

# To succeed globally, disperse locally: effects of local pollen and seed dispersal on tetraploid establishment

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Newly formed tetraploid plants in sympatry with their diploid progenitors should face significant obstacles to persistence and population establishment because of low-fitness triploids formed by cross-ploidy pollinations. Prior models have found restrictive conditions for a minority tetraploid subpopulation to persist. A stochastic spatial model, parameterized using snow buttercups (*Ranunculus adoneus*), was used to examine the influence of limited seed and pollen dispersal distances on the success of minority tetraploids and the interaction of these factors with different rates of self-pollination and tetraploid advantage. Higher rates of self-pollination and increased tetraploid advantage increase the

probability of tetraploid persistence. Limiting the dispersal of seeds and pollen further increases the positive impact of any given level of self-pollination and tetraploid advantage. Taxa with short-distance seed and pollen dispersal should face much less stringent barriers to sympatric polyploid speciation than taxa with long-distance dispersal patterns. With short-distance seed and pollen dispersal, polyploid speciation should be possible in the absence of ecological differentiation or recurrent polyploid formation through unreduced gametes.

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## Introduction

Polyploid speciation differs from other speciation processes in the obstacles posed by matings between progenitor and descendant species. In most parapatric and sympatric speciation processes, divergence may be hindered by mating between the two incipient species. By contrast, chromosome doubling leads to immediate, substantial postzygotic reproductive isolation. Polyploid speciation has played an important role in the generation of plant diversity: 30–70% of plant species have four or more sets of chromosomes (Stebbins, 1970; Masterson, 1994), and at least 2–4% of speciation events have involved chromosome doubling (Otto and Whitton, 2000). Allopolyploidy, in which interspecific hybrids undergo chromosome doubling, is thought to be the more common source of successful new species than autopolyploidy, which occurs without hybridization (Ramsey and Schemske, 1998).

In contrast to the long-term success of polyploid taxa, the establishment and persistence of newly originated tetraploid plants, both auto- and allopolyploid, should be hindered by frequency-dependent mating success. In both cases, the polyploid individuals originate in sympatry with their diploid progenitors. Allopolyploids, due to their hybrid origin, may have greater ecological differentiation from their parental species than autopol-

yploids, and so may be better able to escape from sympatry via colonization of a novel habitat (Levin, 2002). However, both auto- and allopolyploids will likely face an initial period of sympatry with their progenitors. Matings between diploid and tetraploid plants result in triploid embryos; frequent failures of triploid seed provisioning and low triploid fertility lead to a loss of fitness from cross-ploidy fertilizations. Newly formed tetraploid plants will face no reproductive cost if they are completely self-pollinating (although inbreeding and the resulting loss of genetic diversity might hinder establishment). The proportion of self-pollinating species is higher in allopolyploids than in autopolyploids (Stebbins, 1957; Galloway *et al.*, 2003). However, taxa with mixed mating systems or obligate outcrossing are known for both types of polyploids (Husband and Schemske, 1997; Stanton *et al.*, 1997; Cook and Soltis, 1999, 2000; Mable, 2004). The combination of outcrossing and an initial sympatry of diploid and polyploids suggests that minority cytotype disadvantage (Levin, 1975) should be a common obstacle in polyploid speciation.

Theoretical studies of polyploid speciation have examined a variety of mechanisms that facilitate tetraploid population establishment in sympatry with their diploid progenitors. The earliest model examined how increased selfing rates could decrease the disadvantage suffered by the minority cytotype (Levin, 1975), although this only slowed the rate of exclusion. Later models broadened the consideration of mechanisms that reduce the loss of fitness due to cross-cytotype fertilizations, including pollinator discrimination, pollen incompatibility, and ecological differentiation (Fowler and Levin, 1984; Rodriguez, 1996a,b). Finally, some models consider

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how tetraploid persistence and success are influenced by levels of triploid fitness and the frequency with which unreduced gametes are produced by diploid and triploid plants by modeling a continuous influx of new tetraploids into the population (Felber, 1991; Felber and Bever, 1997; Ramsey and Schemske, 1998; Li *et al.*, 2004).

All models of tetraploid establishment to date suggest that self-fertilization is by itself insufficient to allow tetraploid success. Completely selfing, novel tetraploids that are ecologically equivalent to self-pollinating diploid progenitors should be lost from a population in the same way that novel neutral alleles are lost by drift due to stochastic processes (Levin, 1975; Felber and Bever, 1997). Ecological differentiation that reduces cross-ploidy pollination improves the odds of tetraploid persistence, but still requires a significant competitive advantage in order to offset the remaining reproductive disadvantage (Fowler and Levin, 1984; Rodriguez, 1996a, b). If unreduced gametes are sufficiently common and triploids sufficiently fit, tetraploids can persist at low levels in a population, even when they are at a severe reproductive disadvantage, a phenomenon similar to mutation – selection balance (Felber, 1991; Felber and Bever, 1997; Li *et al.*, 2004). In situations where continued genesis of new tetraploids is insufficient to maintain tetraploids at a low level, tetraploids must have a dramatic competitive advantage in combination with significant selfing to invade and persist within diploid populations.

Most of the previous models share an important feature: they assume that all individuals in a population experience the same average competitive and reproductive environment. With limited seed and pollen dispersal, or through clonal reproduction, tetraploids may form local majorities and produce local frequencies that differ from overall population frequencies. Therefore, spatial structure may ameliorate the minority cytotype disadvantage and increase the probability of tetraploid persistence, even when tetraploids are otherwise ecologically similar to their diploid progenitors. One recent study has considered the effect of local pollen and seed dispersal (Li *et al.*, 2004); however, their model did not examine the effect of spatial structure within a patch or the role of self-pollination.

