Priority effects between annual and perennial plants

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ABSTRACT

Dominance by annual plants has traditionally been considered a brief early stage of ecological succession preceding inevitable dominance by competitive perennial plants. A more recent, alternative view suggests that interactions between annuals and perennials can result in priority effects, causing annual dominance to persist for decades if they are initially more common. Such priority effects would complicate restoration of native perennial grasslands that have been invaded by exotic annuals. However, the conditions under which these priority effects occur remain unknown. Using a simple simulation model, we show that long-term (equilibrium) priority effects are possible only when the plants have low fecundity and show an establishment-longevity tradeoff, with annuals having competitive advantage over perennial seedlings. However, transient (but long-lasting over decades) priority effects are more likely and does not require the tradeoff. Our results provide a theoretical basis for predicting when restoration of annual-invaded grasslands requires active removal of annuals and timely reintroduction of perennials.
1. INTRODUCTION

Plants of many species live for several years and reproduce multiple times, while others are annual, reproducing only once before senescing. Which of these strategies dominates over the other when they compete? This question has attracted ecologists for decades [1–4]. Moreover, it also has implications for conservation as many grasslands around the world are threatened by exotic annual plants that are invading native plant communities consisting primarily of perennial species [5–9]. In California, for example, more than nine million hectares of former perennial grasslands have been invaded by exotic annual plants [10].

Annual dominance in grasslands has often been considered a short, early stage of plant succession that is realized when a disturbance event (e.g. fire, grazing, agriculture) opens up space, but replaced quickly by perennials [11–14]. This view stems from the idea that the annual life cycle is an adaptation to cope with high adult mortality caused by frequent disturbance or drought [3,4]. Restoration of perennial dominance in annual-invaded grasslands should then be possible by reducing disturbance intensity. However, a more recent, alternative view suggests that annual-perennial interactions are sometimes characterized by priority effects, where dominance is determined by initial conditions [5,6,15–18]. According to this view, restoration of perennial dominance may require manually establishing a high density of perennial cover by removing exotic annuals and reintroducing perennials in a timely fashion. This restoration practice is gaining popularity in recent years and being applied in many grasslands despite its high costs [8,19]. However, few studies have investigated the mechanisms leading to priority effects within a theoretical model [but see 20], leaving it unclear when priority effects occur.
In this paper, we seek to provide a new perspective on the conditions for priority effects at different time scales by incorporating a neglected ecological tradeoff into a simple model of annual-perennial interactions. Most previous models have assumed a tradeoff between competitive ability and colonization [21,22]. Under this tradeoff, annuals are better colonizers of empty microsites because of their higher fecundity [23,24], whereas perennials are better competitors, being able to displace annuals [6,7]. This tradeoff can explain annual dominance during early stages of plant succession followed by eventual perennial dominance at local sites [12]. It also predicts coexistence of annuals and perennials at larger spatial scales [25,26]. However, these models overlook the possibility that annuals are often more competitive than seedlings of perennial plants. Evidence suggests that perennials’ advantage of higher longevity often comes at the cost of lower competitive ability at the establishment stage [5,27–29]. Several studies show that this establishment advantage results from earlier germination of annuals which provide them an initial size advantage [30,31]. Furthermore, perennials often have lower specific leaf area, leaf mass fraction, and specific root length [23,32]. All these traits increase longevity but reduce resource acquisition and therefore competitive ability during the establishment phase.

With our model, we show that this establishment-longevity tradeoff is necessary for priority effects to last permanently, but that it is not required for priority effects that are transient, but can last several decades.

2. THE MODEL

We built an individual-based, spatially implicit model describing population dynamics of sessile organisms where the local site is comprised of number of patches (cells), each of which can
accommodate only one adult individual [e.g. 33]. The model describes competition among two species, one annual (semelparous) and one perennial (iteroparous), interpreted as two dominant species or two functional groups with minor differences within each group.

