

Alternative States in Plant Communities Driven by a Life-History Trade-Off and Demographic Stochasticity

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ABSTRACT: Life-history trade-offs among species are major drivers of community assembly. Most studies investigate how trade-offs promote deterministic coexistence of species. It remains unclear how trade-offs may instead promote historically contingent exclusion of species, where species dominance is affected by initial abundances, causing alternative community states via priority effects. Focusing on the establishment-longevity trade-off, in which high longevity is associated with low competitive ability during establishment, we study the transient dynamics and equilibrium outcomes of competitive interactions in a simulation model of plant community assembly. We show that in this model, the establishment-longevity trade-off is a necessary but not sufficient condition for alternative stable equilibria, which also require low fecundity for both species. An analytical approximation of our simulation model demonstrates that alternative stable equilibria are driven by demographic stochasticity in the number of seeds arriving at each establishment site. This site-scale stochasticity is affected only by fecundity and therefore occurs even in infinitely large communities. In many cases where the establishment-longevity trade-off does not cause alternative stable equilibria, the trade-off still decreases the rate of convergence toward the single equilibrium, resulting in decades of transient dynamics that can appear indistinguishable from alternative stable equilibria in empirical studies.

Keywords: alternative stable states, bistability, competition-colonization trade-off, annual plants, drift, priority effects.

Introduction

The assembly of ecological communities is often affected by life-history trade-offs among species (Pianka 1970; Tilman 1994; Calcagno et al. 2006). Early models investigated how environmental conditions select for different life-history strategies that result in trade-offs (Pianka 1970;

Charnov and Schaffer 1973). Other studies investigated the effects of life-history trade-offs on species coexistence, with a focus on the competition-colonization trade-off (Hastings 1980; Tilman 1994; Calcagno et al. 2006). One aspect of life-history trade-offs that remains poorly understood is their role in driving alternative community states, scenarios where competitive dominance and exclusion of species depend on initial abundances, leading to historical contingency in community assembly. Some theoretical studies have shown that alternative community states are possible under a life-history trade-off (Kisdi and Geritz 2003; Baudena et al. 2010), but since the primary goal of these studies has been to understand mechanisms of coexistence, the conditions for alternative states remain largely unknown. In addition to advancing curiosity-driven research, this basic knowledge that is currently lacking should help improve the conservation and restoration of plant communities in degraded systems (Scheffer et al. 2001; Suding et al. 2004; Kadowaki et al. 2018).

In this article, we propose that alternative community states can be easily caused by a life-history trade-off. We focus on one of the trade-offs that should be common in plants: the establishment-longevity trade-off, where greater longevity is associated with lower competitive ability during individual establishment. Evidence suggests that traits that increase longevity reduce competitive ability during establishment in many plant communities. For example, comparisons between annual and perennial plants suggest that perennials' longevity is associated with lower specific leaf area, leaf mass fraction, and specific root length (Garnier 1992; Vico et al. 2016). All of these traits increase longevity but reduce resource acquisition and therefore competitive ability during establishment relative to annuals (Vaughn and Young 2015). Similarly, the establishment-longevity trade-off arises when grasses have a shorter life span than trees but can outcompete their seedlings (Baudena et al. 2010).

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Alternative community states arise when each species cannot invade a community dominated by its competitor (i.e., species are at a disadvantage when rare; Ke and Letten 2018). We hypothesized that this outcome of mutual exclusion could be realized by the establishment-longevity trade-off. For example, a short-lived species (e.g., annual plants) may be at a disadvantage when rare since its seedlings cannot replace established adults of a long-lived species (fig. 1*a*). Conversely, the long-lived species may be at a disadvantage when rare if its seedlings are outcompeted by

