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Competition as a demolition derby: why tolerating
competitors is more important than suppressing them. –
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Appendix 1

Individual-based models: ODD protocol

Purpose. The purpose of these models was to compare the relative effects of tolerance and suppression ability on the overall competitive ability of a native plant, and to determine how indirect interactions among conspecific competitors influence the relative importance of tolerance and suppression, by comparing outcomes of the multiplayer and pairwise models.

Entities, state variables and scale. Individual plants populated a two-dimensional grid, the cells of which constituted the entity in our model. Each grid cell could be either unoccupied, occupied by a single native individual (e.g. *Pseudoroegneria*), occupied by a single invasive individual (e.g. *Centaurea*), or occupied by one individual of each species. While the invasive plant was characterized only by its presence or absence, the native plant could vary in its tolerance ability (*T*) and suppression ability (*S*). As such, each cell was characterized by three state variables: the presence or absence of an invader and the tolerance (*T*) and suppression (*S*) ability of a single native, if present. Tolerance and suppression were invariant through the life of an individual native plant, although it could die and be replaced. There was no variable for age or size.

The model landscape consisted of a 100×100 cell grid (total: 10 000 cells). This landscape ‘wrapped’ in such a way that cells on the edge of the landscape were considered adjacent with their immediate neighbors, as well as cells at the opposite end of the landscape (Yamamura et al. 2004). A cell is interpreted as the spatial area occupied by a single *Pseudoroegneria* (roughly 0.25 m^2). All

cells were identical. Each time-step represented a year, in which individuals of both species were allowed to produce propagules and in which survival of both species was evaluated stochastically.

Process overview and scheduling. At each time-step native and invasive survival was evaluated simultaneously for all cells. Following this, state variables were updated for all cells. Next, seed production occurred, followed by establishment. The state variables updated again following establishment and the model advanced one time-step. Multiplayer models proceeded until 5000 time-steps had elapsed. This was sufficient to allow equilibration, with drift becoming the dominant process affecting species and ecotype abundance. Pairwise models proceeded until 2000 time-steps had elapsed. This was done because the pairwise models tended to equilibrate quickly and additional steps were unnecessary.

Design concepts: basic principles. We chose to model the interaction between native and invasive plants in the simplest fashion that our data allowed. One consequence of this is that we modelled competition as a phenomenological process rather than a mechanistic one. Doing so enabled us to test relative changes in the importance of tolerance and suppression ability directly without interference from confounding correlations between tolerance and suppression that can arise in a mechanistic model. However, the simplicity of our models prevents us from accurately forecasting the outcome of invasion of *Pseudoroegneria* populations by *Centaurea*. Rather, our models are designed only to shed light on the relative importance of tolerance and suppression, and how this might change under different ecological scenarios.

Specifically, we were interested in comparing the relative importance of tolerance and suppression in multiplayer models (in which a native population containing multiple ecotypes/genotypes competed against an invasive population containing a single genotype) as compared to pairwise models (in which a native population containing a single ecotype/genotype competed against an invasive population containing a single genotype). These scenarios differ in the presence of indirect interactions among native ecotypes/genotypes, which manifest in the multiplayer models but not in the pairwise models. Comparing models allows us to test how indirect

interactions among conspecific competitors influence the relative benefits of tolerance and suppression. Here we chose to represent pairwise competition as an interaction between two genetically identical populations for consistency with the multiplayer models, in which a genetically diverse native population competed with a genetically identical invasive population.

Design concepts: emergence. The population dynamics we observed were an emergent consequence only of direct interactions among individuals. There was no behavioral adaptation in either species and the environment was static.

Design concepts: interaction. Two direct interactions existed in our models: 1) native and invasive individuals that shared a cell interacted directly by reducing one another's survival probability, and 2) propagules of each species competed for empty space. In ecotypically/genetically diverse native populations, these interactions in turn produced a positive indirect interaction among native ecotypes/genotypes, whereby ecotypes/genotypes that suppressed the invader benefitted others in the system by reducing the abundance of the invader.

