Understanding the emergence of contingent and deterministic exclusion in multispecies communities

Chuliang Song[1,2,3], Lawrence H. Uricchio[4], Erin A. Mordecai[5], Serguei Saavedra[1]

[1]Department of Civil and Environmental Engineering, MIT,
77 Massachusetts Av., 02139 Cambridge, MA, USA

[2]Department of Biology, McGill University,
1205 Dr. Penfield Avenue, Montreal, H3A 1B1 Canada

[3] Department of Ecology and Evolutionary Biology, University of Toronto,
25 Willcocks Street, Toronto, Ontario M5S 3B2 Canada

[4]Department of Integrative Biology, University of California, Berkeley,
Berkeley, CA, USA

[5]Biology Department, Stanford University, Stanford,
California 94305 USA

Abstract

Competitive exclusion can be classified as deterministic or as historically contingent. While competitive exclusion is the norm in nature, it has remained unclear when multispecies communities should be dominated by deterministic or contingent exclusion. Here, we provide a general theoretical approach to explain both the emergence and sources of competitive exclusion in multispecies communities. We illustrate our approach on an empirical competition system between annual and perennial plant species. First, we find that the life-history of perennial species increases the probability of observing contingent exclusion by increasing their effective intrinsic growth rates. Second, we find a shift from contingent exclusion to dominance with increasing numbers of competing species. Third, we find that the probability of observing contingent exclusion increases with weaker intraspecific competition, and not by the level of hierarchical competition. Our work provides a framework to increase our understanding about the predictability of species survival in multispecies communities.

Keywords: ecological communities, competitive exclusion, contingent exclusion, deterministic exclusion, structural stability

Introduction

Species coexistence is one of the most studied topics in ecology (Vellend, 2016); however, competitive exclusion is the norm rather than the exception in nature (Hardin, 1960; Goldford et al., 2018; Blowes et al., 2019). Competitive exclusion can be broadly classified into two ecologically different categories (Mordecai, 2011; Grainger et al., 2019). One category is *deterministic exclusion* (also known as dominance). That is, the order of species arrivals does not affect which species is competitively excluded. The other category is *contingent exclusion* (also known as priority effects). That is, the order of species arrivals does affect which species is competitively excluded. Importantly, knowing whether competitive exclusion in a community is deterministic or contingent is fundamental to understand the role of predictability and randomness in community assembly (Lawton, 1999; Fukami, 2015), which has empirical implications for conservation management (McGeoch et al., 2016), invasion ecology (Bøhn et al., 2008), and disease transmission (Keesing et al., 2010).

Since the 1930s, theoretical and empirical research has systematically documented and expanded our understanding of competitive exclusion between two competing species (Gause, 1932; Ayala, 1969; Brown, 1971; Gilpin and Justice, 1972). Moreover, in recent decades, theoretical studies have started to provide an overarching framework to synthesize data across different competition systems (Mordecai, 2013; Johnson and Bronstein, 2019; Ke and Wan, 2020). This theoretical development started by focusing on the conditions leading to deterministic exclusion (Chesson, 2000; Adler et al., 2007), and then it was extended to investigate the conditions for contingent exclusion (Mordecai, 2011; Fukami et al., 2016; Ke and Letten, 2018). Similarly, on the empirical side, extensive research started to examine the sources of deterministic exclusion (Mayfield and Levine, 2010; Violle et al., 2011; Adler et al., 2010), and more recently it has moved to the analysis of contingent exclusion (Grainger et al., 2018, 2019; Song et al., 2020*a*). Specifically, this body of work has shown that deterministic exclusion is more likely to occur when the competitively inferior species has a lower intrinsic growth rate and when intraspecific interactions are stronger than interspecific interactions. The opposite patterns have been shown to operate under contingent exclusion (Ke and Letten, 2018; Song et al., 2020*a*). Yet, it remains unclear whether these clear conditions at the two-species level also operate in larger communities, where more complex outcomes, including non-hierarchical competition and higher-order interactions, can occur (Levine et al., 2017; Saavedra et al., 2017*b*).

We still lack a full understanding about competitive exclusion in ecological communities of more than two species. One of the main reasons is that the overarching theoretical formalism used to study two-

species communities (which based on studying the growth rates when rare) does not generalize well to larger communities (Barabás et al., 2018; Song et al., 2019). It is therefore necessary to further develop the existing theory or to establish new approaches to tackle the problem of competitive exclusion in multispecies communities. In this line, the *structural approach* in ecology has provided an alternative theoretical perspective to study competitive exclusion in multispecies communities (Saavedra et al., 2017*b*; Song et al., 2018*b*). In general, the structural approach posits that how likely a particular outcome of competition is to occur can be understood through the full range of environmental conditions compatible with that qualitative outcome. While the structural approach was initially devised to investigate species coexistence as the qualitative outcome (Rohr et al., 2014; Saavedra et al., 2017*b*), it can also be extended to study competitive exclusion (Song et al., 2020*a*). Here, we apply the structural approach to investigate the emergence and sources of competitive exclusion in multispecies communities as a function of species' intrinsic growth rates, community size (number of competing species), and competition structure (i.e., the interaction matrix).

As an empirical application for our framework, we use empirical data on five grass species from California grasslands. The invasion of exotic annual species has competitively excluded native perennial species in many regions (Seabloom et al., 2003). Indeed, empirical evidence suggests that coexistence of multiple annual and perennial species is highly unlikely (Uricchio et al., 2019). However, most theoretical (Crawley and May, 1987; Rees and Long, 1992; Kisdi and Geritz, 2003; Uricchio et al., 2019) and experimental studies (Hamilton et al., 1999; Corbin and D'Antonio, 2004; Seabloom et al., 2003; Mordecai et al., 2015) have primarily focused on the competitive exclusion between two species (i.e., one annual species and one perennial species). Thus, it is unclear how these ecological dynamics are expected to play out among multiple annual and perennial species. To this end, we apply our investigation to field experiments on three exotic annual species (*Bromus hordeaceus*, *Bromus diandrus*, and *Avena barbata*) and two native perennial species (*Elymus glaucus* and *Stipa pulchra*) that occur in California grasslands (Uricchio et al., 2019). Previous simulation-based work showed a complex pattern of coexistence, deterministic exclusion, and contingent exclusion among these species (Uricchio et al., 2019). In addition, competition among these species is intransitive (non-hierarchical), and stronger between species than within species (i.e., self-regulation is weak). Here, using a structural approach, we systemically disentangled the contributions of life-history traits, community size, and competition structure in shaping whether competitive exclusion is expected to be deterministic or contingent in California grasslands.