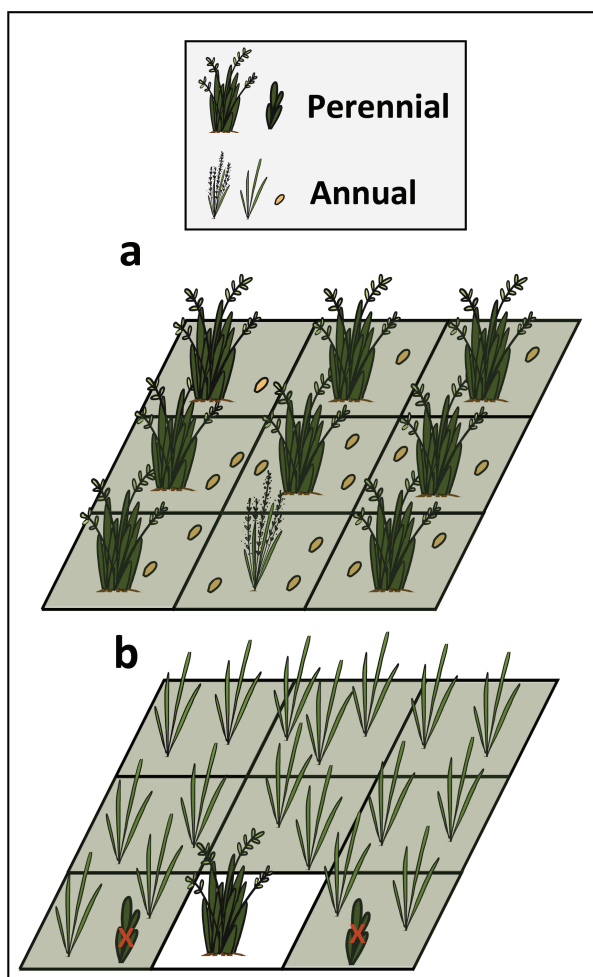


Figure 1: Simplified illustration of alternative stable states driven by the establishment-longevity trade-off. Under this trade-off, a long-lived species (perennial) is less competitive than a short-lived species (annual) during the establishment phase. Alternative stable states arise when both species are at a disadvantage when rare. *a*, An annual plant cannot invade a perennial-dominated community because its seeds cannot establish in recruitment sites that are occupied by adult perennials. *b*, A perennial plant cannot invade an annual-dominated community because its seedlings are outcompeted by annual seedlings.

the seedlings of the short-lived species (fig. 1*b*). In both cases, the species that happens to be initially more abundant will dominate the community permanently, resulting in alternative stable equilibria.

Alternative stable equilibria are not the only mechanism leading to historical contingency in community assembly, however. When communities that vary in initial species abundances do not converge for a long time, their long-term transient dynamics can also result in a large amount of historical contingency even when communities would eventually converge into a single equilibrium given enough time (alternative transient states, as opposed to alternative stable states, *sensu* Fukami and Nakajima 2011, 2013). Long-term transient dynamics are a characteristic feature of systems in the vicinity of a point in which a given state becomes unstable (Hastings et al. 2018). Therefore, in many cases, there can be a parameter region of alternative transient states in the periphery of the region where alternative stable states occur (Scheffer et al. 2009).

We developed a simulation model to understand how the establishment-longevity trade-off might affect community assembly, considering both alternative stable and transient states. We investigated possible conditions under which competitive dominance depends on initial abundances, hereafter referred to as priority effects (Fukami 2015). In this analysis, we sought to distinguish priority effects resulting in alternative stable states from priority effects resulting in long-lasting transient dynamics. As we detail below, our simulation model and its analytical approximation show that the establishment-longevity trade-off can cause both alternative stable states and alternative transient states. Our analysis also shows that whether alternative stable or transient states occur depends on other life-history traits, especially fecundity.

Methods

We implemented an individual-based, spatially implicit model describing population dynamics of plants where the local site is comprised of many patches (cells), each of which can accommodate only one adult individual (e.g., Mouquet et al. 2002). In this model, plants compete for empty cells, but the specific limiting resource is implicit to keep the model general. This approach is well suited for studying life-history trade-offs (Hastings 1980; Kisdi and Geritz 2003; Calcagno et al. 2006), as it explicitly considers fecundity and mortality. Our simple model describes the dynamics of two grassland species, one annual (semelparous) and one perennial (iteroparous), interpreted as two dominant species or two functional groups with minor differences within each group. As mentioned above, evidence suggests that perennials' advantage of higher longevity often comes at the cost of lower competitive ability at the

establishment stage (Bartolome and Gemmill 1981; Dyer and Rice 1997; Hamilton et al. 1999; Young et al. 2015).

We simulated three processes each year: establishment (competition over recruitment cells), seed production, and mortality. First, at the beginning of the growing season, the establishment of recruits (annuals and perennial seedlings) occurs only in patches with no adult perennials (i.e., adult perennials are not affected by annuals or by perennial seedlings). As in similar spatially implicit models, dispersal is assumed to be global (Hastings 1980; Kisdi and Geritz 2003; Calcagno et al. 2006). Therefore, the number of viable seeds of each species arriving at an empty cell is a random Poisson number (a different number for each cell) with the expected value (and SD) equal to the species' mean seed rain (N). Mean seed rain is the per capita net fecundity times the proportion of cells occupied by a given plant species in the previous time step. If at least one seed arrives in an empty cell, then the probability of an annual occupying that cell is determined by a weighted lottery (Kisdi and Geritz 2003):

$$\frac{C \cdot N_{a(t)}}{(N_{p(t)} + C \cdot N_{a(t)})},$$

where N_a and N_p represent the mean seed rain of the annuals and perennials and C is a weighting factor describing differences in competitive ability among the two species (Kisdi and Geritz 2003). When $C = 1$, the establishment is completely neutral (i.e., the probability of winning is determined only on the basis of seed density). Higher values of C imply that the annual seeds have higher competitive ability than perennials during the establishment phase (i.e., an establishment-longevity trade-off).