In this paper, I explore the consequences of limited seed and pollen dispersal on tetraploid establishment, with a focus on local, within-patch interactions. Models that focus on within-patch dynamics are appropriate for examining interactions such as competition and reproduction that occur at a very small spatial scale (Bolker and Pacala, 1999). Using simulation models, parameterized on a well-studied buttercup species, *Ranunculus adoneus* (Stanton and Galen, 1989, 1997; Scherff *et al.*, 1994; Galen and Stanton, 1999; Baack, 2004), I compare the relative importance of limited seed and pollen dispersal to increased selfing and tetraploid advantage in determining the success of minority tetraploids.

## Methods

### Model overview

The model is written in C++ (Borland C++ version 5.02, 1997, Scotts Valley, CA, USA); source code is

available from the author upon request. Plants are randomly assigned coordinates on a continuous landscape (Pacala and Silander, 1985). Each plant receives pollen from neighbors within radius  $r_1$  and competes with plants within radius  $r_2$ . Plants produce seeds as a function of competition, pollen availability and ploidy, and degree of selfing. Seeds are dispersed using a gamma distribution of mean and variance  $r_3$ . Disturbances remove all adults in patches covering 20% of the habitat each year. Finally, seeds germinate and plants establish in gaps left by disturbance.

I use a continuous space modeling approach for this simulation, with discrete generations. Discrete spatial models, such as those in which every square on a grid is either empty or occupied by a single plant, impose a spatial structure difficult to compare to natural conditions. In contrast, continuous spatial models can be parameterized based on empirical data (Pacala and Silander, 1985).

To maximize realism, I use field estimates for seed dispersal distance, pollen dispersal distance, plant density, and disturbance frequency for snow buttercups (*Ranunculus adoneus* Gray: Ranunculaceae). Snow buttercups are long-lived perennials with a mixed mating system (Stanton and Galen, 1989) restricted to late-melting snowbeds and alpine seeps (Scherff *et al.*, 1994). Diploid and tetraploid *R. adoneus* share very similar floral morphologies, phenologies, and habitat requirements (Baack, 2003), making them appropriate case to model speciation without ecological differentiation. While snow buttercups provided values for particular parameters, tests with other values suggest that the results obtained here should apply broadly to plant species with short-distance pollen and seed dispersal (see 'model generality' below).

I model diploid and tetraploid plants as equivalent competitors with comparable habitat requirements, suffering symmetrical reproductive interference, and having the same selfing rates and seed dispersal distances. The two cytotypes differ only in their initial frequency in the population. The assumption of ecological equivalence is conservative; if ecological differentiation led the two cytotypes to occupy different habitats, this would minimize reproductive interference. In addition, I vary the maximum seed set and the germination probability of the tetraploid plants to examine how an advantage in scramble competition influences tetraploid success under different dispersal distances.

### Initial conditions

Each plant is assigned a location in  $20 \times 20$  m<sup>2</sup> continuous space. Initial densities average 50 plants/m<sup>2</sup>, matching field observations (Baack, 2003). Plants have a minimum spacing of 5 cm throughout the model to prevent unnaturally high densities from occurring. Initially, one plant out of 1000 is tetraploid.

### Reproduction

For simplicity, I discuss only female reproductive success; however, the same processes would result in symmetrical changes in male fitness. Plant reproduction in the model depends upon the selfing rate, the number of resource competitors, and the cytotype of neighboring plants within the range of pollen dispersal. Plant

fecundity is determined by the following equation:

$$\text{Seeds} = mK^e \left( s + (1-s) \frac{c}{c + (Bh) + a} \right) \quad (1)$$

Seed set is determined by the maximum seed set,  $m$ ; the number of resource competitors,  $e$ , and the effect of each competitor,  $K$  ( $0 < K < 1$ ); the proportion of seeds set due to selfing,  $s$ ; the number of pollen donors of the matching cytotype,  $c$ , and the other cytotype,  $h$ ; the relative probability of the other cytotype fertilizing an ovule,  $B$ ; and a saturation constant,  $a$ .

The maximum seed set for diploids,  $m$ , is set arbitrarily to 20 for these simulations; the maximum seed set for tetraploids will be increased by the percent tetraploid advantage. Resource competition reduces seed set from this maximum by  $K^e$ , where  $K$  is a constant determining the effect of each additional competitor (arbitrarily set to 0.6; using other competition functions did not yield different qualitative simulation results) and  $e$  is the number of resource competitors within 10 cm. For simplicity,  $K$  does not vary with the ploidy of the neighbor: differentiation in resource use between cytotypes would result in a lower  $K$  for interploidy competition. Competition was not detected in field studies of snow buttercups (Galen and Stanton, 1999); I include it here to increase model generality as competition will restrict the benefits of limited dispersal.

Seeds result from self-pollination or pollination by other plants. The potential seed set is composed of the fraction fertilized due to selfing ( $s$ ) and the fraction dependent upon outcrossed pollen ( $1-s$ ). Diploid and tetraploid plants have the same selfing probability, which is independent of the availability of outcross pollen for ease of comparing the impact of self-pollination to that of other factors. I evaluated the full range of breeding systems from complete selfing to complete outcrossing.