Design concepts: stochasticity. Stochasticity influenced whether an individual survived a time-step, where its propagules were distributed, and which propagule recruited into an empty cell. To account for stochasticity, multiplayer models were replicated 50 times. Pairwise models involving the 23 *Pseudoroegneria* ecotypes were replicated 100 times, and pairwise models involving the 256 artificial genotypes were replicated 18 times.

Design concepts: collectives. Collective behavior was not explicitly modeled, but it manifested in two ways: 1) individuals acted independently in the monotypic single-ecotype models, but they functioned collectively, because they acted in concert to influence invader abundance and because their propagules did not experience intraspecific competition (being exchangeable). 2) In the multiplayer models with dispersal limitation, *Centaurea* occurred primarily in patches of *Pseudoroegneria* with low suppression ability and high tolerance ability. These patches were maintained by mutually facilitative interactions between invaders and weak-suppressor natives.

Design concepts: observation. The total number of lattice cells containing *Centaurea* and each *Pseudoroegneria* ecotype were censused at the end of the first 200 time-steps, every 10 time-steps between 210 and 2500 time-steps, and every 50 time-steps between 2550 and 5000 time-steps. These data were used to calculate competitive ranks, depending upon final abundance for surviving ecotypes, and time to extirpation for extirpated ecotypes.

Initialization. The first step in initialization was to determine the identity of the native ecotypes/genotypes to be used and their tolerance and suppression abilities (T and S). In the real-ecotype models, these were the experimentally measured values of T and S . In the simulated-genotype models, these were the simulated values described above.

In the pairwise models, at initialization each of the 10 000 cells contained an individual native plant belonging to one chosen ecotype/genotype. In the multiplayer models all of either the 23 *Pseudoroegneria* ecotypes or the 256 artificial genotypes were randomly distributed, such that each cell contained exactly one native individual and all ecotypes/genotypes were as evenly represented as possible. In all models, 100 of the 10 000 cells were randomly chosen to also contain *Centaurea*. During initialization we also specified the maximum survival probability P_{max} as being either 0.8 or 0.975 for either species. A maximum survival probability $P_{max} = 0.8$ resulted in a 3.1-step life expectancy for an individual experiencing no competition, and $P_{max} = 0.975$ resulted in a 27.4-step life expectancy. These values were chosen because they correspond roughly to the life expectancies of *Centaurea* and *Pseudoroegneria* in Montana (with a time-step being equivalent to one year) and because they represent about an order of magnitude of variation in life expectancy. In the models with artificial genotypes we varied the life expectancy of both species independently. We also independently specified the mode of dispersal of each species (*i.e.*, determining whether to use the local or global dispersal submodel).

Input data. The model does not contain any external input of driving variables.

Submodels: survival. When filled *Centaurea* and *Pseudoroegneria* cells overlapped, survival probability (P) was determined as:

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

for *Centaurea* individual 'j': $P_j = P_{max,C} * (1 - S_i)$

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 . If an individual died, it was not allowed to disperse a propagule, and the state variable of its resident cell was updated to reflect that it was empty.

Submodels: dispersal. Each surviving individual produced a single propagule, which was dispersed either globally or locally. For *Pseudoroegneria*, this propagule was given the same values of T and S of the originating individual. During local dispersal, a propagule was dispersed into one cell randomly selected from the eight cells adjoining the parent cell. A propagule was not dispersed into the parent cell. During global dispersal, each propagule was dispersed to a randomly selected cell in the entire grid, including the parent cell.

Submodels: establishment. A propagule established if it arrived in a cell that did not already contain an individual of the same species, including those cells whose occupants died during the immediately preceding survival step. If multiple *Pseudoroegneria* propagules arrived in the same cell, one propagule was randomly selected to establish, and that cell was assigned the T and S values of the randomly selected propagule. If multiple *Centaurea* propagules arrived in a cell, the cell was simply considered to be established by *Centaurea*. There was no difference between cells established by one propagule or multiple propagules. If a cell did not receive any propagules, recruitment did not occur. There was no interspecific interaction among propagules, and a *Centaurea* propagule had the same probability of establishing in a cell containing only a *Pseudoroegneria* as it did establishing in a completely empty cell. The same was true for *Pseudoroegneria*. A successfully established propagule was considered mature, had its survival checked, and was able to produce a single propagule in the following time-step.