The next process after establishment is seed production by annuals and adult perennials, assuming that perennial seedlings cannot produce seeds (Mordecai et al. 2015). 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 several processes, including seed production, seed viability, 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

external factors (e.g., disturbance, drought) or as an endogenous 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. 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 (β): $F_p = \beta \cdot F_a$. This coefficient, ranging from 0 to 1, determines the strength of fecundity advantage. When $\beta = 1$, the two species have equal fecundity. As β decreases, the perennial species suffers from a lower fecundity. This modeling choice allows us to disentangle the effect of fecundity advantage (determined by β) and the effect of varying the net fecundity of both species simultaneously (determined by F_a).

The parameter space (table 1) was selected on the basis of empirical data. We aimed to represent a wide range of demographic traits. The range of each parameter was based on the extreme values of herbaceous plants from Sweden (Jakobsson and Eriksson 2000), Israel (Dirks et al. 2017), Australia (Wainwright et al. 2018), California (Mordecai et al. 2015), Texas (Fowler 1995), and Montana (Tuomi et al. 2013) to increase generality while keeping the results relevant to real plants.

We assumed that annual net fecundity (taking into account both seed production and germination fraction) was in the range of 3–300 (Jakobsson and Eriksson 2000; Dirks et al. 2017; Wainwright et al. 2018). 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. We assumed that seedling survival was always 0.3 (Mordecai et al. 2015) and that perennial adult survival was 0.8–0.99 (Fowler 1995; Tuomi et al. 2013; Mordecai et al. 2015). In additional simulation runs (app. S1; apps. S1–S4 are available online), we implemented lower survival rates (the entire range, 0–1), which are possible in highly disturbed systems (e.g., arable fields). We did not find any relevant data for parameterizing C or β 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

Table 1: Parameters of the models

Symbol	Description (unit)	Value(s)
C	Competitive difference among seedlings (no unit)	1, 3, 30
F_a	Net fecundity of annuals (viable seeds/year)	3, 10, 300
β	Ratio between annual and perennial fecundities (fraction)	.3–1
S_s	Survival probability of perennial seedlings (fraction/year)	.3
S_p	Survival probability of adult perennials (fraction/year)	.8–.99

community) and as invaders (10% of the community). We chose this high abundance of invaders and large community size (10,000 patches) to reduce the possibility of stochastic extinction caused by small population size. Preliminary simulations confirmed that this large community size ensures that the same results are obtained in different iterations of the model. However, high invader abundance does not necessarily mean that stochasticity plays a minor role in the dynamic; another source of stochasticity associated with seed competition turns out to be important, as described below.

We investigated the dependency on initial conditions (priority effects) in several time steps (individuals were censused after the establishment phase and before mortality occurs). In this article, we define priority effects as the situation where, after multiple generations of population dynamics, the annual species has abundance above 50% when started with high initial abundance but below 50% when started with low initial abundance. We fitted a nonlinear regression between simulation length (t) and the proportion of the parameter space where priority effects occur (y) using an asymptotic function:

$$y = b_0 + \frac{b_1 \cdot t}{b_2 + t}.$$

This regression was used to estimate the equilibrium value of y and to assess whether equilibrium was reached within the timeframe of our simulation runs. We found that after 1,000 time steps, all simulations (asymptotically) reached an equilibrium (see app. S2 for longer simulations). Therefore, priority effects after 1,000 time steps represent alternative stable states (multiple equilibria), while priority effects in shorter time scales can also represent alternative transient states that undergo slow convergence to a single equilibrium.

To better understand the mechanisms leading to alternative stable states, we simplified the simulation model by assuming an infinite community size and a single life-stage population structure for perennials (i.e., reproduction starts from the first year and $S_s = S_p$). An infinite community size implies no demographic stochasticity in adults. However, it does not remove stochasticity in seed rain (i.e., the number of seeds in each cell was a random discrete quantity in our model). We used this simple model to test whether stochasticity in seed rain resulting from low fecundity can cause alternative states (app. S3).

Results

Consistent with previous models of life-history trade-offs (Charnov and Schaffer 1973; Iwasa and Cohen 1989), our model predicts that dominance by annuals decreases as

the survival of adult perennials increases (fig. 2; app. S1); that is, annuals are favored when perennial adult survival is low. Nonetheless, dominance is also affected by initial frequency under some conditions, leading to either alternative stable states (fig. 2c, 2d) or alternative transient states (fig. 2e, 2f).