The number of seeds set due to outcrossing will depend on several factors. First, the proportion of the pollen reaching the stigma from the matching cytotype is calculated as the ratio of neighbors with the matching cytotype ( $c$ ) within the pollen dispersal distance, over the total neighbors within the pollen dispersal distance,  $c + h$ , where  $h$  is the number of alternate-cytotype pollen neighbors. Pollen tube success may vary with cytotype, so the amount of pollen from the other cytotype fertilizing ovules is weighted by  $B$ , the pollen performance coefficient. For this simulation I used  $B = 0.7$  based upon past pollination experiments (unpublished data), indicating that a pollen grain from a diploid plant on a tetraploid stigma has 70% of the chance of fertilizing an ovule, compared to a pollen grain from a tetraploid plant; a symmetrical disadvantage occurs for pollen from tetraploid plants on a diploid stigma. Finally, the outcross seed production is reduced by a saturation coefficient,  $a$ , arbitrarily set to 0.6, to allow for seed set to increase with increasing pollen loads while never exceeding the maximum seed set. The pollen dispersal distance was varied from 0.5 to 1.5 m in this set of simulations to model different pollen dispersal distances.

Several assumptions underlie this equation. First, triploid seeds are assumed to have no fitness. In field observations of triploid snow buttercups, triploid plants had 10% of the fertility of diploid or tetraploid plants, with none of the triploid plants producing tetraploid

seed (Baack, 2003). Therefore, pollen from diploid plants fertilizing a tetraploid flower results in the usurpation and loss of ovules, and likewise for pollen from tetraploid plants fertilizing diploid flowers. Second, the selfing rate is independent of the availability of outcross pollen; isolated plants receiving low amounts of outcross pollen cannot opt to self, nor do plants receiving high levels of outcross pollen reduce their self-pollination. While facultative self-pollination occurs in some taxa (eg Galloway *et al*, 2003), ignoring this possibility here simplifies comparisons of the influence of self-pollination to that of other factors on tetraploid establishment. The intrinsic selfing rate could correspond to alterations of floral morphology and phenology that alter the probability of mature self-pollen reaching a receptive stigma. Third, seeds produced by selfing and outcrossing have an equivalent fitness in this model: that is, there is no inbreeding depression. I address the potential impact of this assumption in the discussion section.

### Dispersal

Seeds disperse individually in a random direction from each maternal plant with the dispersal distance determined by the gamma distribution (Press *et al*, 1992) with equal mean and variance. The gamma distribution allows for a peak of seed dispersal to occur at short distances away from the parent, although seeds could still disperse to the location of the maternal plant. This is the case in snow buttercups, in which seed stalks fall over and so disperse the majority of seeds a short distance from the maternal plant (Scherff *et al*, 1994). Seeds dispersing beyond the boundaries of a patch are lost. I examined the effects of mean seed dispersal distances from 0.1 to 0.5 m, which are reasonable estimates for gravity-dispersing seeds such as those of *R. adoneus* (Scherff *et al*, 1994). Diploid and tetraploid plants were assigned identical seed dispersal curves.

### Survival and germination

In the snowbed habitat, most mortality of the long-lived snow buttercups is due to disturbance caused by gophers or soil slumping (Thorn, 1982). In the model, all mortality is due to randomly distributed  $0.2 \times 0.2 \text{ m}^2$  patches of disturbance that affect up to 20% of the total area each year, which is within empirical estimates (Thorn, 1982; Stanton *et al*, 1994). After disturbance, seeds more than 5 cm from an adult neighbor germinate and mature. The germination probability varied between diploid and tetraploid plants in the model: a 20% advantage for tetraploids is equivalent to tetraploids having a 6% germination probability, compared to a 5% germination probability for diploids. Within any 5 cm radius, the first seed to disperse and germinate is able to exclude all others. There is no seed dormancy; each year, the seed bank is regenerated. This differs slightly from the field situation in snow buttercups, in which most seeds remain dormant for 1 year before germinating.

### Overall dynamics

The diploid and tetraploid populations compete for germination sites. Individual plants have negative density-dependent reproduction due to resource competition, which is independent of the cytotype of neighbors. At the same time, plants have positive frequency-

dependent reproductive success, which depends on the cytotype of their neighbors. Seed dispersal distance may alter scramble competition by determining the propagule pool that can disperse to a germination site. In addition, seed dispersal will alter the local frequencies of the two cytotypes. Self-pollination will reduce the strength of the positive frequency-dependent reproduction, while the size of the pollen dispersal distance will determine the scale at which the positive frequency dependence occurs.

### Model output

Each simulation ran for 500 years. Each set of parameters was run in 300 replicate simulations (chosen to balance the need for precise estimation of the probability of success with limited computer time). For each set of parameters, I calculated the proportion of replicates in which tetraploids drove the diploids extinct or coexisted with diploids, comprising a tetraploid population of at least 50 plants in the  $20 \times 20 \text{ m}^2$  patch at the end of the run.

### Parameter space

I investigated the effect of four different parameters on the probability of tetraploid success: selfing rate (from 0 to 1, by 0.2 increments), tetraploid advantage (from 0 to 60%, by 20% increments), average seed dispersal distance (from 0.1 to 0.5 m), and pollen dispersal distance (from 0.5 to 1.5 m). The last two factors examine how a spatially explicit modeling framework will alter the probability of tetraploid success. I include the first two factors to compare the relative impact of local interactions, as compared to nonspatial factors examined in several previous models of tetraploid establishment. All combinations of these parameter values were examined.

### Model generality

Simulation models face the criticism that their results are dependent upon the particular set of conditions. I performed several trials to assess the impact of spatial scale, time scale, and disturbance regime on model outcomes. A set of model runs that proceeded for 5000 years were compared to the results for 500 year runs in order to detect transient tetraploid persistence. Model runs at  $100 \times 100 \text{ m}^2$  scale were produced to examine the effect of the smaller,  $20 \times 20 \text{ m}^2$  habitat size. Disturbance intensity, initially set to 20% per year, was modified to 6 and 50%, and disturbance scale changed from  $0.2 \times 0.2$  to  $0.1 \times 0.1$  and  $1.0 \times 1.0 \text{ m}^2$ .

