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Weed Suppression Success Can Depend on Removal Pattern and Gene Dispersal Distance: Modeling Callery Pear

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Substantial resources are spent each year on weed control, but in many cases eradication projects are incomplete. Here we used the computer program NEWGARDEN to model whether alternate geometric patterns of incomplete removal (99% removed) of the increasingly invasive Callery pear from an isolated fragment differentially affect the rate of population recovery and genetic diversity retention. Geometric patterns of remaining founders within the fragment (1% of the fragment area) included: (A) a long rectangular strip centered on one edge; (B) a square at one corner; (C) a central square; or (D) scattered randomly throughout the entire fragment. Population re-growth and genetic diversity retention measures for each geometric removal pattern were modeled under two contrasting gene dispersal patterns (via both offspring and pollen): short versus long dispersal (both leptokurtic relative to the pistillate plant). After 14 bouts of mating, the greatest difference in census size among comparative recovery populations amounted to 393% (centered founders, long gene dispersal > scattered founders, short gene dispersal). The best pattern of removal for suppressing population regrowth was to leave founders scattered throughout the fragment when gene dispersal was short, or at one corner if gene dispersal was long. The only removal pattern that differed substantially in population genetics characteristics was when remnant individuals were left scattered throughout the fragment and dispersal was short (alleles continued to be lost; observed heterozygosity dropped 13.3% and was still rapidly declining; and inbreeding and/or subdivision were moderate ($F_{it} = 0.12$) and still rapidly increasing). Such comparative modeling can be used to suggest removal patterns that might greatly outperform other removal modalities in terms of suppressing the return of weed populations. The effectiveness of such modeling will be improved by acquisition of accurate life history information of targeted species.

Nomenclature: Callery pear, *Pyrus calleryana* Decne.

Key words: Biological suppression, invasive control, plant population biology, plant population genetics, weed management.

Globally, weed and invasive plant species control and eradication expenditures amount to many billions of dollars every year (e.g., Pimentel et al. 2000; Pimentel et al. 2005). Weed removal efforts are often not conducted to completion for a number of reasons such as exhaustion of project funding or failure to treat all targeted individuals uniformly. Here we use computer modeling to investigate the question: If the same amount of resources is expended to partially remove a weed population, does the geometric pattern of removal affect the rate of population recovery and retention of genetic variation following cessation of control measures?

Several studies have explored, using computer simulations, how different spatial patterns of weed control can affect the subsequent population diffusion dynamics and management economics of such species. The primary focus of several of these analyses has been on economic considerations (e.g., Deen et al. 1993; Finnoff et al. 2010) and are based on large scales with relatively simplified dispersal modalities (e.g., dispersal of propagules is one or a few adjacent cells on a grid per unit time and/or pollen dispersal distances are not considered; e.g., Epanchin-Niell and Wilen 2012; Murphy and Johnsons 2012; Pichancourt et al. 2012; and their references). Some modeling studies suggest that investing resources in reducing connectivity among patches (e.g., Blackwood et al. 2010), or suppressing nascent foci (Moody and Mack 1988) can greatly improve the efficiency of control efforts.

However, many eradication projects will be conducted on smaller, relatively isolated areas (25 km^2 or less), and determining whether some geometric patterns of incomplete weed removal are more effective at suppressing re-invasion in such cases might result in reducing treatment costs. At such scales, differing life history characteristics of different weeds might alter re-invasion outcomes. For example, the role of varying gene dispersal, especially the interplay of variation in

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seed versus pollen dispersal limitations, has been little investigated. How weeds with different age-specific reproduction or mortality schedules respond to different removal geometries is poorly understood. Further, we have been unable to find other studies that explore how different removal geometries might affect subsequent population genetics of weed populations. To underscore the importance of such considerations, partial eradication of a weed in a particular geometric pattern may lead to increased random genetic drift of allele frequencies and loss of alleles, potentially resulting in erratic or reduced evolutionary response potential due to genostasis (Gomulkiewicz and Shaw 2012). If a particular weed is known to be sensitive to inbreeding depression, then removal geometries that increase F_{it} (a measure of inbreeding and differentiation among subpopulations; e.g., Hartl 1987) may result in populations that are less fit, and thus less competitive.