Methods

Structural approach to competitive exclusion

The structural approach in ecology is built on a systematic and probabilistic understanding of how likely a given qualitative dynamics is to occur (Song et al., 2020*b*; Saavedra et al., 2020). Here, the qualitative dynamics of interest are deterministic exclusion and contingent exclusion. The structural approach simplifies ecological dynamics as a function of abiotic and biotic conditions (Saavedra et al., 2017*b*). Abiotic conditions are phenomenologically represented by *intrinsic growth rates* (the maximum growth rate a species can have in isolation) and they are assumed to change in response to environmental changes. Biotic conditions are phenomenologically represented by the *competition structure* (the matrix whose elements correspond to the competitive effect of one species on another) and are assumed to be fixed across time. This characterization and set of assumptions allows us to calculate the domain of abiotic conditions compatible with a given qualitative outcome as a function of biotic conditions. Importantly, the larger this domain is, the higher the probability that the observed abiotic conditions (drawn uniformly at random) match with one inside the domain, leading to the realization of the corresponding qualitative outcome.

Formally, the structural approach uses the *feasibility domain* as the domain of abiotic conditions compatible with a given qualitative outcome. The feasibility domain describes the full range of intrinsic growth rates compatible with positive abundances of all species in the community (i.e., feasible equilibrium). While the competition structure determines the *shape* of the feasibility domain (Song et al., 2018*b*, 2020*a*; Tabi et al., 2020), the observed intrinsic growth rates determine whether the community is inside or outside of the feasibility domain (Saavedra et al., 2017*b*). In addition to the shape of the feasibility domain, it is also important to consider the *orientation* of the feasibility domain. The orientation refers to whether the feasible equilibrium in the feasibility domain is dynamically stable or not. The importance of the orientation is that stable feasibility leads to coexistence, whereas unstable feasibility leads to contingent exclusion (Case, 1999; Fukami et al., 2016). The orientation of the feasibility domain is mainly driven by the ratio of intra- to interspecific interactions (Song et al., 2020*a*). In sum, following the structural approach, whether competitive exclusion is deterministic or contingent should be driven by the orientation of the feasibility domain (determined by the observed competition structure), and the match between the observed intrinsic growth rates (mainly constrained by life-history processes) and the shape of the feasibility domain (determined by the observed competition structure).

By way of example, focusing on two-species communities (see Figure 1 for a graphical illustration), one can establish three key intuitions about competitive exclusion derived from the structural approach (Song et al., 2020*a*): (i) For contingent exclusion to occur, it is necessary that species depress their competitor's per capita growth rate more than their own (changing the orientation of the feasibility domain). (ii) The larger the intrinsic growth rate of the competitively inferior species, the more likely contingent exclusion is to occur. (iii) The larger the feasibility domain, the more likely contingent exclusion is to occur. Note that these intuitions are aligned with the theoretical expectations from frameworks based on growth rates when rare that are explicitly justified for two-species communities (Adler et al., 2007; Fukami et al., 2016). Because the theoretical formalism of the structural approach is the same for two-species and multispecies communities (Saavedra et al., 2017*a*), these three intuitions can be expected to operate in multispecies communities as well. It is worth noting that on average, the size of the feasibility domain decreases with the number of species in a community (Grilli et al., 2017; Song et al., 2018*b*). Thus, following these premises, contingent exclusion should be more likely to be observed in ecological communities (i) with few number of species, (ii) with species that more strongly depress their competitor's growth rate relative to their self-regulation, and (iii) where life-history processes increase the intrinsic growth rate of competitively inferior species.

Empirical data

We based our analysis on an experimental study conducted in 2015-2016 in Jasper Ridge Biological Preserve, located in San Mateo County, California (377°24'N, 122°13'30"W; 66–207 m) (Uricchio et al., 2019). The experimental study investigated five focal grassland species with three exotic annual species (*Avena barbata*, *Bromus diandrus*, and *Bromus hordeaceus*) and two native perennial species (*Stipa pulchra* and *Elymus glaucus*). These species were studied because they were abundant and widespread in California grasslands. This experimental study measured key demographic rates that determined species growth, including seed overwinter survival, germination, establishment, adult bunchgrass survival, and the effects of competition on per-capita seed production (Uricchio et al., 2019). In addition, the study measured competition experimentally and observationally in 1-m^2 plots. This covered a broad range of naturally occurring plant densities. Competition and growth parameters were inferred via Markov-Chain Monte Carlo based on population dynamics models developed for the three annual and two perennial grass species. We used 2000 samples from the posterior distribution of each of these parameters to conduct our study.

Population dynamics of annual and perennial species

To study ecological dynamics under a structural approach, it is necessary to assume the governing laws of population dynamics (Cenci and Saavedra, 2018). Annual and perennial species have different population dynamics. A key difference is that annual species only carry over between growing seasons as seeds, while perennial species carry over between growing seasons as both seeds and adults. To simplify the notation, for each species i we hereafter denote annual seeds as N_i, perennial seeds as N_i^S, and perennial adults as N_i^A.

Focusing on annual species, we assume the classic seed-banking annual plant model with Beverton-Holt competition (Levine and HilleRisLambers, 2009; Godoy and Levine, 2014). For annual plants, these dynamics can be written as (illustrated in Figure 2A)

$$N_i(t+1) = \underbrace{N_i(t) g_i \frac{\lambda_i}{1+\sum_j \alpha_{ij} D_j(t)}}_{\text{germinated seeds under competition}} + \underbrace{N_i(t)(1-g_i)}_{\text{non-germinated seeds}} , \tag{1}$$

where N_i is the number of seeds of species i, g_i is the germination fraction, λ_i is per-capita seed production in the absence of competition, and α_{ij} is the per-capita competitive effect of species j on species i. The summation of the germinated density D_j is established over all species of annual germinants, perennial germinants, and perennial adults. Specifically, the germinated density D_j of competitors from species j is

$$D_j = \begin{cases} g_j N_j, & \text{if } j \text{ is annual seed,} \\ g_j N_j^S, & \text{if } j \text{ is perennial seed,} \\ N_j^A, & \text{if } j \text{ is perennial adult.} \end{cases} \tag{2}$$

Perennial seed population dynamics can be written as (illustrated in Figure 2B)

$$N_i^S(t+1) = \underbrace{N_i^A(t) \frac{\lambda_i}{1+\sum_j \alpha_{ij} D_j(t)}}_{\text{seeds produced from adults}} + \underbrace{N_i^S(t)(1-g_i)}_{\text{non-germinated seeds}} , \tag{3}$$

which is a slight modification of the annual plant model. Specifically, perennial seeds are generated when adults A_i reproduce, and reduced by both species competition (first term in Eqn. 3) and the survival of non-germinating perennial seeds (second term in Eqn. 3). The competition coefficients α_{ij} and densities D_j are defined as above (Eqn. 2).