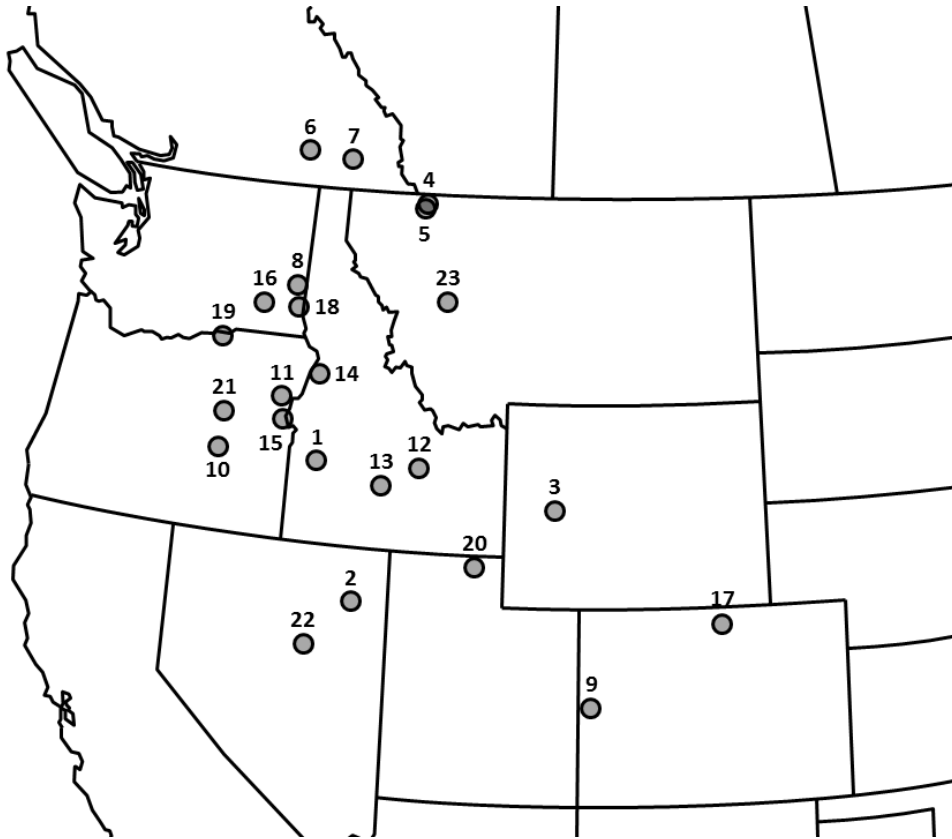


Figure A1. Map of the *Pseudoroegneria* accessions used in this study.