Here, computer modeling the increasingly invasive Callery pear (*Pyrus calleryana* Decne.; Rosaceae; Culley and Hardiman 2007), we explore whether different geometric patterns of removal in an incomplete eradication project can affect the subsequent rate of repopulation and genetic diversity retention. We demonstrate that the computer program NEWGARDEN, designed to model the development of newly founded, isolated populations, can be used to search for preferred patterns of weedy plant removal. NEWGARDEN differs from other modeling programs in that it allows users to explore how differing life history and situational conditions, such as varying gene dispersal distances via offspring versus pollen, or varying age-specific reproduction or mortality, may affect population dynamics after partial extirpation (see below). Further, NEWGARDEN can be used to explore how comparative weed removal patterns affect the subsequent population genetics of the targeted species. Employing more optimal abatement patterns that better suppress, and perhaps lead to more efficient eradication of, weed species would provide increased returns per unit investment in control activities.

Materials and Methods

Premise. Our hypothesis was that certain geometric patterns of Callery pear removal from isolated urban stands are more effective than others at suppressing autochthonous re-invasion rates. An additional hypothesis was that such different geometric removal patterns would generate variation in the retention of genetic diversity in comparative expanding recovery populations. We modeled an isolated stand since these are often the targets of weed control, and studies have shown that most population growth in such stands is often driven locally (e.g., Hutchinson and Vankat 1997). To test our hypotheses, our premise was that an isolated square open field measuring 1.84 km on a side has been invaded by a developing population of Callery pear for the past 15 yr (naturalization of this species is recent and expanding; Culley and Hardiman 2007), growing to a total randomly-distributed population of 17,200 individuals of various ages. Holding all other conditions constant we used NEWGARDEN modeling to explore autochthonous population recovery after the stand is culled down to 1% of those individuals with survivors (founders) being situated in different geometric patterns. Specifically, we investigated whether population recovery rates (population size and genetic diversity retention) were affected by interactions between founder geometric patterning and differing gene dispersal differences.

NEWGARDEN and Statistical Analyses. NEWGARDEN is a spatially-explicit, individually-based program that simulates the development of plant populations from a specified number of founders positioned as determined by the user (Pelikan and Rogstad 2013; Rogstad and Pelikan 2011). Populations develop through time (bouts of mating; each bout is considered one increment of "age") from processes intended to simulate those occurring naturally (e.g., mating, mortality, dispersal, etc.), conditioned by user-specified input parameter values (see below). One set of input values is called a "trial," and for a given trial, the user can stipulate the number of replicate populations ("runs") to be generated using the input conditions for that trial. For all of the trials here, there were 100 replicate runs. For each trial, NEWGARDEN reports total population mean output values across runs, with standard deviations, after each bout of mating for population size, the number of founding alleles retained, observed and estimated heterozygosity, and F_{it} (a measure of population inbreeding and/or subdivision interpreted here according to Hartl 1987). The effects of changing one or more input conditions (e.g., survivor placement; gene dispersal distances) between comparative trials were tested using *t*-tests of means. In this study, the mean values between two trials are said to differ if the P-value $\leqq$ 0.05 (with Bonferroni corrections).

Input Parameters Held Constant Across Trials. These NEWGARDEN populations developed on a grid system where individuals can only establish on grid points. The distance between grid points, here designated as 2 m, represents the average minimum distance at which two mature pears can establish and mature. The fragment was a 920 by 920 grid points square.

The genetic "constitution" of each founder is established by selecting two alleles at random for each of 20 loci, the alleles being drawn from a "source population" at Hardy-Weinberg equilibrium in which each allele has a frequency of 0.01 (there are 100 different alleles at each locus). We use such low frequency alleles since they make the effects of random genetic drift more easily detectable (Rogstad and Pelikan 2011). Of the 172 founders, individuals were randomly selected within each of the following age class groups: 77 were ages from zero to two; 52 were ages from three to six; 26 were ages 7 through 10; and 17 were aged between 11 and 14. For each run, these founders were placed in a new random positioning within their respective founding geometric patterns (see below). All individuals were designated as cosexual with no selfing (Culley and Hardiman 2009).

The mean age-specific offspring production schedule was zero offspring through age 6; 1.4 offspring per individual for ages 7 through 10; and two offspring per individual from ages 11 and older. For each bout of mating, offspring production does not meet these numbers exactly for each individual, but rather, total production is distributed among eligible individuals according to the Poisson distribution. Age-specific pollen production begins earlier with individuals aged three to six set to a relative provisioning rate of 0.5 compared to individuals aged 7 to 50 with a relative rate of 1 (full productivity). Pollen contribution is distributed at random among eligible individuals.