## Results

All parameters (pollen and seed dispersal distance, selfing rate, and tetraploid advantage) have strong effects on tetraploid success. Tetraploid establishment probabilities generally increase with shorter pollen and seed dispersal distances, larger selfing rates, and increasing tetraploid advantage (Figure 1). The effect of a change in any one parameter depends upon the values of the other parameters.

### Effect of tetraploid advantage

With no advantage (leftmost column of Figure 1), novel tetraploids have very low probabilities of persistence. As the advantage in seed set and germination increases for

tetraploid plants, so does their persistence (moving to the right in Figure 1). For instance, with an average seed dispersal distance of 0.1 m, a pollen dispersal radius of 1.0 m, and a 40% selfing rate, changing the tetraploid advantage from 40 to 60% changes the persistence probability from 14 to 27.7% (see bars marked with arrows in Figure 1o and p).

### Effect of self-pollination

With no self-pollination, tetraploid plants did not persist (data not shown). Just 5% self-pollination resulted in low levels of tetraploid persistence (bottom row of Figure 1u–x). Tetraploid persistence increases as the rate of self-pollination increases (moving up a row in Figure 1). For example, with a 40% tetraploid advantage, 1.0 m pollen dispersal distance, and 0.1 m mean seed dispersal distance, changing the selfing rate from 40 to 60% yields a change in persistence from 14 to 19.8% (see bars marked with an arrow in Figure 1o and k).

### Effect of average seed dispersal distance

Lower mean seed dispersal distances generally led to higher tetraploid persistence. For example, with 40% tetraploid advantage, 80% self-pollination, and 0.5 m pollen dispersal distance, changing the mean seed dispersal distance from 0.1 to 0.2 m yielded a change in tetraploid persistence from 32 to 27% (see bars marked with arrows in Figure 1g). At higher tetraploid advantage, 0.1 and 0.2 m seed dispersal distances resulted in similar probabilities of tetraploid persistence: changing the mean seed dispersal distance from 0.1 to 0.2 m resulted in a change from 25.7% tetraploid persistence to 29.3% persistence at 20% self-pollination, 60% tetraploid advantage and 0.5 m pollen dispersal distance (see bars marked with arrows in Figure 1t).

### Effect of pollen dispersal distance

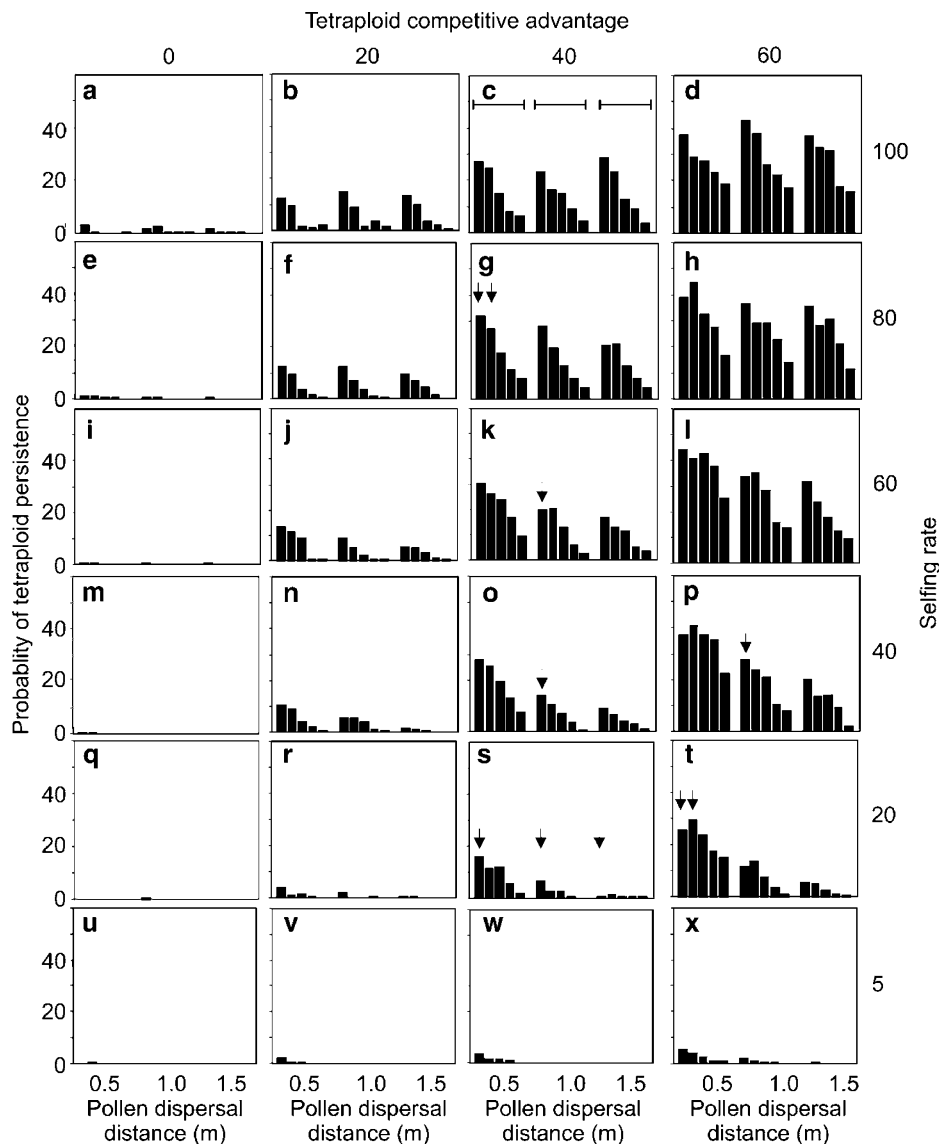
The pollen dispersal distance has no simple effect on tetraploid persistence, but interacts with the selfing rate. At selfing rates of 100%, pollen dispersal distance has no effect (compare the three bracketed sets in Figure 1c). As the selfing rate decreases, shorter pollen dispersal distances result in higher tetraploid persistence. For example, with 40% tetraploid advantage, 20% self-pollination, and a mean seed dispersal distance of 0.1 m, pollen dispersal distances of 0.5, 1.0, and 1.5 m result in tetraploid persistence of 12.0, 2.3, and 0.7%, respectively (see bars marked with arrows in Figure 1s).