In the model, we simulate three processes each year: establishment (competition over recruitment sites), seed production, and mortality. First, at the beginning of the growing season, establishment of new recruits (annuals and perennial seedlings) occurs in patches with no adult perennials (i.e. adult perennials are not affected by annuals[18]). The number of seeds of each species arriving to an empty patch is a random Poisson number with expected value (and SD) equal to the species’ mean seed rain. Mean seed rain is the per-capita net fecundity times the proportion of cells occupied by a given plant species. The yearly probability of an empty cell to be occupied by an annual is determined by a weighted lottery: 

\[
\frac{C \cdot S_a(t)}{C \cdot S_p(t) + S_a(t)},
\]

where \(S_a\) and \(S_p\) represent the number of viable seeds of the perennials and annuals and \(C\) is a weighting factor describing establishment differences. When \(C = 1\), establishment is completely neutral (i.e. the probability of winning is determined only based on seed density). Higher values of \(C\) imply that the annual seeds have higher competitive ability than perennials during the establishment phase.

The next process after establishment is seed production by annuals and adult perennials assuming perennial seedlings cannot produce seeds, [18,34]. The net per-capita fecundity for annuals and perennials \((F_a, F_p)\) is the number of viable seeds per individual of annuals and adult perennials. Biologically, this parameter represents the combined effect of a number of processes including seed production, seed viability, germination fraction, seed predation, and pathogens. For simplicity the model does not incorporate seed dormancy.
The last process each year is mortality occurring after seed set (i.e. after the end of the growing season). The yearly survival probability could be viewed as a result of an external factor (e.g. disturbance, drought) or as an endogenic demographic trait of the perennials. Survival probability differs between perennial seedlings ($S_s$) and perennial adults ($S_p$). Seedlings that do not die become adults the next year [18,34]. All annuals die at the end of each growing season.

The fecundity of the annual species ($F_a$) is a free parameter of the model. The fecundity of the perennial species ($F_p$) is a function of annual fecundity and the fecundity coefficient ($\beta$): $F_p = \beta \cdot F_a$. This coefficient, ranging from zero to one, determines the strength of fecundity advantage. When $\beta = 1$, the two species have equal fecundity. As $\beta$ decreases, the perennial species suffers from a greater fecundity disadvantage. This modeling choice allows one to disentangle the effect of fecundity advantage (determined by $\beta$) and the effect of varying the net fecundity of both species simultaneously (determined by $F_a$).

The parameter space we investigated (Table 1) was designed to represent a wide range of demographic traits from various systems around the world. We assumed that annual net fecundity (taking into account both seed production and germination fraction) was in the range of 3-300 [35–37] and perennial adult survival was 0.8-0.99 [34,38,39]. Since preliminary investigations showed that the effect of varying perennial seedling survival was qualitatively similar to varying adult survival, we report only the effects of the latter, i.e. we assumed that seedling survival was always 0.3 following [34]. We did not find any relevant data for parameterizing $C$ or $\beta$ and therefore investigated a wide range (1-30 and 0.3-1, respectively).

For each combination of parameters, we investigated two initial conditions, annuals as residents (90% of the community) and as invaders (10% of the community). We chose this high
abundance of invaders to reduce the possibility of extinction by demographic stochasticity (although preliminary simulation showed that the model results were robust to the exact portion of the invader).

Our operational definition of priority effects in this paper is situations in which dominance depends on initial conditions (i.e. when the annual species has abundance above 50% when started with higher initial abundance but below 50% when starting in low abundance). We investigated model results at several time points, to study two types of priority effects, which we refer to as equilibrium and transient. Equilibrium priority effects (or alternative stable states sensu [40]) occur in systems characterized by multiple stable equilibria. Transient priority effects (or alternative transient states sensu [40]) occur when the effects of initial conditions on dominance lasts for many generations even when all communities eventually converge to a common equilibrium. Transient priority effects are relevant for restoration, but frequently ignored in theoretical ecology [40–43].

In all simulation runs, the community was comprised of 10,000 patches in order to reduce the effects of drift. We estimated the equilibrium conditions by fitting an asymptotic function describing the proportion of priority effects as a function of time ($y = b_0 + \frac{b_1 \cdot x}{b_2 + x}$). After 1000 timesteps, all simulations have (asymptotically) reached the equilibrium (Figure S1).
3. RESULTS

In accordance with previous predictions [3,4], our model predicts that dominance by annuals decreases as the survival of adult perennial increases (Fig. 1). Nonetheless, dominance is also affected by initial frequency under some conditions, leading to equilibrium (Fig. 1c-d) or transient (Fig. 1e-f) priority effects.