Specifically, alternative stable states (priority effects lasting for 1,000 years) occur in the intermediate parameter space between annual dominance and perennial dominance (fig. 3). We also found that alternative stable states require the establishment-longevity trade-off (i.e., $C > 1$) and low fecundity for both species (as explained above, F_a affects the fecundity of both species simultaneously). Within 1,000 years, the less dominant species always reaches abundance below 1%, which we interpret as competitive

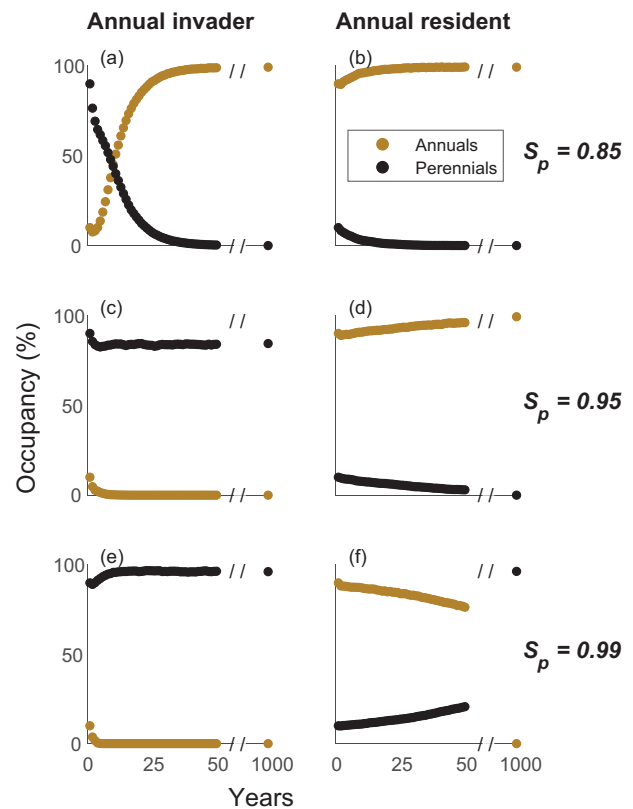


Figure 2: Representative examples of population dynamics of annuals (yellow lines) and perennials (black lines) as affected by initial conditions and perennial adult survival probability (S_p). In the left column, annuals are the minority of the initial community (10%). In the right column, annuals are the majority initially (90%). Low survival probability (0.85) leads to annual dominance (a, b). Intermediate survival ($S_p = 0.95$) leads to alternative stable states where exclusion depends on initial conditions. High levels of adult survival lead to long-term transient dynamics where initial conditions affect community dominance for decades, although the perennial species dominate in the long-term. Parameter values: $S_s = 0.3$, $F_a = 5$, $\beta = 0.5$, $C = 10$.