### Interactions of factors

Lower mean seed dispersal distances, increased tetraploid advantage, and increased rates of self-pollination interact nonadditively to increase tetraploid persistence (Figure 1). At lower rates of self-pollination, decreased pollen dispersal distances likewise interact with decreased seed dispersal and increased tetraploid advantage (panels i–x of Figure 1) to increase tetraploid persistence.

### Relative effects of each factor

The effect of a change in each factor depends upon the values held by the other three factors. I quantify the effect of changes in dispersal on tetraploid persistence relative to changes in selfing and tetraploid advantage



**Figure 1** Effects of tetraploid advantage, selfing rate, pollen dispersal distance, and seed dispersal distance on tetraploid persistence. Each panel reflects a different selfing rate (from 5 to 100%, labeled on the right axis) and tetraploid advantage (from 0 to 60%, labeled on the top axis). Within each panel, the three sets of bars are for three different pollen dispersal distances (0.5, 1.0, and 1.5 m, labeled on the bottom axis). Five seed dispersal distances (0.1, 0.2, 0.3, 0.4, and 0.5 m, moving left to right) are shown for each pollen dispersal distance. Arrows mark particular cases discussed in the text.

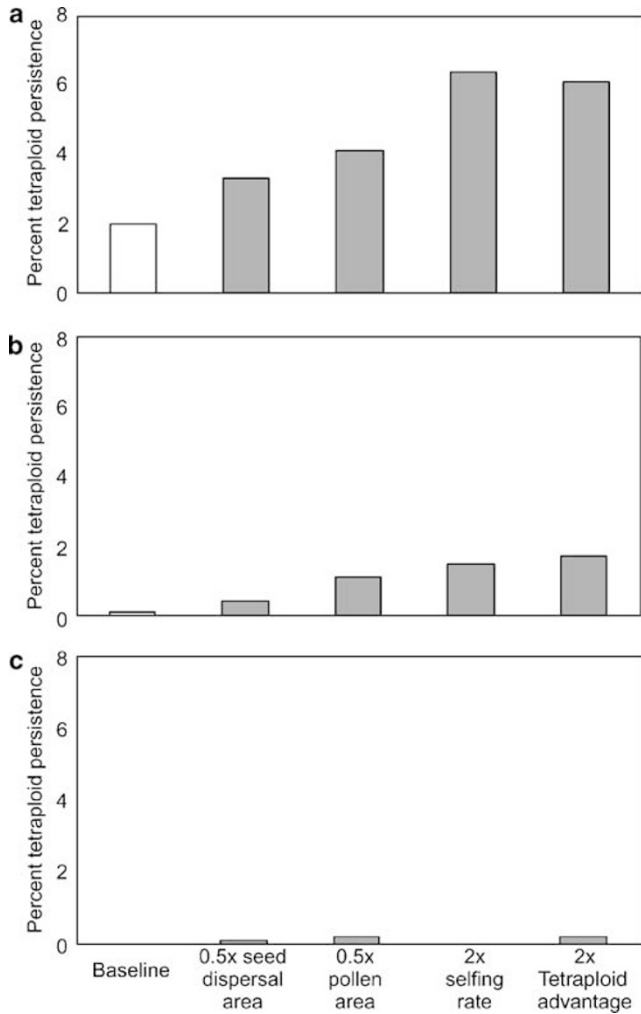
under three different dispersal scenarios: short, medium, and long. In each scenario, I examine the sensitivity to proportional changes in one factor while holding the others constant. In all scenarios, plants have a 20% selfing rate and a 20% tetraploid advantage. In the 'short' scenario, plants have pollen and seed dispersal distances of 0.7 and 0.2 m respectively; in 'medium', these are 1.0 and 0.3 m; and in the 'long' scenario, 1.4 and 0.5 m. I examine the impact of doubling the tetraploid advantage or selfing rate, or halving the area of pollen or seed dispersal, holding the other three factors constant (Figure 2a–c). Doubling the tetraploid advantage from 20 to 40% always has the largest impact on the tetraploid success in comparison to changes in other parameters (Figure 2a–c). However, halving pollen dispersal area has a strong impact as well in all three scenarios. For plants with longer dispersal distances, doubling the selfing rate has

no impact, although the absolute change due to changes in the other parameters was small as well.

#### Model generality

Running the model for 5000 years did not change the results: tetraploid plants that persisted for 500 years persisted for 5000 years. Likewise, increasing the scale of the simulation to  $100 \times 100 \text{ m}^2$  did not alter the qualitative outcome.