Over the long-term (Fig. 2), priority effects (marked in blue in Fig. 2) occur in the intermediate parameter space between annual dominance and perennial dominance, where ecological fitness differences (sensu 35) are small. In addition, equilibrium priority effects require the establishment-longevity tradeoff (i.e. $C > 1$) and a low fecundity level for both species (as explained above $F_a$ affects the fecundity of both species simultaneously). Within 1000 years, the less dominant species always reaches abundance below 1%, which we interpret as competitive exclusion (preliminary simulations showed that complete exclusion depends on the arbitrary choice of the number of patches).

The parameter region of transient priority effects is larger and requires neither competitive advantage of annuals over perennial seedlings nor low fecundity (Figure 3). The proportion of the parameter space that shows transient priority effects slowly declined over time from c. 37% after 30 years to c. 16% after 100 years and down to c. 8% at equilibrium (Figure 4, Figures S1-S5).

We obtained qualitatively similar results when we introduced environmental variability to the model (Figures S6-S8).
4. DISCUSSION

Taken together, our analysis indicates a previously unrecognized set of possible conditions for priority effects in annual-perennial interactions. First and foremost, it reveals low fecundity and the establishment-longevity tradeoff as necessary conditions for equilibrium priority effects. The analysis also suggests that these conditions are not necessary for priority effects that are transient, but lasting for several decades, which require only small fitness difference. Below we will elaborate on these conditions for priority effects, place our results in the context of existing knowledge from previous studies, discuss limitations of our findings, and end with implications for restoration.

(a) Conditions for priority effects

As recently shown, coexistence and equilibrium priority effects occur when fitness difference is relatively small [45], which is found, in our case, between the parameter space of annual dominance and that of perennial dominance (e.g. when mortality levels are intermediate). In this intermediate parameter space, negative frequency dependence would lead to coexistence by allowing both species to increase when rare, whereas positive frequency dependence would disadvantage species with low abundance, leading to priority effects [45,46]. Our model produces only priority effects, so which assumption leads to positive frequency dependence?

One assumption we had was higher fecundity of the annual species [3,4]. The resultant fecundity-longevity tradeoff could not produce positive or negative frequency dependence and therefore the species with the highest life-time fecundity should always win in the absence of any additional tradeoff [47]. In accordance, priority effects occur even when this tradeoff is relaxed (i.e. when fecundity ratio [$\beta$] is 1 in Fig. 2).
Another assumption of our model was competitive advantage of annuals over perennial seedlings [27,29,31]. This assumption leads to an establishment-longevity tradeoff, which we find here to be a necessary condition for priority effects in the long term. The establishment advantage of annuals reduces the population growth rate of perennials when they are rare since their seedlings are outcompeted by the annual species (the probability of a patch being empty from annual seeds by chance is low due to the high density of annuals). Conversely, high cover of perennials reduces the population growth rate of the annuals by reducing the availability of open patches which are necessary for their recruitment each year. Since annuals are short-lived, they are particularly prone to extinction when none of their seedlings can find a vacant patch.

In addition, the model suggests that decreasing net fecundity of both species simultaneously (as affected by $F_a$) increases the likelihood of priority effects. In our model, priority effects are driven by low recruitment of the rare species. Increasing fecundity reduces this recruitment limitation, thereby decreasing priority effects. We are not aware of any study that discussed this intuitive effect of fecundity on priority effects, although it also occurs in other patch occupancy models [20,48]. In Lotka-Volterra models, however, there is no effect of intrinsic growth rate on priority effects [45]. We speculate that it is related to Lotka-Volterra models lumping mortality and fecundity into the intrinsic growth rate.

The low net fecundity required for equilibrium priority effects raises the question whether they can really occur given that some herbaceous plants produce more than 1000 seeds per individual [36]. Still, low levels of net fecundity could arise due to high probability of seed loss caused by pathogens, mechanic decay, and seed predation. Consistent with this expectation, the proportion of seeds becoming seedlings can be low, especially in species with high seed output [49,50].
In contrast to the strict assumptions for equilibrium priority effects, our model indicates a large parameter space of transient dynamics lasting for decades (longer than most “long-term” experiments). Transient priority effects do not require an establishment-longevity tradeoff. Still, they are more likely (i.e. occur in a larger parameter space) when this tradeoff exists (Figures 3, S1-4). The parameters that were used included some arbitrary choices due to data limitation, but our results suggest that slow convergence to equilibrium might be common (see Figure S1).