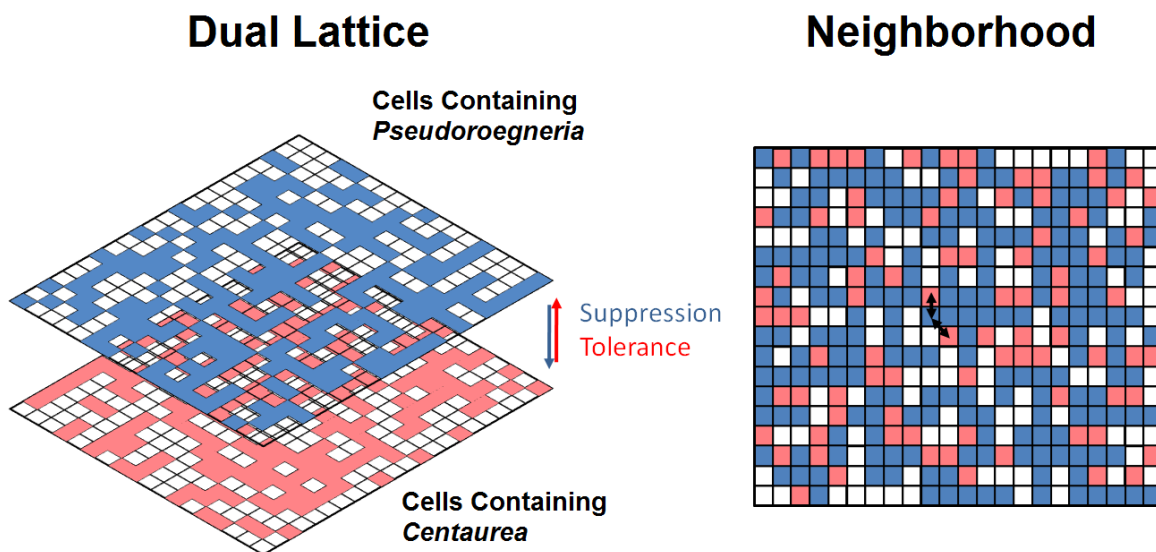


Figure A2. Dual-lattice versus neighborhood models. In this study we used dual lattice models in keeping with our goal of using the simplest and most conservative model appropriate to our data. In dual lattice models, species in lattice A interact only with their neighbor in an overlapping cell in lattice B. All other interactions among community members are indirect. In neighborhood models, species interact directly with their neighbors and both species coexist in a single lattice. Neighborhood models require a larger set of parameters because all possible pairwise interactions must be input. However they model neighborhood interactions rather than just the pairwise and demographic processes reported in this study.

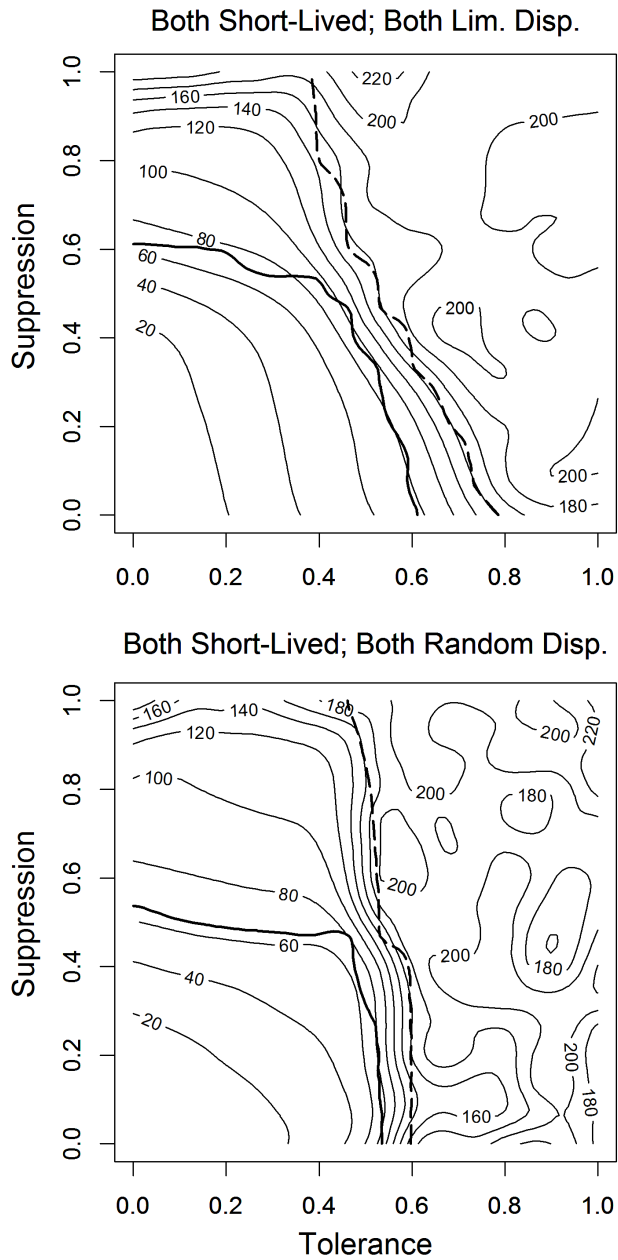


Figure A3. Results of pairwise models with artificial accessions. Note that the entire available parameter space for T and S is plotted. Contour lines show competitive rank. The heavy solid line shows the combinations of T and S that allowed the native species to persist (any values above or to the right of the line). The heavy dotted line shows the combinations of T and S that caused competitive exclusion of the invader (any values above or to the right of the line). In the region between these lines the native and invader coexisted.