Model results showed some sensitivity to the details of the disturbance regime. At higher levels of disturbance intensity (50% of habitat disturbed each year), tetraploid persistence probabilities declined. However, the relative advantages of local dispersal were not changed. Disturbance scale interacted with self-pollination to alter the optimal seed dispersal distance (Figure 3). At 20%

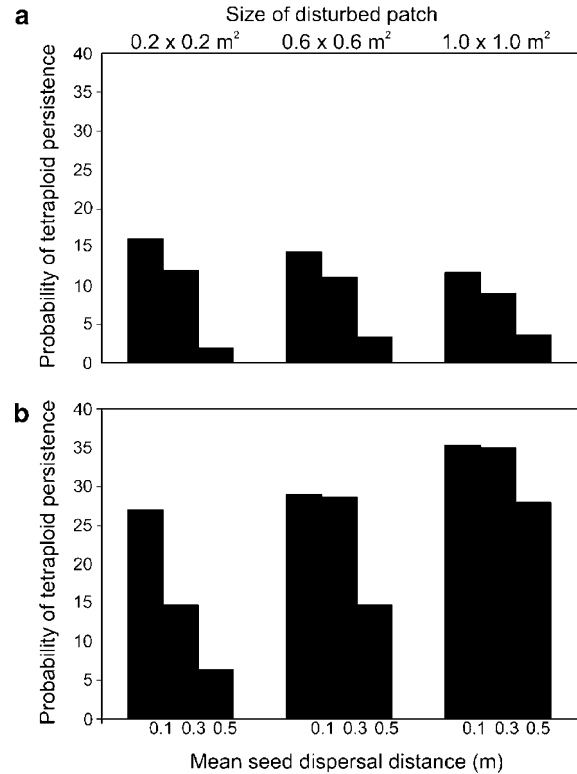


**Figure 2** Relative impact of factors on tetraploid establishment. For each of three dispersal scenarios (short (a), intermediate (b), or long (c)) one factor was altered while holding the others constant at the baseline value. The areas encompassed by the pollen dispersal distance and the mean seed dispersal distance were halved in their respective alternate scenarios, while selfing rate and tetraploid advantage were doubled. In all scenarios, plants had baseline selfing rates of 20% and baseline tetraploid advantage rates of 20%. Baseline mean seed dispersal distances were 0.2, 0.3, and 0.5 m for the short, medium, and long scenarios. Baseline pollen dispersal distances for each scenario were 0.7, 1.0, and 1.4 m, respectively. Baseline tetraploid establishment probabilities are shown by the clear bar in each chart, while the establishment probabilities resulting from altering each factor in turn are shown in the respective gray bars.

self-pollination and 20% disturbance intensity, the smallest seed dispersal distance was favored at all sizes of disturbance ( $0.2 \times 0.2$  to  $1.0 \times 1.0$  m<sup>2</sup>; Figure 3a). However, at 100% self-pollination and 20% disturbance intensity, intermediate seed dispersal distances were nearly as effective as shorter distances as the size of the disturbed area increased (Figure 3b).

## Discussion

The results presented here indicate that spatial structure increases the probability of tetraploid persistence in sympatry with diploid progenitors. Prior models exam-



**Figure 3** Effect of disturbance scale and self-pollination on optimal seed dispersal distance. Each graph shows the effect of mean seed dispersal distance (0.1, 0.3, or 0.5 m) on the probability of tetraploid persistence, with 40% tetraploid advantage and 0.5 m pollen dispersal radius. Disturbance affected 20% of the habitat each year in both panels. The three sets in each graph reflect different sizes for disturbed patches:  $0.2 \times 0.2$  m<sup>2</sup>,  $0.6 \times 0.6$  m<sup>2</sup>, and  $1.0 \times 1.0$  m<sup>2</sup>. (a) Results for 20% self-pollination; (b) results for 100% self-pollination.

ining sympatric tetraploid speciation have found the conditions for successful persistence to be fairly stringent, but in the framework of global interactions (which in this model are approximated by longer seed and pollen dispersal distances). They have therefore not shed light on the relative importance of spatial structure of cytotypes within populations. The predictions generated by this model qualitatively differ from those drawn from previous models of tetraploid persistence. With local seed and pollen dispersal, even very low levels of self-pollination and tetraploid advantage result in nonzero probabilities of tetraploid persistence. Tetraploid speciation need not involve ecological differentiation, high triploid fitness, or high rates of tetraploid formation due to unreduced gametes.

Local dispersal effectively separates the two cytotypes and thereby decreases the reproductive interference occurring between them. This is analogous to studies of competition, which have found that spatial structure can decrease interspecific competition and promote coexistence (Neuhauser and Pacala, 1999; Molofsky *et al*, 2001; Molofsky and Bever, 2002).

### Local dispersal and self-pollination

In this model, tetraploids had an initial numerical disadvantage, comprising just 0.1% of the population,

leading them to suffer usurpation of their ovules by pollen from diploid plants. Complete self-fertilization allowed tetraploid plants to escape reproductive costs due to their minority status. In the same way, local seed and pollen dispersal allowed tetraploids to establish local majorities despite their global minority status. Seed and pollen dispersal interacted positively: local pollen flow was more beneficial when low seed dispersal distances created more homogeneous patches of plants (Figure 1). Since local dispersal limited the influx of alternate-cytotype pollen, it could partially replace self-fertilization (Figure 1).

The three factors limiting reproductive interference between cytotypes – self-pollination, local pollen movement, and local seed dispersal – interacted with tetraploid advantage (Figure 1). As local dispersal or increased self-fertilization decreased the cost of minority status, the relative importance of tetraploid advantage increased. Thus, a small change in the advantage of tetraploid plants and seeds had a large effect when the reproductive cost of minority status has been ameliorated, but a negligible effect when minority tetraploids exchange pollen frequently with diploid plants.

The decline in tetraploid persistence with increasing dispersal distance is due to two factors. With outcrossing, local dispersal creates local majorities, reducing cross-ploidy pollinations. The advantages for local dispersal under complete self-pollination are due to the scale of disturbance (Figure 3b). If the average seed dispersal distance is too large, plants miss nearby disturbance patches while competing with a larger number of competitors for more distant patches. Altering the size of disturbed patches did not quantitatively alter the impact of reduced seed dispersal for outcrossing plants (Figure 3a).