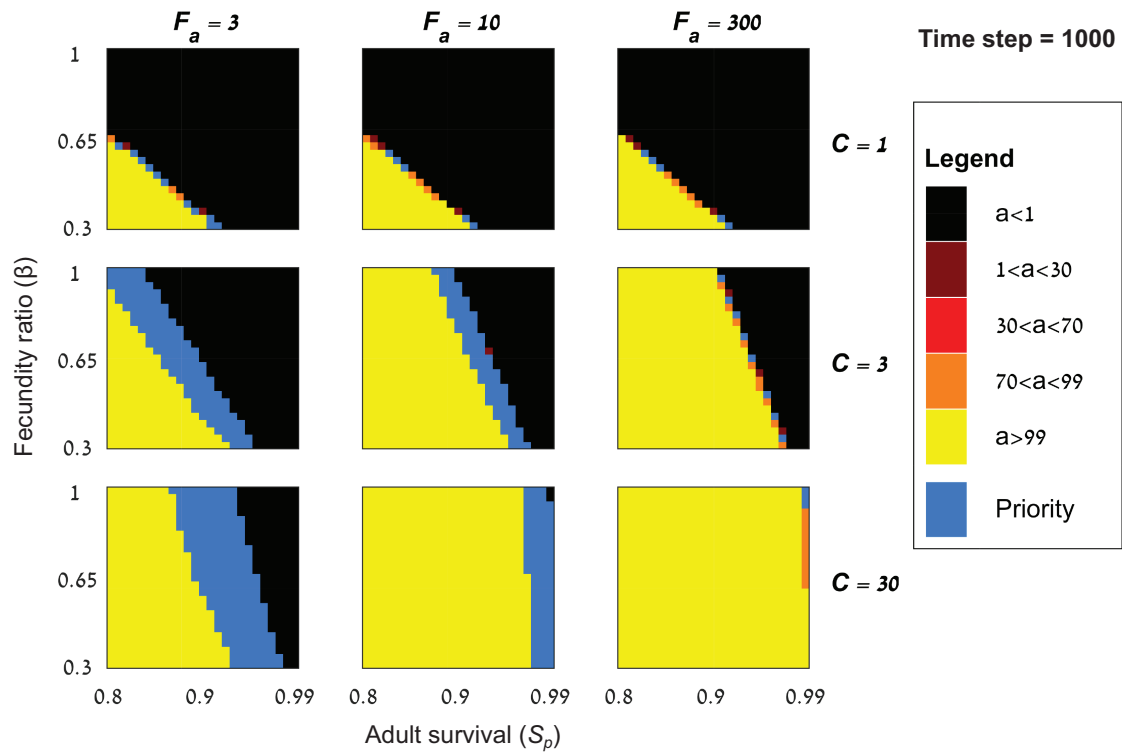


Figure 3: Proportion of patches occupied by the annual species (a in the legend) after 1,000 years (equilibrium results) as affected by competitive differences among seedlings (C), annual fecundity (F_a), fecundity ratio (β), and adult survival (S_p). The results (of each parameter combination) are the 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.

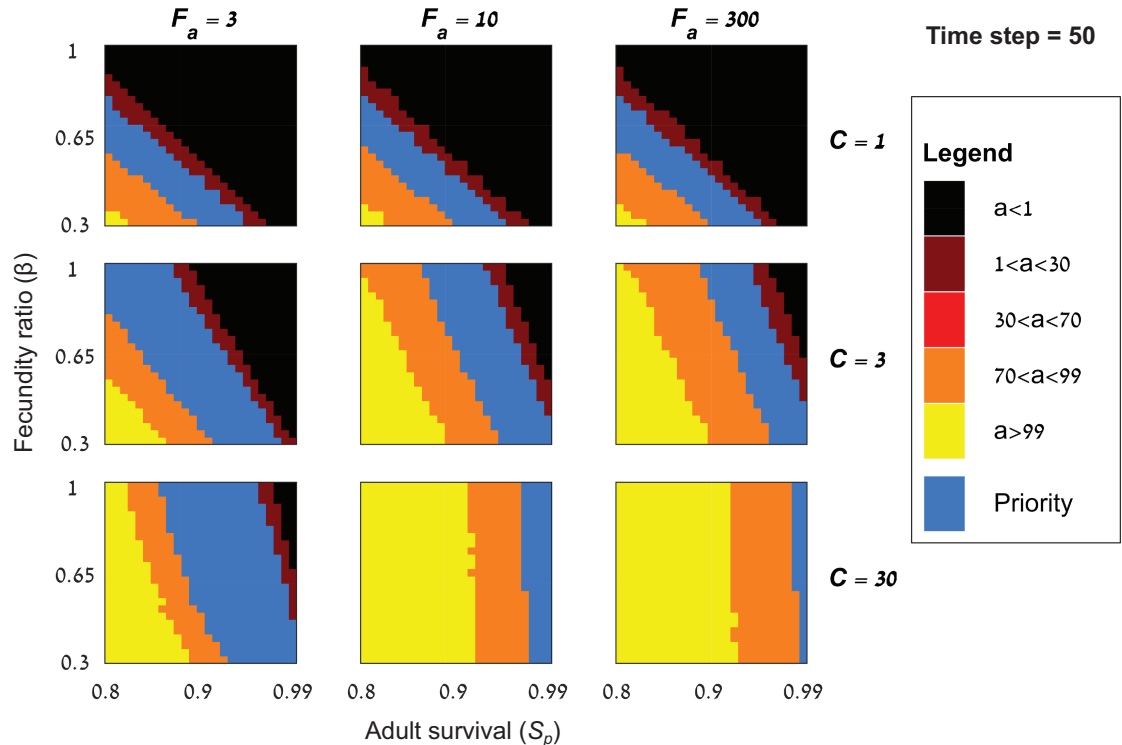


Figure 4: Proportion of patches occupied by the annual species (a in the legend) after 50 years (transient results). The results (of each parameter combination) are the mean proportion of two simulations starting from different initial abundances (10% and 90% of annuals). Black regions represent perennial 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.