Age-specific mortality runs from 10% of individuals remaining in each age class through age 13, this probability decreasing linearly from 5% for individuals of age 14 to 1% when individuals reach age 50 (individuals that die are selected at random). All trials were run for 14 bouts of mating (i.e., 14 years).

Depending on conditions submitted in the input file, individuals can die (be removed from any further analyses) in ways other than due to the age-specific mortality statement described above. For example, if an offspring is dispersed off the grid (fragment), it dies. If an offspring randomly lands on a grid point already occupied by an established individual, the offspring dies. If an offspring is dispersed to a vacant point to which other offspring are also simultaneously dispersed, one is selected at random to establish, and the others die. If for a given mating event, no eligible pollen donor can be found within the selected distance frame, the mating fails. All of the cases above are tallied as single "mating events," but a new offspring may fail to establish.

Input Parameters that Varied Among Comparative Trials. The different founding geometric patterns in which the 172 survivors were positioned randomly were: (A) a long rectangular strip (736 by 46 m) centered on one edge (hereafter called the "strip" treatment); (B) a square (184 m on a side) at one corner ("corner" treatment); (C) a central square (184 m on a side; "center" treatment); or (D) scattered randomly throughout the entire fragment ("scattered" treatment; Figure 1).

Further, we studied population recovery from each of these geometric patterns of survivors first under "short," and then under "long" gene dispersal conditions. Gene dispersal distances via offspring or pollen are controlled by the user as a specified series of nested, square distance "frames" surrounding the offspring-generating plant in a given mating event (Rogstad and Pelikan 2011). Each frame is defined by the input minimum and maximum *x* and *y* dispersal distances. The probability of an offspring establishing within one of the distance frames, and the probability of pollen coming from one of the distance frames (given that an eligible pollen donor is present in that frame), surrounding the offspring generating plant is included in the input statements. For either the short or long distance gene dispersal trials, the distance frames and probabilities of dispersal to (offspring) or from (pollen) the offspring generating plant in a particular mating were identical. For the short gene dispersal trials, the distance frames and probabilities were: one to six grid points, 60% probability; 7 to 20 grid points, 20% probability; 21 to 41 grid points, 13% probability; 42 to 199 grid points, 4% probability; and 200 to 299 grid points, 3% probability. For the long gene dispersal trials, the distances and probabilities were: 1 to 59 grid points, 50% probability; 60 to 119 grid points 30% probability; 120 to 179 grid points, 10% probability; 180 to 239 grid points 6% probability; and 240 to 899, 4% probability.

Results

After 14 bouts of mating, alternate patterns of removal of Callery pear resulted in mean rates of

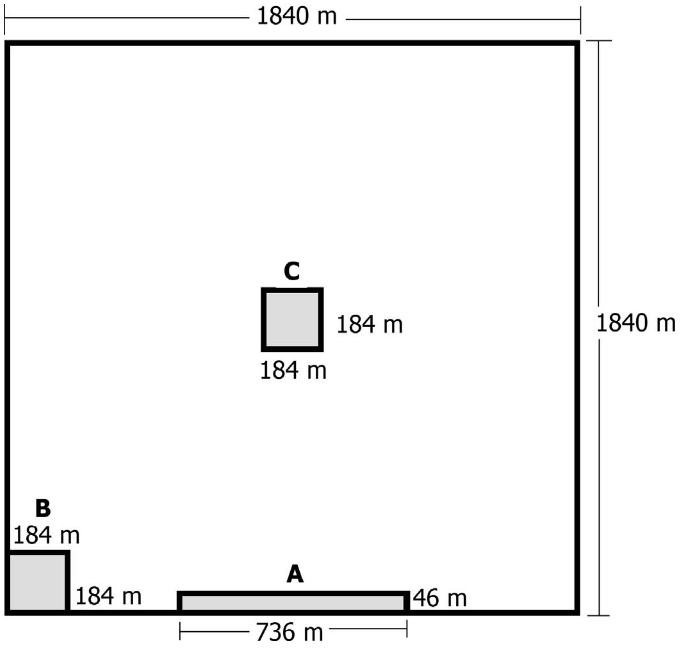

Figure 1. Map of the isolated Callery pear population showing the different geometries of the 1% areas and founders (shaded regions) used in the comparative NEWGARDEN trials. A = strip; B = corner; C = center. The positioning of the founders in a fourth trial type, in which the 1% of remaining individuals were scattered randomly throughout the fragment (scattered), is not shown.