Finally, the population dynamics of perennial adults can be written as (illustrated in Figure 2B)

$$N_i^A(t+1) = \underbrace{N_i^A(t)\omega_i}_{\text{surviving adults}} + \underbrace{N_i^S(t)\frac{g_i v_i}{1+\sum_j \beta_{ij} D_j(t)}}_{\text{seeds germinating into adults}}, \tag{4}$$

where ω_i is the over-summer survival fraction of perennial adults, and v_i is the fraction of over-summer maturation from perennial seedlings into adults for the following year (in the absence of competition). Note that perennial adults are generated by both surviving perennial adults A_i (first term in Eqn. 4) and seeds S_i that germinate and survive over the summer to become adults. Again, the abundance of perennial adults are reduced by species competition (second term in Eqn. 4).

Understanding the sources of competitive exclusion

To understand the emergence of deterministic and contingent exclusion, it is necessary to understand their sources. For this purpose, here we focus on three key ecological properties: life-history processes, community size, and competition structure. Following a structural approach, we investigate these three sources in the California grassland study system.

Life-history processes

Annual and perennial species differ in their strategies for persisting between growing seasons, either solely as seeds or additionally as surviving adults (Lundgren and Des Marais, 2020)—as we have exemplified in our population dynamics models. To understand the contribution of this life-history difference to the emergence of competitive exclusion, we applied the structural approach to the population dynamics of species with and without modeling the life-history difference between annual and perennial species.

By removing over-summer survival of adult perennials and assuming that germinating seeds produce new seeds within the same growing season, thereby removing the life-history difference between annual and perennial species (i.e., removing the dashed links in Figure 2B), the feasibility condition of a multispecies community reduces to

$$\lambda_i - 1 = \sum_{j\in\mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j\in\mathcal{P}} \alpha_{ij} g_j N_j^S, \ \forall i, \tag{5}$$

where N_j represents either the annual or the perennial species, $\mathcal{A}$ represents the set of all annual species, and $\mathcal{P}$ represents the set of all perennial species.

Alternatively, incorporating the life-history processes of perennial species (i.e., keeping the dashed links in Figure 2B), the feasibility condition is

$$\lambda_i - 1 = \sum_{j\in\mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j\in\mathcal{P}} \alpha_{ij} g_j \left(1 + \sqrt{\frac{v_j}{\lambda_j(1-\omega_j)}}\right) N_j^S, \text{ if species } i \text{ is annual} \quad (6)$$

$$\sqrt{\frac{\lambda_i v_i}{1-\omega_i}} - 1 = \sum_{j\in\mathcal{A}} \alpha_{ij} g_j N_j + \sum_{j\in\mathcal{P}} \alpha_{ij} g_j \left(1 + \sqrt{\frac{v_j}{\lambda_j(1-\omega_j)}}\right) N_j^S, \text{ if species } i \text{ is perennial,} \quad (7)$$

where again N_j represents either the annual or the perennial species, $\mathcal{A}$ represents the set of all annual species, and $\mathcal{P}$ represents the set of all perennial species. The derivations can be found in Appendix B.

Importantly, the feasibility domain of the multispecies communities is the same excluding (Eqn. 5) or including (Eqn. 6 and 7) perennial life-history processes. The mathematical rationale of this identity comes from the column scaling invariance of the feasibility domain (Song et al., 2020*b*) (Appendix D). The ecological rationale can be interpreted by the fact that perennial life-history processes affect only the absolute equilibrium abundances, and not the competition coefficients (Saavedra et al., 2017*b*). Thus, for the assumed population dynamics, the feasibility domain of the multispecies community is uniquely determined by the competition structure $\{a_{ij}\}$ summarized in the interaction matrix, but not by any other parameter. This result additionally implies that life-history processes only affect the patterns of competitive exclusion (whether it is dominated by deterministic or contingent exclusion) by changing the effective intrinsic growth rates. Specifically, life-history processes change the effective intrinsic growth rates of the perennial species from $(\lambda_i - 1)$ to $(\sqrt{\frac{\lambda_i v_i}{1-\omega_i}} - 1)$ (see Appendix B for variations of assumptions).

We test the effects of life history differences on competitive exclusion in the species present in our empirical data of California grasslands. As we show theoretically, the effects can only come through the effective intrinsic growth rates. It is unclear *a priori* whether the life-history processes increase or decrease the effective intrinsic growth rates of the perennial species in the empirical data.

Community size

As described above, following a structural approach, deterministic exclusion is expected to dominate over contingent exclusion in large communities (see section *Structural approach on competitive exclusion*, Figure 1). However, in a multispecies community, more complex outcomes of competitive exclusion are possible: some species can be deterministically excluded while others can be

contingently excluded. This implies that we cannot always classify the competition dynamics of a community simply as either deterministic or contingent. Instead, this reveals that competitive exclusion in multispecies communities should be analyzed at the species level. That is, in order to investigate the contribution of community size to the patterns of competitive exclusion, we need to analyze how the probabilities of observing deterministic and contingent exclusion for each species change as a function of community size. Importantly, while the theory suggests that we should get more deterministic exclusion as community size increases, it is possible that the observed parameters from empirical communities do not support this pattern. Here we test whether these theoretical patterns hold in our empirical data from California grasslands.