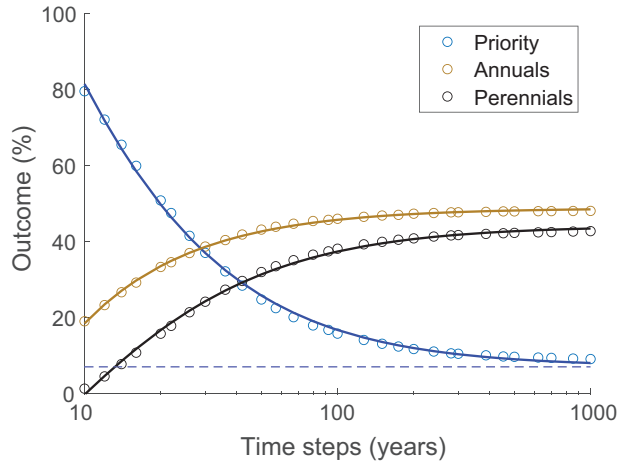


Figure 5: Proportion of communities experiencing priority effects (where dominance is determined by initial conditions), annual dominance, and perennial dominance as a function of simulation time (based on the total parameter space shown in figs. 3, 4). Circles indicate simulation results, and solid lines indicate asymptotic predictions ($y = b_0 + (b_1 \cdot t)/(b_2 + t)$). The blue dashed line indicates the asymptotic proportion of priority effects at equilibrium (i.e., alternative stable states; $b_0 + b_1 \approx 8\%$). Note the logarithmic scale of the X-axis. Estimated parameters for priority effects: $b_0 = 296$, $b_1 = -288$, and $b_2 = 3$. Estimated parameters for annuals: $b_0 = -2,938$, $b_1 = 2,987$, and $b_2 = 0$. Estimated parameters for perennials: $b_0 = -72$, $b_1 = 116$, and $b_2 = 6$.

exclusion (preliminary simulation showed that complete exclusion depended on the arbitrary choice of the number of patches).

Priority effects lasting for 50 years occur in a larger region of the parameter space (fig. 4) compared with equilibrium results (fig. 3). These findings indicate that in many cases dependency on initial conditions results in long-term transient dynamics rather than alternative stable states. Such alternative transient states do not necessarily require the establishment-longevity trade-off, but they occur more often when this trade-off is present (compare upper panels with middle and lower panels in fig. 4). The proportion of the parameter space that shows priority effects slowly declined over time from 37% after 30 years to 16% after 100 years and down to 8% at equilibrium (figs. 5, S1–S5; figs. S1–S12 are available online). We obtained qualitatively similar results when we introduced environmental variability to the model (figs. S6–S8).

The analytical approximation of our simulation model clarifies the role of fecundity (F_a) as a necessary condition for alternative stable states (see app. S3 for details). Low fecundity increases the demographic stochasticity in seed rain because the number of seeds arriving at each cell is a discrete entity. Therefore, demographic stochasticity in seed rain occurs even when community size is infinite, and its effect strengthens at low fecundity. In other words, under

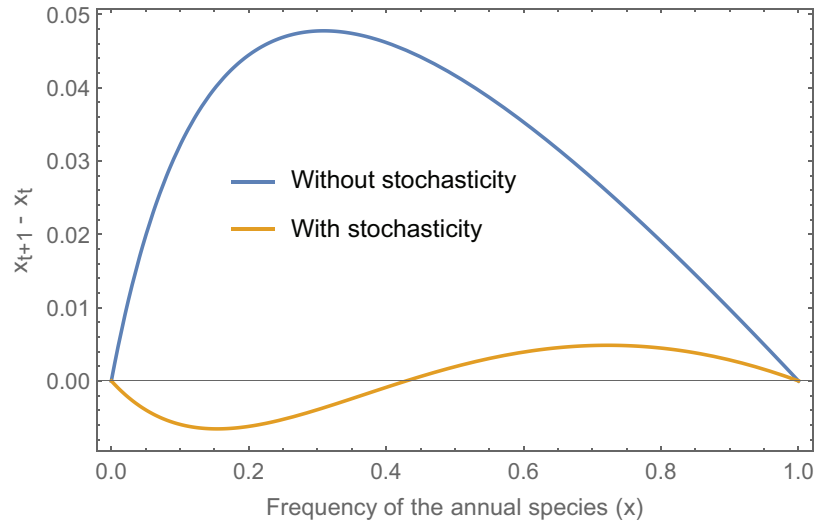


Figure 6: Change in frequency of the annual species ($x_{t+1} - x_t$) as the function of annual frequency (x) with and without stochasticity. Without demographic stochasticity, the number of seeds of each species in each cell is equal to its expected value rather than a Poisson-distributed variable. Without stochasticity (blue line), the annual species dominates the community and excludes the perennial species regardless of initial frequency (change in frequency is never negative). In contrast, when stochasticity is incorporated (yellow line), the growth rate is frequency dependent, thereby causing alternative stable states. Below the threshold frequency (0.45), the annual will be excluded by the perennial (i.e., negative change in frequency), and vice versa above it. Results are based on the analytical approximation of the model. Parameter values: $\beta = 0.4$, $C = 2$, $F_a = 3$, and $s = 0.7$.

low fecundity, seed rain is low and highly variable from cell to cell regardless of the number of cells.