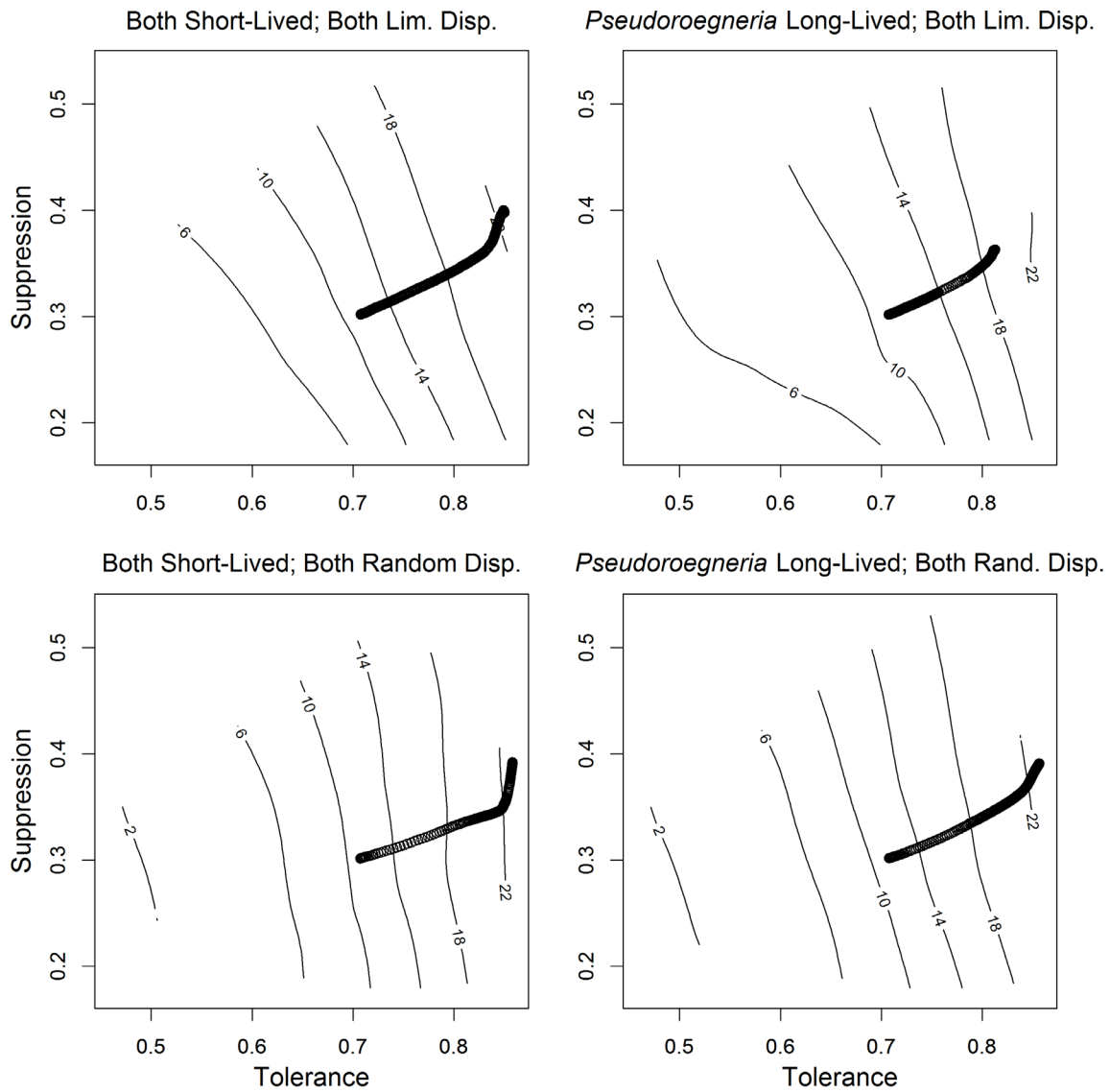


Figure A4. Outcome of the simulations involving 23 *Pseudoroegneria* accessions. Each panel shows a contour plot of how competitive rank varied according to tolerance and suppression ability. The trace in the middle of each plot shows how tolerance and suppression ability changed over time. Please note 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.