Competition structure

Ecological communities are characterized by non-random competition structures (Thébault and Fontaine, 2010; Song et al., 2018*a*; Song and Saavedra, 2020). Indeed, Figure 5A shows the inferred competition structure (the direction and strength of species competition) of annual and perennial species in the California grassland data. This figure reveals two key features of the empirically studied competition structure. First, the intraspecific competition (self-regulation) is generally weaker than the interspecific competition. Second, interspecific competition forms an intransitive structure (also known as a non-hierarchical structure). The importance of these two features has been a central question in ecological research (Uricchio et al., 2019; Fukami, 2015).

To test the overall effect of the competition structure on the patterns of competitive exclusion, we investigate how the competition structure changes the size of the feasibility domain in the empirical parameter space estimated for California grassland species. Recall that it is expected that contingent exclusion dominates multispecies communities with larger feasibility domains. We compute numerically the size of the feasibility domain from Eqns. (6) and (7) (Song et al., 2018*b*). Additionally, to separate the specific contributions of the two structural features of competition (i.e., intraspecific competition and intransitive competition), we use model-generated communities with four types of competition structures: (i) communities with either weak (intraspecific<interspecific) or strong (intraspecific>interspecific) intraspecific competition, and (ii) communities with either a hierarchical or intransitive competition structure. Focusing on the first structural combination, we consider strong intraspecific competition when the intraspecific competition of a given species is larger than the sum of the interspecific competition that this species experiences from other species (the opposite for weak intraspecific competition). Focusing on the second structural combination, we generate a random Erdős-Rènyi structure where each competition strength is independently sampled

from a uniform distribution $[0, 1]$ (Song and Saavedra, 2018), and then we arrange the competition structure as either hierarchical or intransitive. We investigate which combinations can reproduce the associations between competitive exclusion and feasibility domain observed in the empirical data. We have additionally tested other parameterizations to test the robustness of the results (Appendix F).

Results

We first analyzed the effects of perennial life-history processes on whether a community is dominated by deterministic or contingent exclusion. The structural approach argues that contingent exclusion is more likely when the competitively inferior species has a higher intrinsic growth rate (Figure 1). Theoretically, perennial life-history processes only regulate the intrinsic growth rates—via their effects on survival and fecundity in the absence of competition—but not the feasibility domain, which exclusively depends on competition structure. Because the perennial species included in this study were generally competitively inferior to the annual species, we expected that incorporating perennial life-history processes would yield a higher frequency of contingent exclusion by increasing perennial species intrinsic growth rates.

Focusing on all possible two-species communities with one annual and one perennial species, Figure 3 confirms the expectation above. To illustrate this effect, we used a standard graphical representation of ecological dynamics for two species: the niche-overlap-fitness-ratio space (Song et al., 2020*a*). Specifically, Figure 3 shows that by adding perennial life-history processes to the model, the fitness of perennial species increases, which leads to a higher frequency of contingent exclusion, rather than deterministic exclusion. In addition, we found that incorporating life-history processes can change the outcome of the dynamics when subject to different types of environmental perturbations acting on parameters (Song et al., 2020*a*). That is, we found that communities exhibit robustness to perturbations acting on intrinsic growth rates but not on competition strength when life-histories are excluded, while they exhibit robustness to perturbations acting on competition strength but not on intrinsic growth rates when life-histories are incorporated (see Appendix C). Importantly, multispecies communities exhibit qualitatively identical patterns (see Figure 4).

Next, we analyzed the effects of community size on the patterns of competitive exclusion. The structural approach argues that contingent exclusion is less likely—and deterministic exclusion more likely—when the community size is larger (Figure 1). Figure 4 confirms this expectation in the em-

pirical data. We found that the percentage of deterministically excluded species rises from 33% in two-species communities to 74% in five-species communities. By contrast, the percentage of contingently excluded species falls from 31% in two-species communities to 14% in five-species communities. Note that we are studying the patterns of competitive exclusions on a species level here (i.e., whether a species persists, is deterministically excluded, or is contingentally excluded). In addition, we found that the effect of community size acts more strongly on annual than perennial species (Appendix E). The effect of community size remained consistent with and without incorporating perennial life-history processes (Appendix E).

Lastly, we analyzed the effect of competition structure on the patterns of competitive exclusion. The empirical competition structure (Figure 5A) exhibits two key features: relatively weak intraspecific competition, and intransitive competition. The structural approach establishes that contingent exclusion is more likely when a community has a larger feasibility domain. Figure 5B confirms this expectation in our empirical data. That is, the figure shows that under contingent exclusion, communities have larger feasibility domains (right orange histograms) than the ones generated under deterministic exclusion (left green histograms). Note that the size of feasibility domain decreases as a function of community size, and coexistence (middle blue histograms) is only observed in two-species communities (Fig. 5B). Additionally, we found theoretically (using simulations, as detailed in Methods) that the empirical relationship between competitive exclusion and the size of the feasibility domain emerges by generating weak intraspecific competition structures, regardless of being intransitive or hierarchical (Fig. 5C). These results are robust to different parameterizations in simulations (Appendix F).

Discussion

Despite the recent research focus on understanding the mechanisms underlying stable coexistence (Levine and HilleRisLambers, 2009; Adler et al., 2007; Chesson, 2000; Godoy et al., 2014; Kraft et al., 2015), competitive exclusion occurs frequently in nature, and the drivers of deterministic versus contingent exclusion remain poorly understood (Fukami, 2015; Fukami et al., 2016; Uricchio et al., 2019; Mordecai et al., 2015; Mordecai, 2013). In multispecies communities, complex outcomes that combine deterministic and contingent exclusion among groups of species are possible, challenging the extension of results from two-species communities (Case, 1995; Uricchio et al., 2019). Here, we provide a theoretical framework following a structural approach to understand the emergence and sources

of competitive exclusion in multispecies communities, specifically to distinguish when competitive exclusion is dominated by deterministic or contingent exclusion. We have evaluated three key expectations derived from our theoretical framework: (i) For contingent exclusion to occur, it is necessary that species have a greater negative effect on their competitor's per capita growth rate than on their own self-regulation. (ii) The larger the intrinsic growth rate of the competitively inferior species, the more likely contingent exclusion occurs. (iii) The larger the feasibility domain of a community, the more likely contingent exclusion can be observed. We tested these expectations in an empirical study system composed of five annual and perennial grasses occurring in California grasslands, which exhibit both deterministic and contingent exclusion and several biologically interesting features, including variation in life history strategy, weak self-regulation and strong interspecific competition, and intransitive (non-hierarchical) competition (Uricchio et al., 2019). Specifically, we investigated the impact of perennial life-history processes, community size, and competition structure dictate the dynamics of competitive exclusion in this system using the structural approach, which applies to communities larger than two species.

