neighbour suppression in *Arabidopsis thaliana*. – J. Evol. Biol. 23: 1412–24.

Yamamura, N. et al. 2004. Evolution of mutualism through spatial effects. – J. Theor. Biol. 226: 421–428.