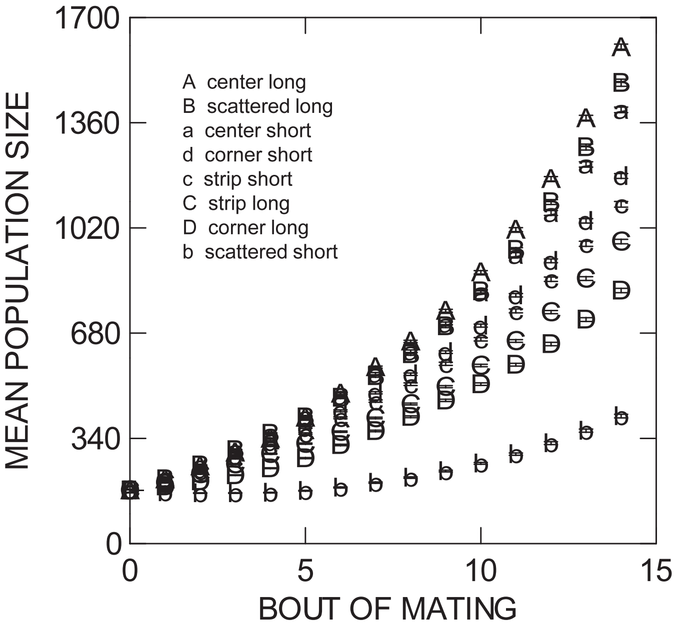

Figure 2. Population growth for comparative culled trial populations of Callery pear across 14 bouts of mating that differ in founding geometry (center, corner, scattered, strip) and gene dispersal distance (short versus long). Trial type is indicated by the legend in the figure with trials listed according to decreasing size. See text for more details. Data denote means ± standard error.

population growth that were statistically different from one another both within and among trials with short versus long gene dispersal (Figure 2). Although all of these populations regenerated from 172 individuals, the greatest difference in population recovery amounted to an increase of 393% (the increase in center long versus scattered short trials; Figure 2 trial A versus trial b, respectively). For a species with long distance dispersal conditions, the greatest population suppression occurs if plants are removed down to one corner (trial D), while leaving remaining individuals in a central square induces the population to grow back most rapidly (trial A; an approximate 200% increase). However, when gene dispersal is short, leaving the last 1% of individuals scattered throughout the fragment (trial b) is the most inhibiting removal treatment, while culling individuals to leave a central square (trial a) allows the greatest return rate (an increase of 343%). In terms of decreasing population re-growth rates, the order of geometric removal pattern effects from highest to lowest differs among trials when gene dispersal is short (center trial a, corner trial d, strip trial c, and scattered trial b) versus when it is long (center trial A, scattered trial B, strip trial C, and corner trial D).

Measures of how founding genetic diversity was altered through mating episodes differed to varying degrees among trials. After 14 bouts of mating, populations lost from 4.5% (trial B scattered long) to 9.1% (trial D corner long) of their founding alleles, with trial b (scattered short) being relatively distinct, losing 20.9% of its alleles with a curve suggesting that more alleles will be rapidly lost in future generations (Figure 3). All populations have similarly high values of observed heterozygosity immediately after population removal treatment (ca. 99%; Figure 4), as would be expected due to the numerous, low-frequency alleles available for each locus. However, this diversity begins to decay in different patterns among the trials after about five bouts of mating. After 14 bouts of mating, trials D, A, and C (all with long dispersal) had lost less than 2% of their heterozygosity, while trials d, a, B, and c (all short dispersal except for B with scattered founders) lost approximately 4% of their heterozygosity, and with trial b (scattered short) clearly differing in declining to an observed heterozygosity of 0.858, and still decreasing at a relatively high rate. F_{it} values reflect these heterozygosity trends (Figure 5), with all but one of the populations remaining below 0.05 indicating little or no inbreeding or intrapopulation subdivision have occurred, and with the exception, population b, finishing with an F_{it} value of 0.12, indicating that inbreeding and/or intrapopulation differentiation are moderate and still increasing (there is no sign of leveling off).