First, we found that perennial life history (interannual survival and reproduction of adult bunchgrasses) increases the probability of observing contingent exclusion by increasing perennial species' effective intrinsic growth rates (Figures 3 and 4). These life-history processes contribute only to the effective intrinsic growth rates but not to the effective competition strength. In a two-species community, life-history processes increase the fitness of competitively inferior species, making deterministic exclusion less likely (Figure 3). In multispecies communities, we have shown that these life-history processes also help the competitively inferior species (Figure 4). This reveals the importance of life-history processes for increasing the chance of survival of inferior competitors.

Second, we have shown that the probability of observing contingent exclusion decreases with community size (Figure 4). This result is contrary to the naive expectation that contingent exclusion dominates in larger communities, derived from randomly constructed communities (Zhao et al., 2020). However, it has remained unclear what happens when communities are structured following a strong deterministic component of population dynamics (Fukami, 2015). For example, in our focal system, annual species are generally superior competitors to perennial species. Under this scenario, contrary to the naive expectation, we should expect to see deterministic exclusion dominating larger communities. That is, a larger community is more likely to contain at least one species that has a large enough competitive advantage over the others to deterministically exclude them. This apparently contradictory expectation aligns well with the intuition derived from our structural approach

(Figure 1). Further, these findings reveal that multispecies dynamics may be more predictable than previously thought (May, 1972).

Third, we found that the probability of observing contingent exclusion increases as a function of the size of the feasibility domain defined by the ratio between intraspecific and interspecific competition, and not by the level of hierarchical competition (Figure 5). While many empirical studies have shown that intraspecific competition tends to be stronger than interspecific competition (LaManna et al., 2017; Adler et al., 2018), recent work has questioned the generality of the empirical evidence supporting stronger intraspecific competition (Hülsmann and Hartig, 2018; Chisholm and Fung, 2018; Detto et al., 2019; Broekman et al., 2019). Moreover, we have shown that intransitive (or non-hierarchical) competition is unlikely to explain the outcomes of competitive exclusion in the studied system. By contrast, intransitive competition can play an important role in shaping species coexistence (Allesina and Levine, 2011; Soliveres et al., 2015; Gallien et al., 2017). Thus, our findings imply that ecological mechanisms may play different roles in coexistence and competitive exclusion.

Although the understanding of species coexistence has been one of the major topics in ecology for decades (May, 1972; McCann, 2000; Ives and Carpenter, 2007; Bastolla et al., 2009; Allesina and Tang, 2012; Rohr et al., 2014), competitive exclusion remains the dominant—if hidden—foundation of ecological community structure. Particularly in light of species invasions and global anthropogenic changes in climate and land use, species increasingly face competitive exclusion, and land managers and conservationists are increasingly tasked with maintaining populations of disappearing species. We know surprisingly little about the frequency of and mechanisms underlying deterministic versus contingent exclusion, but uncovering these mechanisms is paramount to understanding the role of historical contingency in ecological communities. Indeed, coexistence of all species is often too much to ask in ecological communities (Sigmuiud, 1995; Friedman et al., 2017; Goldford et al., 2018). While recent studies have started to focus on the fraction of species that can coexist starting from an initial pool (Bunin, 2017; Barbier et al., 2018; Serván et al., 2018), this line of research does not distinguish whether the excluded species are deterministically or contingently excluded. Recent theoretical work has advanced our understanding of the mechanisms underlying contingent exclusion (Fukami et al., 2016; Ke and Letten, 2018), but empirical studies rarely examine contingent and deterministic exclusion simultaneously.

Our key results—that contingent exclusion is more likely in smaller communities, with species that are more competitively equal (e.g., due to equalizing differences in life history), and among species with low self-regulation relative to interspecific competition, regardless of whether it is hierarchical—

are testable in a wide range of study systems using the same study designs that investigate species coexistence (Levine and HilleRisLambers, 2009; Godoy et al., 2014; Adler et al., 2018). Further research that integrates empirical work with mathematical models could reveal a previously overlooked diversity of contingent and deterministic exclusion occurring among species, which would not be detectable either through empirical studies or two-species models alone. Thus, our work provides a new perspective on the rich and potentially predictable dynamics of competitive exclusion in multispecies communities.

Authors' contributions: All authors conceived the ideas and designed the methodology. C.S. performed the study. S.S. supervised the study. C.S. and S.S. wrote a first version of the manuscript. All authors contributed with substantial revisions. E. M. and L. U. compiled and provided data.

Data availability: The data of the California grassland community have previously been archived on https://www.journals.uchicago.edu/doi/abs/10.1086/701434.