(b) Comparison with previous studies

Counterintuitively, we found that the tradeoff between longevity and competitive advantage, which had previously been suggested as a major coexistence mechanism [22,51], led instead to priority effects. In our model, the better competitor (annual) cannot invade a community dominated by the inferior competitor (perennial), since seeds cannot replace established adults (replacement competition, sensu [52]). In contrast, in previous models [22,51], seeds of the best competitor immediately replace established individuals of the inferior competitor (displacement competition, sensu [52]) and therefore the less competitive species cannot prevent invasion. In the context of annual-perennial competition, evidence suggests that our replacement assumption (where seedlings cannot replace established adults) may be more realistic [52,53].

The analytical model by Kisdi & Geritz [20] relaxed the assumption of replacement competition. In contrast to other models focusing on competition-colonization tradeoff, theirs showed that a competitive advantage of the species with the lower life-span causes alternative stable states. Hence, their model could be viewed as the analytical analog to our simulation model. A main difference is that our simulation model allows incorporating more specific assumption regarding the biology of annual and perennial herbaceous species such as differential survival between
seedlings and adults and more relevant parameter space. Nonetheless, the finding that the results of our simulation model after 1000 years were qualitatively similar to the analytical model and are adequately described by an asymptotic function (Figures 4, S1) suggests that priority effects in the time scales of centuries represent alternative stable states, rather than long-lasting transient states.

Kisdi & Geritz’s model also incorporated a scenario of competition-colonization tradeoff that allowed coexistence [20]. In contrast, in the parameter space that we investigated here, there was no competition-colonization tradeoff. We assumed that annuals were better competitors and more fecund (i.e. better colonizers), and therefore our model did not produce a stable coexistence (only a transient co-occurrence lasting for decades, Figures 3, S2-S5). Our assumption of higher or equal competitive ability of annual seedlings is probably valid for most systems [5,27–29]. Still, it is possible that, in some systems, perennial seedlings are better competitors, which can allow stable coexistence via a competition-colonization tradeoff. We speculate, however, that coexistence is often promoted by other mechanisms such as resource partitioning and spatial and temporal variability (e.g. inferior competitor may survive in microsites with special conditions).

Empirical tests of equilibrium priority effects remain scarce probably because of logistical challenges and, as far as we know, are confined to grasslands in California. The study by Seabloom et al. [7] is probably the most direct test. Using seed addition (1,000 seeds/m²), they showed that perennials were able to invade annual-dominated communities and vice versa, a result interpreted as evidence against multiple stable equilibria. However, their experimental manipulation removed recruitment limitation, which is a necessary condition for equilibrium priority effects in our model. Alternative approach is estimating demographic parameters of co-occurring annual and perennial species and building a system specific model. This approach
provided variable results. A model of grassland in northern California [54] suggests that annuals are better competitors and are therefore capable of invading perennial monocultures, whereas a model for southern California grasslands suggests that competitive outcomes depend on nitrogen availability [18]. Under low nitrogen availability perennials dominate, under high availability annuals dominate, and under intermediate levels priority effects are expected. This result is in accordance with the predictions of our model of priority effects occurring under intermediate conditions between annual and perennial dominance.

(c) Limitations of our model

One limitation of our approach is the implicit assumption that annuals and perennials have the same adult size (since only one individual can occupy each patch). We used this common approach to modeling population dynamics of sessile organisms [21,22,25,26,51,53] to facilitate comparison with other models. Nonetheless, since plants vary in size, our model should be viewed as having the extent of cover, rather than the number of individuals, as the focal unit of abundance. Therefore, system-specific parametrization of simple models like ours should focus on quantifying fecundity per unit area rather than per capita and incorporate vegetative growth (i.e. the capability of perennials to fill space without the need for establishment).