The probability of establishment of the annual species (P_a) in an empty cell that received at least one seed is $P_a = Cn/(Cn + m)$, where n and m are the numbers of seeds of the annual and perennial species, respectively. In our model, these numbers are drawn from Poisson distributions with means $\bar{n} = F_a x$ and $\bar{m} = F_a \beta(1 - x)$, where x and $(1 - x)$ are the relative frequencies of the annual and the perennial species. Without stochasticity in seed rain (i.e., assuming n and m in each cell are equal to their expected value), the fecundity (F_a) does not affect the dynamic of the model because it is canceled out (appears in both the numerator and the denominator). However, when demographic stochasticity is incorporated, fecundity can affect the competitive outcome because of nonlinear averaging (app. S3). Under the establishment-longevity trade-off (when $C > 1$), demographic stochasticity in seed rain reduces the probability of the establishment of the annual species. Therefore, the annual species can be excluded under those conditions where it could have won in the deterministic scenario. This negative effect of stochasticity is frequency dependent, and its strength weakens as annual frequency grows. Alternative stable states occur when the annual has a positive growth only above a threshold frequency and therefore each species is excluded when rare (fig. 6; app. S3). In sum, the analytical approximation of the simulation model demonstrates that the combination of the establishment-longevity trade-off and low fecundity produces alternative stable states and that the underlying mechanism is demographic stochasticity in seed rain, which operates against the annual species under low frequency.

Discussion

In our simple model, the establishment-longevity trade-off sometimes causes alternative stable states, but the conditions for alternative stable states are complex because the establishment-longevity trade-off interacts with other traits, especially fecundity. In addition, even when the trade-off does not produce alternative stable states, it can still decrease the rate of convergence into the dominance of the species with the best strategy, causing alternative transient states. Below, we elaborate on the conditions for alternative states, discuss some limitations of our model, and place our results in the context of existing knowledge on life-history trade-offs.

Conditions for Alternative Stable States and Alternative Transient States

In our model, the establishment-longevity trade-off is a necessary but not sufficient condition for alternative sta-

ble states. First, alternative stable states cannot occur when one species has a large demographic advantage over the other. When the survival probability of perennials is very high, they dominate regardless of initial abundance, and vice versa for annuals when they have a high fecundity advantage (i.e., β is close to zero). Furthermore, alternative stable states occur only when the fecundity of both species is low (as affected by F_a). Low fecundity increases demographic stochasticity in seed rain, which reduces the growth rate of the annual species. Under some conditions, the change from negative growth rate to positive growth rate is frequency dependent such that the annual species is excluded when rare but takes over the community when abundant.

The low net fecundity required for alternative stable states raises the question of how often they occur, especially in the context of annual-perennial interactions, given that many herbaceous plants produce more than 1,000 seeds per individual (Jakobsson and Eriksson 2000). This low net fecundity could nevertheless be possible because seed loss can be substantial owing to pathogens, mechanic decay, and seed predation. Additionally, the proportion of seeds becoming seedlings is often low, especially in species with high seed output (Muller-Landau 2010; Ben-Hur et al. 2012). Moreover, seeds must fall in specific sites where the conditions are adequate for germination and early establishment, further reducing the effective number of seeds produced by each individual (Boeken 2018). We therefore speculate that systems characterized by low fecundity (e.g., under stressful environmental conditions) are more likely to experience alternative stable states driven by the establishment-longevity trade-off.

In many cases when the establishment-longevity trade-off cannot produce alternative stable states, the positive feedback created by this trade-off can still lead to alternative transient states, which may be indistinguishable from alternative stable states in empirical studies, as transient dynamics can last for decades (Fukami and Nakajima 2011; Hastings et al. 2018).

Comparison with Previous Studies

Unlike this study, most previous studies considered the trade-off between longevity and competitive advantage as a mechanism of coexistence, not alternative states (Tilman 1994; Chave et al. 2002). This difference is likely to reflect different assumptions about competition. In our model, the better competitor (annual) cannot invade a cell occupied by the inferior competitor (perennial) because seeds cannot replace established adults (replacement competition *sensu* Yu and Wilson 2001). In contrast, previous models (Tilman 1994; Chave et al. 2002) have assumed that seeds of the best competitor immediately replace established individuals of the inferior competitor (displacement

competition sensu Yu and Wilson 2001), and therefore the less competitive species cannot prevent invasion. Evidence suggests that our replacement assumption (i.e., that seedlings cannot replace established adults) can be more realistic (Yu and Wilson 2001; Calcagno et al. 2006).

Two previous modeling studies assumed that seedlings cannot replace adults (Kisdi and Geritz 2003; Baudena et al. 2010). Although these studies did not investigate alternative states in detail, both studies found bistability in a parameter space where the better competitor had lower longevity. Kisdi and Geritz's (2003) model also incorporates stochasticity in seed rain, and therefore we suspect that the mechanism leading to bistability in their model is the same as in ours. However, Baudena's (2010) model does not incorporate stochasticity, suggesting that, in some cases, the establishment-longevity trade-off can produce bistability even without demographic stochasticity.