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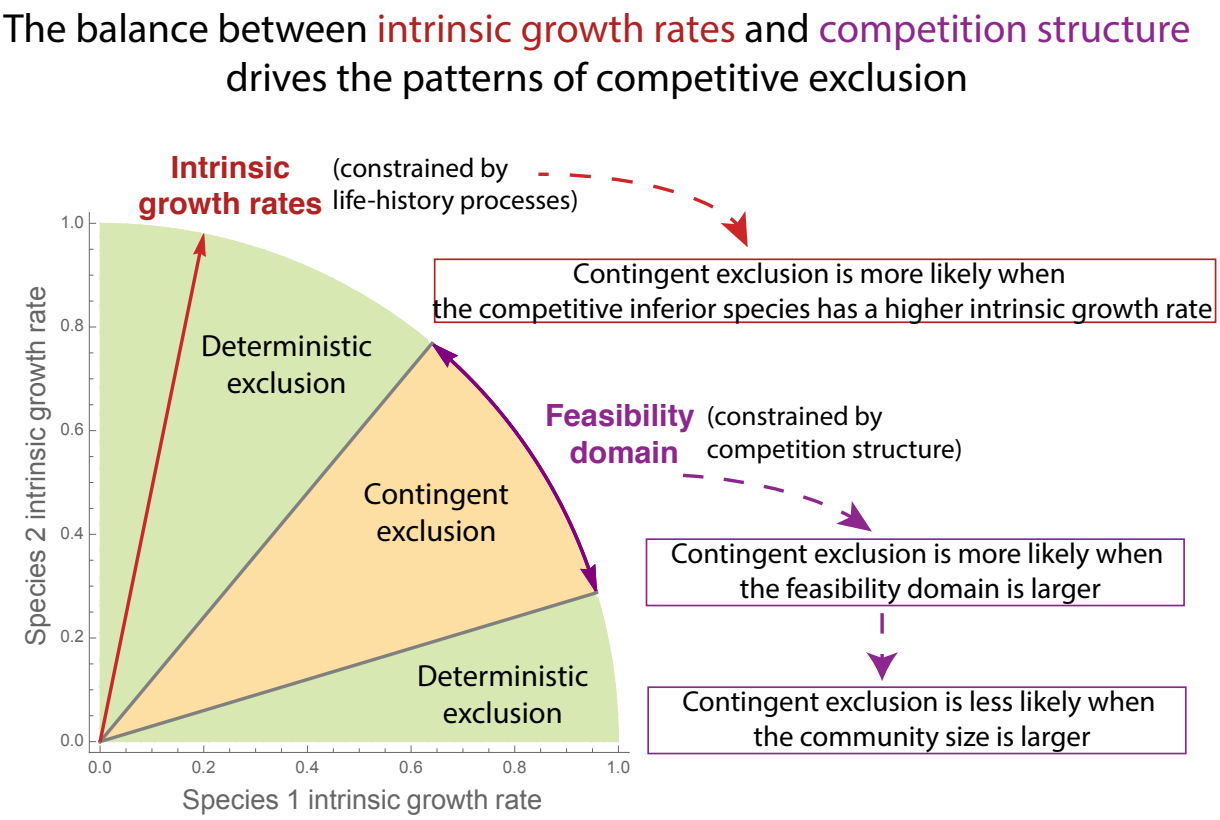

Figure 1: **Three key intuitions on competitive exclusion following a structural approach**. For a hypothetical community with two competing species, the figure shows the parameter space defined by the intrinsic growth rates (phenomenological abiotic conditions) of the two species. The feasibility domain (middle orange region) is the set of all directions of intrinsic growth rates compatible with an *unstable* feasible equilibrium. Note that we only study unstable feasible equilibrium here since our focus is on competitive exclusion (otherwise we would expect stable coexistence). The complement of the feasibility domain (green region) corresponds to the directions of intrinsic growth rates associated with deterministic exclusion. Following the structural approach in ecology (Saavedra et al., 2017*b*), we can derive three key intuitions: (i) Contingent exclusion is expected to be more likely when the competitive inferior species has a higher intrinsic growth rate. (ii) Contingent exclusion is more likely when the feasibility domain is larger. (iii) Contingent exclusion is less likely when the community size is larger. The ecological rational is that adding a new species generally further constrains the feasibility domain to be smaller. Note that the third intuition is a corollary from the second intuition since the feasibility domain generally shrinks with community size.

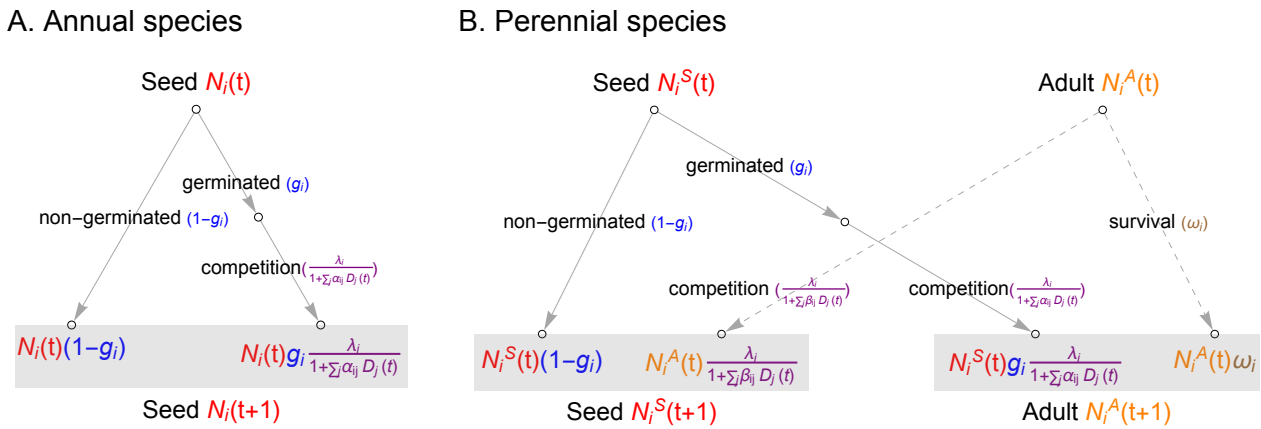

Figure 2: **Population dynamics of annual and perennial plant species.** Panel (A) illustrates the population dynamics of an annual plant species (Eqn. 1). The annual plant has one life stage as seed. Some annual seeds germinate, and the germinated seeds produce seeds and are decreased by competition from other plant species. Panel (B) illustrates the dynamics of a perennial plant species (Eqn. 3 and 4). The perennial plant has two life stages, seed and adult. Some perennial seeds germinate, and the germinated seeds would produce adults and are decreased by competition from other plant species (left side). Perennial life history: some perennial adults survive as perennials, while some perennial adults produce seeds and are decreased by competition from other plant species (right side, dashed lines). Note that the dynamics of perennial plants can be be modeled with or without these perennial life-history processes.