Another simplifying assumption of our model is the absence of seed dormancy. A similar model of annual-perennial interactions has shown that simply incorporating dormancy into the model (i.e. a constant portion of seeds germinate every year) has modest effects on the model predictions [25]. However, this model has also suggested that if dormancy is induced by the presence of established perennials (i.e. annual seeds are able to wait for the right time and
replace dead perennials) many predictions could change [25]. We speculate that such selective germination may reduce the probability for priority effects. Furthermore, interactions between seed bank and environmental variability may lead to complex outcomes depending on the specific characteristics of seed dormancy [25,55], interactions between seed dormancy and other traits [56], and temporal autocorrelation in environmental conditions [57]. We found that a simple addition of environmental variability does not affect the model predictions (SI Appendix, Fig. S6-S8), but the complex interactions between seed bank and environmental variability in time and space remain to be fully investigated.

Lastly, our model focuses on interactions between two species that represent two functional groups with minor interspecific variability (or two dominant species from each group). However, high variation within the two groups may lead to deviation from the predicted patterns e.g. in cases where there is one highly competitive species that is able to outcompete all the rest regardless of initial conditions.

(d) Implications for restoration

When systems are characterized by long-term priority effects, simply restoring historical habitat conditions will not be enough for restoring the historical plant community [58,59]. In the context of restoring perennial dominance, it means that removal of the annual dominants together with reintroduction of the native perennials is needed [5,8]. Our simulation-based approach has allowed us to investigate transient dynamics, which are probably more common than long-term priority effects that have tended to be the primary focus of previous research. Our results have suggested that succession lasts only a few decades when conditions are favorable for perennials
(see [60,61] for empirical examples), whereas succession can take several hundred years to complete when conditions are less favorable for perennials [7,16]. These results raise a restoration dilemma for grasslands invaded by exotic annual species due to past disturbances [6,10]. Namely, are we willing to wait for natural recovery of perennial dominance that can take many decades, or should we actively reestablish perennial dominance? The answer to this question will be specific to each restoration project, and it will involve not just biological, but also social and political considerations. Nevertheless, we suggest that more temporally explicit investigations of priority effects like the initial attempt that we have presented here are needed to better inform restoration efforts.
DATA ACCESSIBILITY

All simulation codes are available on FigShare: https://figshare.com/s/fb208ec97ca7dd0f250f

AUTHORS' CONTRIBUTIONS

N.D. and T.F. conceived and designed the study; N.D. performed the simulations. N.D. and T.F. wrote the manuscript.

COMPETING INTERESTS

We have no competing interests

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FIGURE CAPTIONS

**Figure 1.** Representative examples of population dynamics of annuals (blue lines) and perennials (red lines) as affected by initial conditions and adult survival probability ($S_P$). In the left column, annuals are the majority of the initial community (90%). In the right column, annuals are the minority initially (10%). Low survival probability (0.85) leads to annual dominance (upper panels). Intermediate survival ($S_P=0.95$) leads to equilibrium priority effects. Under high levels of adult survival, there are transient priority effects (for decades), although the perennial species dominates in the long-term. Parameter values: $S_s=0.3$, $F_a=5$, $\beta=0.5$, $C=10$

**Figure 2.** Proportion of patches occupied by the annual species (‘a’ in the legend) after 1000 years as affected by competitive differences among seedlings ($C$), annual fecundity ($F_a$), fecundity ratio ($\beta$), and adult survival ($S_P$). The results (of each parameter combination) are the mean proportion of two simulations starting from different initial abundances (10% and 90% of annuals). Black regions represent perennial dominance while yellow regions represent annual dominance. The cases where the dominant species depends on initial conditions (i.e. when annuals comprised more than 50% in one simulation and less than 50% in the other simulation) are categorized as priority effects.

**Figure 3.** Proportion of patches occupied by the annual species (‘a’ in the legend) after 30 years. Symbols are as in Figure 2.

**Figure 4.** Proportion of communities experiencing priority effects (where dominance is determined by initial conditions), annual dominance, and perennial dominance as a function of simulation time (based on the total parameter space). Circles are simulation results and solid lines indicate asymptotic predictions ($y = b_0 + \frac{b_1 \cdot x}{b_2 + x}$). The horizontal blue dashed line represents the asymptotic proportion of priority effects ($b_0 + b_1$). Note the logarithmic scale of the x-axis. Estimated parameters for priority effects are: $b_0 = 296, b_1 = -288, b_2 = 3$.