#### Model generality

Stochastic simulation models can be sensitive to changes in initial conditions and unexamined parameters. I investigated this sensitivity by varying the minimum plant spacing, seed germination probability, and competitive functions, and found no qualitative changes to the results reported here. Altering the minimum plant spacing does have the effect of altering the optimal mean seed dispersal distance: as the spacing between plants increases, the lowest seed dispersal distances used in this paper are no longer optimal. Altering the function for resource competition had no qualitative effect, as was true for altering the seed germination rate. Finally, running the model at a larger scale (100 × 100 m) did not alter the qualitative outcomes. Local dispersal favors tetraploid success under a wide range of assumptions and initial conditions.

#### Variables not examined

Three potentially significant factors not included in the model – unreduced gamete production, triploid fitness, and initial clumping – would tend to increase the probability of tetraploid success. Adding unreduced gamete production from diploid plants will maintain tetraploid plants in a population indefinitely. Prior models have demonstrated that sufficiently high levels of unreduced gamete production can lead to consistent *diploid* extinction (Li *et al.*, 2004). Levels of tetraploid

production in nonhybrid wild populations based on unreduced gametes are estimated at  $10^{-5}$  (Ramsey and Schemske, 1998). When dispersal is sufficiently local, tetraploid establishment has a nonzero probability of success; adding recurrent tetraploid formation should increase tetraploid persistence. Likewise, increased triploid fitness should tend to decrease the barriers facing minority cytotypes without changing the relative impact of the different factors considered in this model, although triploid plants could compete for resources and occupy spaces that might otherwise be colonized by tetraploid plants. So long as triploid fecundity was lower than that of a tetraploid plant, factors that reduced the number of triploid offspring from tetraploid plants would increase the probability of tetraploid success.

Initial conditions in this model assume that one plant in 1000 is tetraploid, randomly distributed in the population. If tetraploids were to occur at a higher initial density, or if tetraploids were clumped instead of randomly scattered, this would improve the chances for tetraploid success, particularly at lower rates of self-pollination. Environmental stress may increase the rate of nonreduction in meiosis (Bretagnolle and Thompson, 1995; Ramsey and Schemske, 1998), and nonreduced gamete production may have a genetic cause (Bretagnolle and Thompson, 1995). Either mechanism could increase the clumping of tetraploid plants, thereby increasing the odds for tetraploid persistence. Clonal growth would have a similar effect.

Finally, this model does not include inbreeding depression. Inbreeding depression would lower the fitness of seeds from self-pollination and would introduce a cost to local dispersal by penalizing biparental inbreeding. Inbreeding depression resulting from local dispersal would tend to be less severe than inbreeding depression due to selfing, and so on the whole would tend to increase the impact of local dispersal on tetraploid persistence compared to selfing. Theoretical studies vary in their predictions of the impact of inbreeding depression on tetraploids *vs* diploids, predicting milder (Lande and Schemske, 1985), more severe (Bennett, 1976), or detail- (dominance coefficient) dependent outcomes (Ronfort, 1999). Experimental studies of inbreeding depression have been limited, but three comparing wild diploid and tetraploid populations found lower effects of inbreeding depression in the tetraploids (Husband and Schemske, 1997; Rosquist, 2001; Galloway *et al.*, 2003). Overall, including inbreeding depression in a spatially structured model might increase the importance of local dispersal relative to self-pollination and increase the persistence probability for tetraploid plants.

#### Hypotheses

Results reported here provide a number of testable predictions. For example, plant families with limited seed dispersal should have a higher rate of polyploid speciation than families with broader seed dispersal, assuming comparable rates of polyploid formation. Similarly, diploid species in which pollen movement is more local should give rise to tetraploid populations more often than diploid species in which pollination occurs over greater distances. In plant species like the snow buttercup that experience pollination by small flies

and drop their seeds very near the maternal plants, most pollen transfer may occur within 50 cm, and mean seed dispersal distances are near 10 cm. In such species, the barriers to tetraploid persistence should be greatly reduced. It should be possible to test the effects of pollen dispersal distance on tetraploid reproductive success by examining different populations within a species with different pollinator communities. Tetraploid reproductive success should be relatively higher in populations with pollinators having shorter flight distances. Likewise, populations growing in environments differing in their slope or wind exposure should show different degrees of spatial structure and so different reproductive barriers to neopolyploids. Where seed dispersal is longer on average, mixing between the two cytotypes should be greater and reproductive success relatively lower for the minority cytotype.

Levin (1975) concluded his examination of minority cytotype disadvantage by noting that the difficulties facing minority polyploids in sympatry with their progenitors were so severe that perhaps neopolyploids do not establish in sympatry after all. Although neotetraploids must form from diploids, Levin suggested that those that succeed might disperse away from the tetraploid progenitors in order to succeed. The present results suggest the opposite: tetraploids that succeed may be those that disperse least.