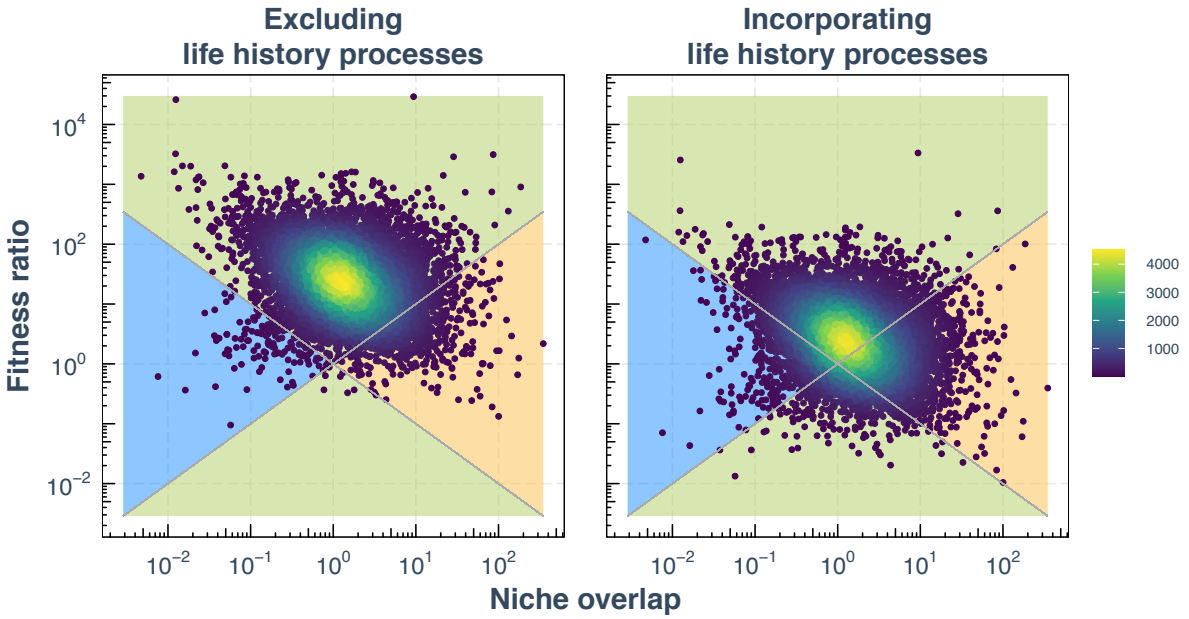

Figure 3: **Perennial life-history processes increase the frequency of contingent exclusion by increasing the effective intrinsic growth rates of perennials.** Plots represent two-species dynamics based on niche overlap (horizontal axis) and fitness ratio (vertical axis) between a pair of one annual species and one perennial species. This space is divided into three regions: deterministic exclusion (green), coexistence (blue), and contingent exclusion (orange). The left panel shows the case when perennial life-history processes are not incorporated into the model, while the right panel shows the case when perennial life-history processes are incorporated. Each point represents a pair of fitness ratio and niche overlap computed from $2,000$ posterior samples from our data (the color map represents the density of the points). Note that the fitness ratio here refers to the ratio of annual fitness to the perennial fitness. Perennial life-history processes only influence the effective intrinsic growth rates, but not the effective competition strength (i.e., life-history processes only change fitness ratios). This implies that including perennial life-history processes allows cases to fall into the contingent exclusion region (orange region). The details of computing fitness ratio and niche overlap can be found in Appendices A and B, and plots for individual pairs can be found in Appendix D.

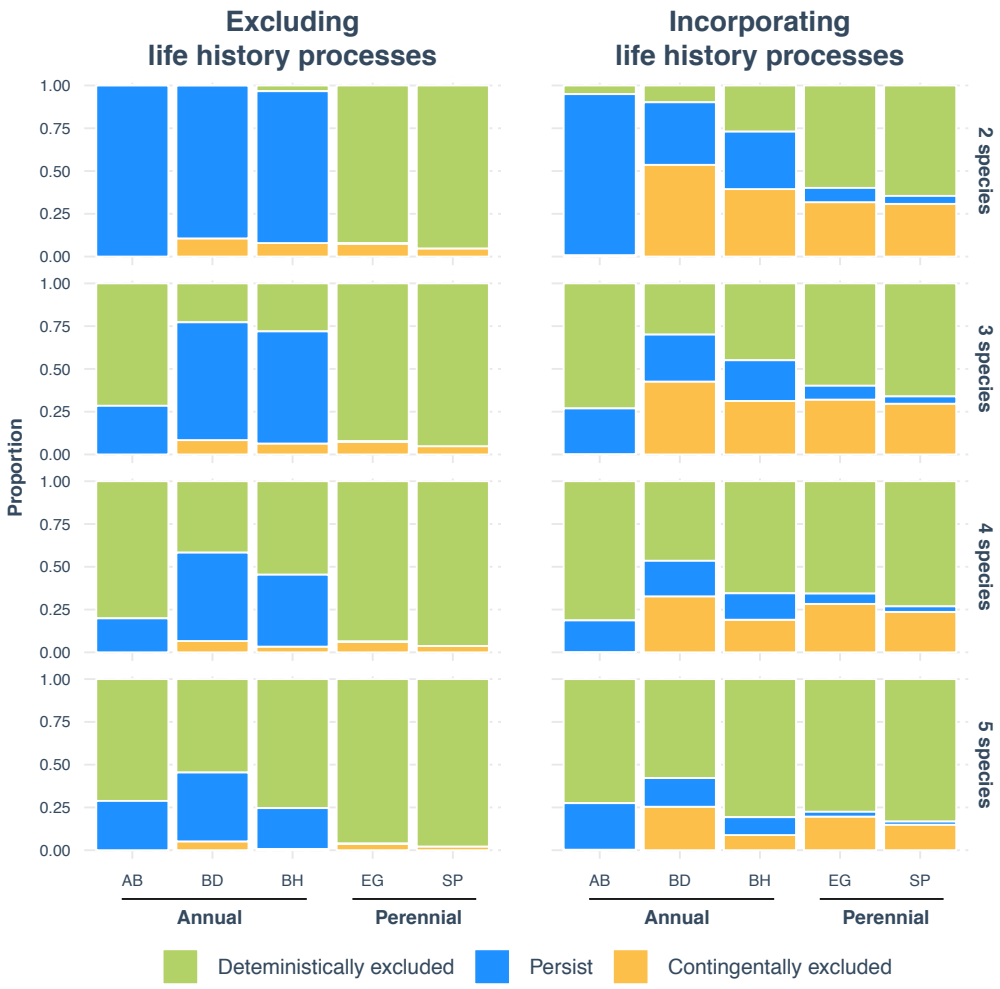

Figure 4: **Contingent exclusion is less likely when the community size is larger**. We show how the proportions of contingent exclusion or deterministic exclusion change with community size. The horizontal axis denotes the plant species, where AB stands for *Avena barbata*, BH for *Bromus hordeaceus*, BD for *Bromus diandrus*, EG for *Elymus glaucus*, and SP for *Stipa pulchra*. AB, BD, and BH are annual species while EG and SP are perennial species. The vertical axis denotes the proportion of posterior 2,000 parameter samples in which the species either is deterministically excluded (green), persists (blue), or is contingently excluded (orange). The left and right panels show the case when perennial life-history processes are excluded and included into the model, respectively. The vertical panels show the patterns in each community size (from two-species communities to five-species communities). We found that the proportion of deterministically-excluded species increases with increasing community size (the opposite patterns for contingent exclusion).