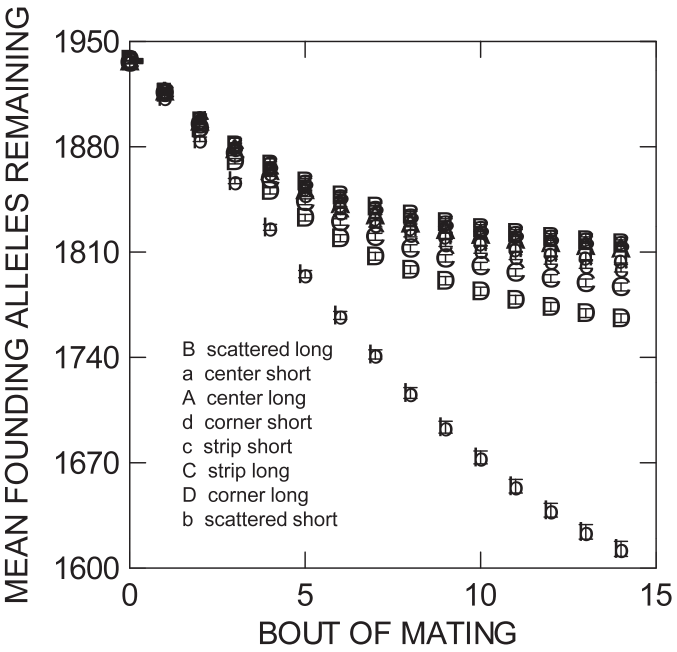

Figure 3. Founding alleles remaining for comparative culled trial populations of Callery pear across 14 bouts of mating that differ in founding geometry (center, corner, scattered, strip) and gene dispersal distance (short versus long). Trial type is indicated by the legend in the figure with trials listed according to decreasing allele number. Data denote means ± standard error.

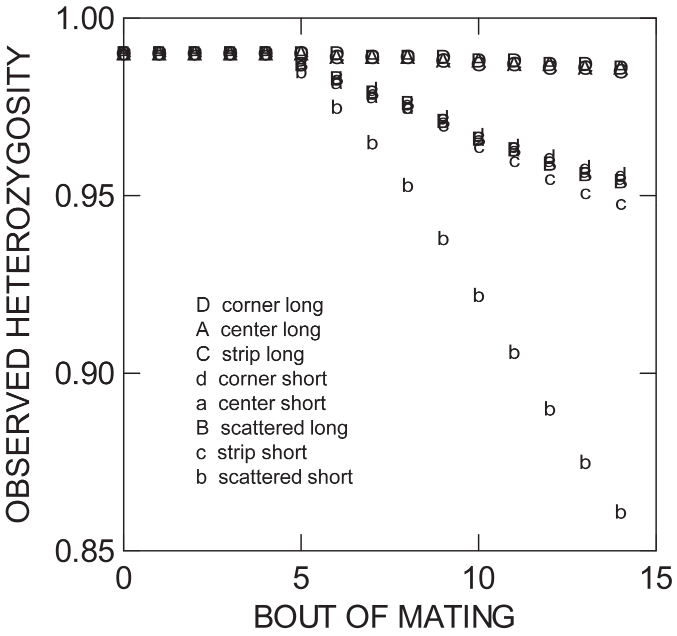

Figure 4. Mean observed heterozygosity for comparative culled trial populations of Callery pear across 14 bouts of mating that differ in founding geometry (center, corner, scattered, strip) and gene dispersal distance (short versus long). Trial type is indicated by the legend in the figure with trials listed according to decreasing heterozygosity. The standard error of the means for these trials at bout of mating 14 ranged from 0.0001 to 0.0012.