Estimated parameters for annuals are: $b_0 = -72, b_1 = 116, 0, b_2 = 6$. Estimated parameters for perennials are: $b_0 = -2938, b_1 = 2987, 0, b_2 = 0$. 
| Symbol | Description (units)                                      | Value(s)  |
|--------|--------------------------------------------------------|-----------|
| C      | Competitive difference among seedlings (unitless)      | 1,3,30    |
| $F_a$  | Net fecundity of annuals (viable seeds/year)           | 3,10,300  |
| $\beta$| Ratio between annual and perennial fecundities (fraction) | 0.3-1    |
| $S_s$  | Survival probability of perennial seedlings (fraction/year) | 0.3     |
| $S_p$  | Survival probability of adult perennials (fraction/year) | 0.8-0.99 |
Figure 1.

Annual invader

Annual resident

\begin{align*}
S_p &= 0.85 \\
S_p &= 0.95 \\
S_p &= 0.99
\end{align*}
Figure 2.

Time step = 1000

Fecundity ratio ($\beta$)

Adult survival ($S_\rho$)
Figure 3.

Time step = 30

Legend
- a<1
- 1<a<30
- 30<a<70
- 70<a<99
- a>99
- Priority

Fecundity ratio ($\beta$)

Adult survival ($S_p$)
Figure 4.
Figure S1. Proportion of communities experiencing priority effects (where dominance is determined by initial conditions), annual dominance and perennials dominance as a function of simulation time (note the logarithmic scale) as affected by competitive differences \((C)\) and annual fecundity \((F_a)\). Results are based on combining all levels of fecundity ratio \([\beta]\) and adult survival \([S_p]\)). Circles are the simulation results and solid lines represent curve fitting of an asymptotic function \((y = b_0 + \frac{b_1 \cdot x}{b_2 + x})\). The dashed blue line represents the equilibrium proportion of priority effects (estimated as \(b_0 + b_1\)).
Figure S2. Proportion of patches occupied by the annual species (a) after 50 timesteps (years). Symbols are as in Figure 2.
Figure S3. Proportion of patches occupied by the annual species (a) after 100 timesteps (years). Symbols are as in Figure 2.
Figure S4. Proportion of patches occupied by the annual species (a) after 200 timesteps (years). Symbols are as in Figure 2.
Figure S5. Proportion of patches occupied by the annual species (a) after 500 timesteps (years). Symbols are as in Figure 2.
Appendix S1

We investigated whether environmental variability reduces the strength of priority effects. Hence, we assumed that competitive difference ($C$) among new recruits varies among years. We chose to vary competitive difference because variation in fecundity always lead to extinction of the annual species (since there is no seed bank in the model). Competitive differences were a random log-normal variable with a mean of 1, 3, or 30, and SD of 3 for the associated normal distributions (Figure S6). This approach allowed incorporating variation in time while keeping the mean conditions as in the main simulations (as presented in Figure 2). We found that the effects of environmental variations were minor (Figure S7-S8).

**Figure S6.** Histograms of competitive differences ($C$) in the simulation (note the logarithmic scale) where environmental variability was incorporated. (a) mean = 1 (b) mean = 3 (c) mean = 30. These values refer to the upper, middle and lower panels in Figure S5.
Figure S7. Proportion of patches occupied by the annual species (a) after 1000 timesteps (years) in a temporally variable environment. Competitive differences in each timestep were drawn from log normal distributions with (geometric) means of 1, 10, and 30. Symbols are as in Figure 2.
**Figure S8.** Proportion of communities experiencing priority effects (where dominance is determined by initial conditions), annual dominance and perennial dominance as a function of simulation time (based on the total parameter space) in a temporally variable environment. Competitive differences in each timestep were drawn from log normal distributions with (geometric) means of 1, 10, and 30. Symbols are as in Figure 4. Estimated parameters for priority effects are: $b_0 = 581, b_1 = -275, b_2 = 2$. Estimated parameters for annuals are: $b_0 = -182, b_1 = .233, 0, b_2 = 3$. Estimated parameters for perennials are: $b_0 = -10674, b_1 = 10716, b_2 = 0$. 