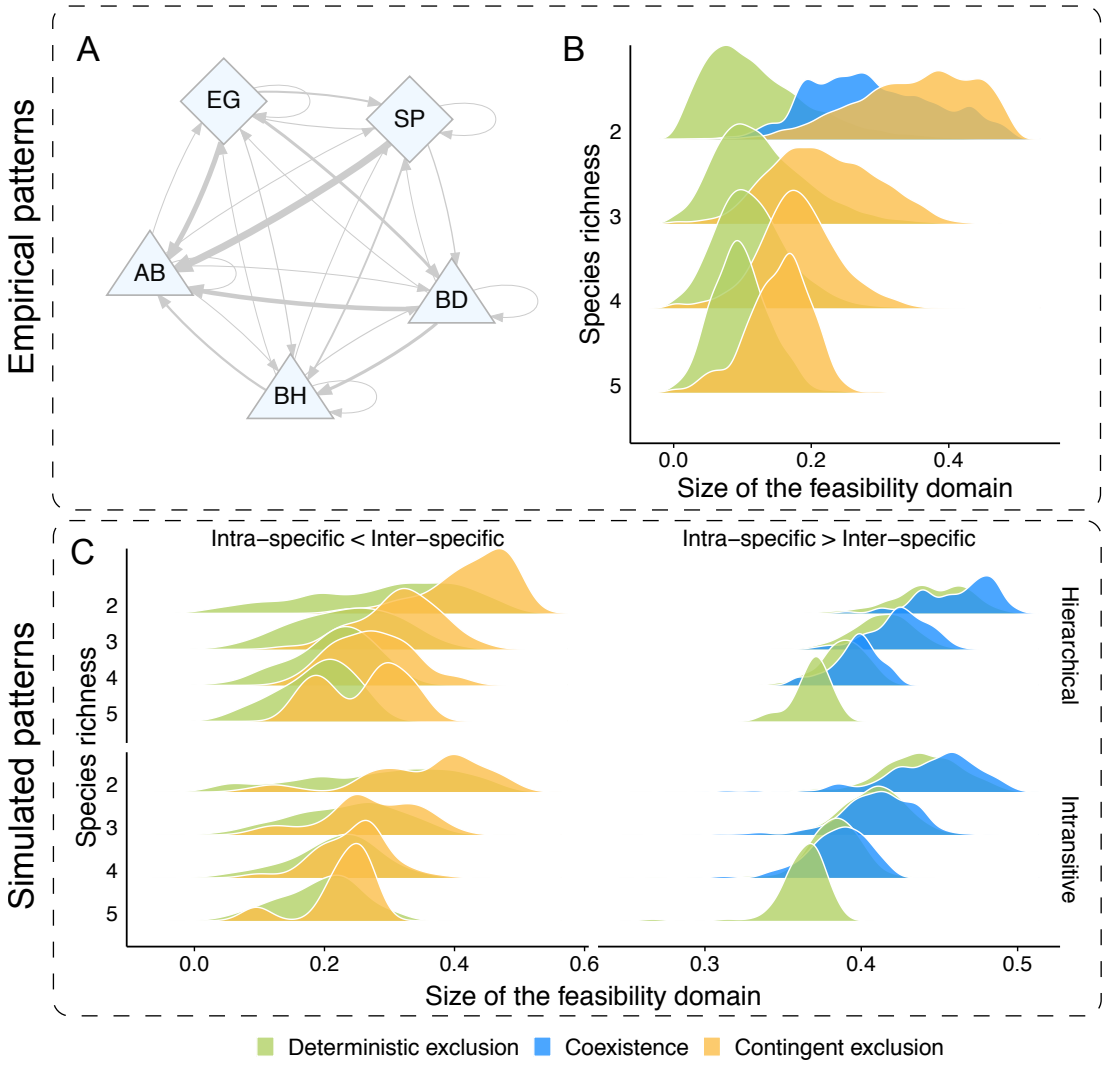

Figure 5: **Weak intraspecific and not intransitive competition drives the patterns of competitive exclusion**. Panel (**A**) shows the competition structure among annuals and perennials in the empirical data from California grassland plant species. Each node represents a plant species, where the triangles (*Avena barbata* (AB), *Bromus hordeaceus* (BH), and *Bromus diandrus* (BD)) are annuals and the rectangles (*Elymus glaucus* (EG) and *Stipa pulchra* (SP)) are perennials. The direction and width of the links represent the directionality and strength (averaged from the posterior samples) of competition. We observe two key structures: (i) intraspecific competition (self-loops) is in general weaker than interspecific competition (edges), and (ii) competition is intransitive (non-hierarchical). Panel (**B**) shows the outcome of competition—deterministic exclusion, coexistence, or contingent exclusion—for each empirically-derived parameter set, grouped into histograms by qualitative outcome. We characterize the competition structure of a community across different community sizes using the normalized size of the feasibility domain (horizontal axis). The empirical data show that deterministic exclusion (green histograms) is mostly characterized by structures with a relatively small feasibility domain. Contingent exclusion (orange histograms) have the opposite patterns. Panel (**C**) shows the theoretical expectations about how competition structure affects the patterns of competitive exclusion. We show model-generated communities with different competition structures. We use two structural combinations: (i) communities with either a low (intraspecific $<$ interspecific) or high (intraspecific $>$ interspecific) intraspecific competition, and (ii) communities with either a hierarchical or intransitive competition structure. We find that the competition structures with weaker intraspecific competition, regardless of being hierarchical or not, produce qualitatively the same patterns as the empirical patterns shown in Panel (**B**).