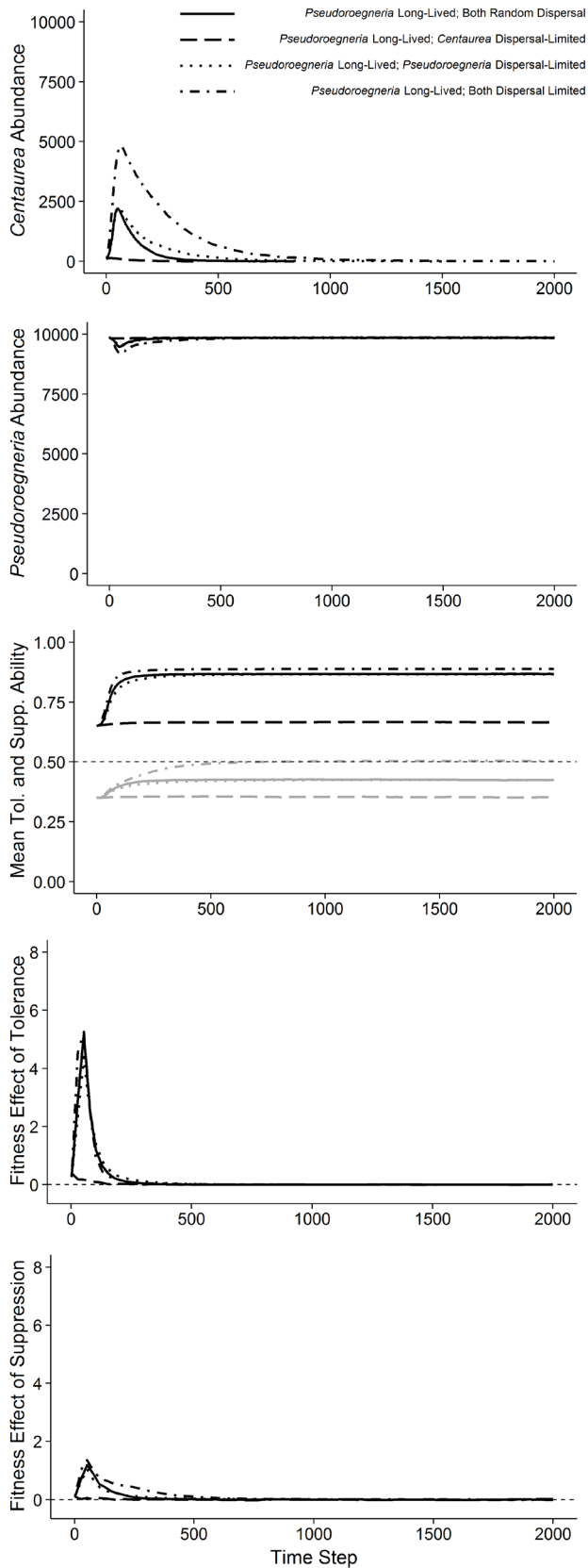


Figure A5. Changes in *Centaurea* and *Pseudoroegneria* abundance, mean tolerance ability (T : black) and suppression ability (S : grey), the fitness benefit of tolerance, and the fitness benefit of suppression as models progressed. Results from models with long life expectancy in *Pseudoroegneria* and varying dispersal limitation are shown.