Our results suggest that the life-history trade-off between establishment (during replacement competition) and longevity can be destabilizing, that is, increasing species' performance as their frequency increases, thereby leading to alternative stable states. We speculate that such a destabilizing life-history trade-off has not been proposed before, because alternative stable states are often analyzed within the classic Lotka-Volterra framework, where fecundity and survival are lumped into a single parameter relative to growth rate (Ke and Letten 2018). In a Lotka-Volterra analog of our model, the competition coefficients would be affected simultaneously by fecundity (F_a) and competitive differences among seedlings (C) with no distinction between the two, while in our model they are treated separately.

Limitations

One limitation of our approach is the implicit assumption that species varying in life-history traits have the same adult size, since only one individual can occupy each patch. We used this common assumption (Crawley and May 1987; Rees and Long 1992; Tilman 1994; Chave et al. 2002; Calcagno et al. 2006) to facilitate comparison with other models. Nonetheless, our model should be viewed as having the extent of cover, rather than the number of individuals, as the unit of abundance.

As in many spatially implicit models (e.g., Tilman 1994; Calcagno et al. 2006), we also assumed global dispersal among cells. In reality, however, communities have a spatial structure due to dispersal limitation and other factors. Such dispersal constraints can change the model behavior in many directions (Chave et al. 2002). Thus, we hope that future extensions of our model will further explore how dispersal kernels interact with life-history trade-offs in producing alternative stable states.

Another simplifying assumption of our model is the absence of seed dormancy. A similar model of annual-perennial interactions has shown that incorporating dormancy into the model (i.e., a constant portion of seeds germinate every year) has modest effects on the model predictions (Rees and Long 1992). However, this model also suggests that if dormancy is induced by the presence of established perennials (i.e., annual seeds can wait for the right time and replace dead perennials), many predictions could change (Rees and Long 1992). We speculate that such selective germination may further reduce the probability of alternative stable states but may also increase the length of transient dynamics. Furthermore, interactions between seed bank and environmental variability may lead to complex outcomes depending on the specific characteristics of seed dormancy (Brown and Venable 1986; Rees and Long 1992), interactions between seed dormancy and other traits (Venable and Brown 1988), and temporal autocorrelation in environmental conditions (Danino et al. 2016). We found that a simple addition of environmental variability does not affect the model predictions (app. S4), but the interactions between seed bank and environmental variability in time and space remain to be fully investigated.

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

Demographic Stochasticity as a Mechanism of Alternative Stable States

We found that alternative stable equilibria are driven by demographic stochasticity in seed rain. Unlike demographic stochasticity in adults that diminishes with increasing community size (Gilbert and Levine 2017; Shoemaker et al. 2020), demographic stochasticity in seed rain is unaffected by community size and affected only by fecundity. Our findings suggest a more prevalent role of stochasticity in community assembly than normally thought (Vellend et al. 2014; Shoemaker et al. 2020) in systems where community size is large, and therefore the role of stochasticity in shaping community structure is considered negligible (Vellend 2016).

We believe that the nonlinear averaging of demographic stochasticity is not a unique attribute of our model and could be relevant to many types of community patterns. For example, the model by Hart et al. (2016) describes how nonlinear averaging in demographic traits affects coexistence patterns. While intraspecific demographic variability in that model was interpreted as genetically driven, it

could be equally interpreted as an outcome of demographic stochasticity.

Conclusion

We have used a simple model to demonstrate how the establishment-longevity trade-off can lead to alternative stable states and alternative long-term transient dynamics. Although we parameterized the model based on grassland species, the establishment-longevity trade-off may exist in other types of plants as well. For example, herbaceous species are often more competitive than seedlings of woody species, while the latter often live longer. Therefore, other interactions, such as tree-grass interactions in the savanna (Baudena et al. 2010) and shrub-herb interactions in Mediterranean systems (Seifan et al. 2010), could also exhibit historical contingency because of the establishment-longevity trade-off. Of course, this trade-off is not the only potential mechanism of alternative community states. We hope that future empirical studies will assess the role of the establishment-longevity trade-off in comparison with other mechanisms, including fire, plant-soil feedback, and allelopathy (Staver et al. 2011; van der Putten et al. 2013).

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Statement of Authorship

N.D. and T.F. conceived and designed the study. N.D. performed the simulations. N.S. developed and solved the analytical model. N.D. wrote the first draft. All authors significantly contributed to the writing of the manuscript.

Data and Code Availability

All simulation codes are available on figshare (<https://figshare.com/s/fb208ec97ca7dd0f250f>) and in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.2fqz612nt>; DeMalach et al. 2021).

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