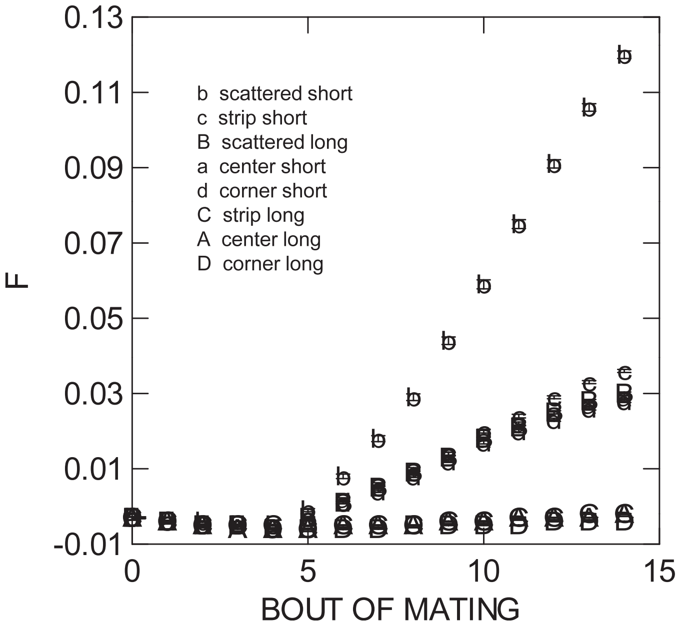

Figure 5. F_{it} for comparative culled trial populations of Callery pear across 14 bouts of mating that differ in founding geometry (center, corner, scattered, strip) and gene dispersal distance (short versus long). Trial type is indicated by the legend in the figure with trials listed according to decreasing values. Data denote means ± standard error.

Discussion

The results of these trials suggest that weed removal projects might be improved by modeling different geometric patterns of removal using approximated life-history and situation-dependent characteristics that apply in particular cases. All of the comparative trials here assumed that an equal amount of effort had been expended on incomplete Callery pear removal, but in different geometric patterns. That differences approaching up to 400% in population size recovery were found implies that resource savings could be substantial if preferred removal patterns are identified and employed. Holding gene dispersal patterns constant, the difference in population recovery between the best and worst geometric removal pattern was 200% for long-distance gene dispersal and 343% for short-distance gene dispersal. These results reinforce the notion that improving weed control can strongly depend on accumulating basic knowledge about the life history characteristics of targeted species. The parameter input values used in these comparative trials represent our initial reasonable estimates that reflect life history characteristics of Callery pear (NEWGARDEN can be used to model species or populations with differing life history characteristics; Rogstad and Pelikan 2011). Obviously, such values may differ due to inaccuracies in our estimations, or values that vary idiosyncratically from one situation to the next, and thus modeling in comparative trials that vary across a range of values can be informative. Highly replicated field experiments to explore the effects of different geometric patterns of weedy plant removal will often be costly or infeasible, and thus NEWGARDEN comparative modeling offers a preliminary alternative. Ultimately, we recognize that field trials are needed to test these hypotheses. But these simulations suggest that conducting such trials could result in significant savings in future efforts.

These results also suggest that even if complete removal is not a realistic goal, different geometric patterns of continuing population suppression might be preferable over others depending on the situation. Genetic diversity suppression through maintenance of populations continually reduced in particular patterns might also be practicable. As noted above, the importance of genetic diversity suppression would have to be demonstrated for any given target species, but if reduced diversity and increased inbreeding depression are thought to reduce fitness or adaptational potential in a particular situation, then continued efforts to reduce populations in particular geometric patterns might be of interest. For example, inbreeding/subdivision continue to rise (Figure 5) for all of the short-distance dispersal trials (especially trial b with scattered founders), and also when individuals are scattered with long-distance dispersal (trial B), even after 13 bouts of mating when populations number well above 850 individuals (population b does not increase above 400 individuals at that point; compare Figures 2 and 5). NEWGARDEN modeling can be used to seek suppression geometries that maintain populations below some target level in selected geometric patterns to best promote continued inbreeding and subdivision.

We emphasize that these results are not exhaustive. Other removal geometries, gene dispersal schedules (e.g., more platykurtic; offspring and pollen dispersal curves can differ in various combinations), different age-specific reproduction or mortality timetables, etc., may produce results that differ from those found here. Every project will have to adjust NEWGARDEN input to match the targeted species and will be situationally dependent. The effects demonstrated here may be influencing natural populations as well. For example, many natural populations are culled by abiotic or biotic factors (e.g., fire, freezing, drought, flooding, herbivores or pathogens) to similar degrees but in different geometric patterns. How might variability in such processes affect the recovery of population numbers and genetic diversity? Further, the approach used in these comparative trials can also be used to seek introduction patterns that better promote population growth for newly introduced species (Kashimshetty et al. 2012; Rogstad and Pelikan 2011), for example, native species plantings intended to suppress weed infestations. NEWGARDEN can thus be used to investigate the effects of different establishment geometries on both weed removal projects and natural culling settings, as well as on artificial introductions or natural population growth and genetics of establishing populations. More information about using the program can be found in Rogstad and Pelikan (2011) and Pelikan and Rogstad (2013), and the NEWGARDEN program and associated materials are available for free at: http://math.uc.edu/~pelikan/NEWGARDEN.

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