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## References

- Baack EJ (2003). Ecological Factors in Tetraploid Speciation in Snow Buttercups (*Ranunculus adoneus*: Ranunculaceae). PhD Thesis, University of California, Davis, CA.
- Baack EJ (2004). Cytotype segregation at regional and micro-geographic scales. *Am J Bot* **91**: 1783–1788.
- Bennett JH (1976). Expectations for inbreeding depression on self-fertilization of tetraploids. *Biometrics* **32**: 449–452.
- Bolker BM, Pacala SW (1999). Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *Am Nat* **153**: 575–602.
- Bretagnolle F, Thompson JD (1995). Gametes with the somatic chromosome number: mechanisms of their formation and role in the evolution of autopolyploid plants. *New Phytol* **129**: 1–22.
- Cook LM, Soltis PS (1999). Mating systems of diploid and allotetraploid populations of Tragopogon (Asteraceae). I. Natural populations. *Heredity* **82**: 237–244.
- Cook LM, Soltis PS (2000). Mating systems of diploid and allotetraploid populations of Tragopogon (Asteraceae). II. Artificial populations. *Heredity* **84**: 410–415.
- Felber F (1991). Establishment of a tetraploid cytotype in a diploid population: effect of a relative fitness of the cytotypes. *J Evol Biol* **4**: 195–207.
- Felber F, Bever JD (1997). Effect of triploid fitness on the coexistence of diploids and tetraploids. *Biol J Linn Soc* **60**: 95–106.
- Fowler NL, Levin DA (1984). Ecological constraints on the establishment of a novel polyploid in competition with its diploid progenitor. *Am Nat* **124**: 703–711.
- Galen C, Stanton ML (1999). Seedling establishment in alpine buttercups under experimental manipulations of growing-season length. *Ecology* **80**: 2033–2044.
- Galloway LF, Etterson JR, Hamrick JL (2003). Outcrossing rate and inbreeding depression in the herbaceous autotetraploid, *Campanula americana*. *Heredity* **90**: 308–315.
- Husband BC, Schemske DW (1997). The effect of inbreeding in diploid and tetraploid populations of *Epilobium angustifolium* (Onagraceae): implications for the genetic basis of inbreeding depression. *Evolution* **51**: 715–723.
- Lande R, Schemske DW (1985). The evolution of self-fertilization and inbreeding depression in plants. 1. Genetic models. *Evolution* **39**: 24–40.
- Levin DA (1975). Minority cytotype exclusion in local plant populations. *Taxon* **24**: 35–43.
- Levin DA (2002). *The Role of Chromosomal Change in Plant Evolution*. Oxford University Press: Oxford.
- Li BH, Xu XM, Ridout MS (2004). Modelling the establishment and spread of autotetraploid plants in a spatially heterogeneous environment. *J Evol Biol* **17**: 562–573.
- Mable BK (2004). Polyploidy and self-compatibility: is there an association? *New Phytol* **162**: 803–811.
- Masterson J (1994). Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. *Science* **264**: 421–424.
- Molofsky J, Bever JD (2002). A novel theory to explain species diversity in landscapes: positive frequency dependence and habitat suitability. *Proc R Soc London B* **269**: 2389–2393.
- Molofsky J, Bever JD, Antonovics J (2001). Coexistence under positive frequency dependence. *Proc R Soc London B* **268**: 273–277.
- Neuhauser C, Pacala SW (1999). An explicitly spatial version of the Lotka–Volterra model with interspecific competition. *Ann Appl Prob* **9**: 1226–1259.
- Otto SP, Whitton J (2000). Polyploid incidence and evolution. *Annu Rev Genet* **34**: 401–437.
- Pacala SW, Silander JAJ (1985). Neighborhood models of plant population dynamics. I. Single-species models of annuals. *Am Nat* **125**: 385–411.
- Press WH, Flannery BP, Teukolsky SA, Vetterling WT (1992). *Numerical Recipes in C: The Art of Scientific Computing*. Cambridge University Press: Cambridge, UK.
- Ramsey J, Schemske DW (1998). Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annu Rev Ecol Syst* **29**: 467–501.
- Rodriguez DJ (1996a). A model for the establishment of polyploidy in plants. *Am Nat* **147**: 33–46.
- Rodriguez DJ (1996b). A model for the establishment of polyploidy in plants: viable but infertile hybrids, iteroparity, and demographic stochasticity. *J Theor Biol* **180**: 189–196.
- Ronfort J (1999). The mutation load under tetrasomic inheritance and its consequences for the evolution of the selfing rate in autotetraploid species. *Genet Res* **74**: 31–42.
- Rosquist G (2001). Reproductive biology in diploid *Anthericum ramosum* and tetraploid *A. liliago* (Anthericaceae). *Oikos* **92**: 143–152.
- Scherff EJ, Galen C, Stanton ML (1994). Seed dispersal, seedling survival and habitat affinity in a snowbed plant: limits to the distribution of the snow buttercup, *Ranunculus adoneus*. *Oikos* **69**: 405–413.
- Stanton ML, Galen C (1989). Consequences of flower heliotropism for reproduction in an alpine buttercup (*Ranunculus adoneus*). *Oecologia* **78**: 477–485.
- Stanton ML, Galen C (1997). Life on the edge: adaptation versus environmentally mediated gene flow in the snow buttercup *Ranunculus adoneus*. *Am Nat* **150**: 143–178.



- Stanton ML, Galen C, Shore J (1997). Population structure along a steep environmental gradient: consequences of flowering time and habitat variation in the snow buttercup, *Ranunculus adoneus*. *Evolution* **51**: 79–94.
- Stanton ML, Rejmanek M, Galen C (1994). Changes in vegetation and soil fertility along a predictable snowmelt gradient in the mosquito range, Colorado, USA. *Arctic Alpine Res* **26**: 365–374.
- Stebbins GL (1957). Self fertilization and population variability in higher plants. *Am Nat* **91**: 337–354.
- Stebbins GL (1970). *Chromosomal Evolution in Higher Plants*. Edwin Arnold: London, UK.
- Thorn CE (1982). Gopher disturbance: its variability by Braun–Blanquet vegetation units in the Niwot Ridge alpine tundra zone, Colorado Front Range, USA. *Arctic Alpine Res* **14**: 45–51.