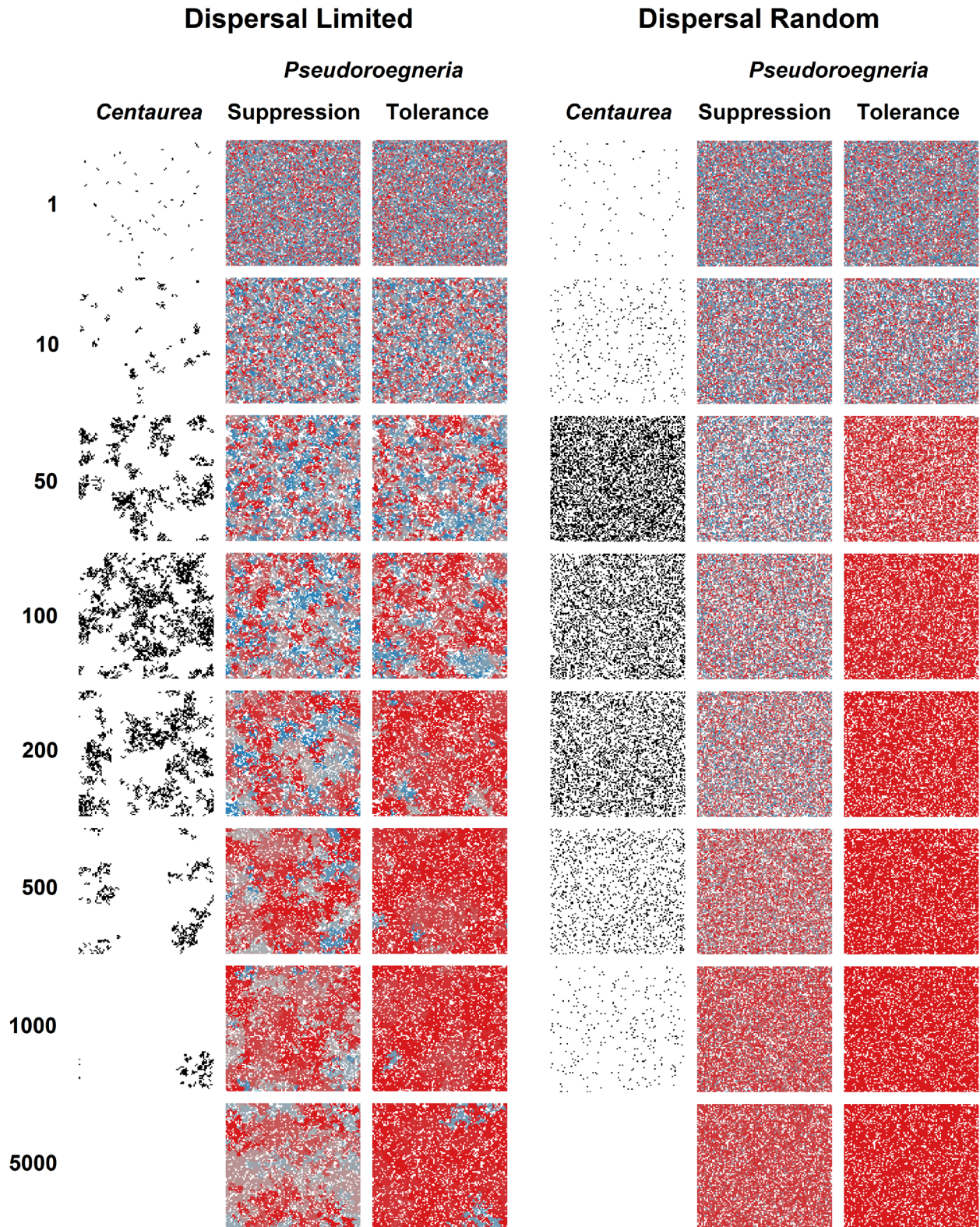


Figure A6. Snapshots of a single model run at multiple time-steps. Each panel shows an overhead view of the plant community (100×100 cell matrix). Both species had short life expectancies. *Centaurea* presence/absence is shown, along with the suppression and tolerance ability of each individual *Pseudoroegneria* (blue is worse, red is better).