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LETTER

# Understanding the emergence of contingent and deterministic exclusion in multispecies communities

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**Abstract**

Competitive exclusion can be classified as deterministic or as historically contingent. While competitive exclusion is common in nature, it has remained unclear when multispecies communities formed by more than two species should be dominated by deterministic or contingent exclusion. Here, we take a fully parameterised model of an empirical competitive system between invasive annual and native perennial plant species to explain both the emergence and sources of competitive exclusion in multispecies communities. Using a structural approach to understand the range of parameters promoting deterministic and contingent exclusions, we then find heuristic theoretical support for the following three general conclusions. 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 that the probability of observing contingent exclusion increases with weaker intraspecific competition, and not with the level of hierarchical competition. Third, we find a shift from contingent exclusion to deterministic exclusion with increasing numbers of competing species. Our work provides a heuristic framework to increase our understanding about the predictability of species persistence within multispecies communities.

**KEYWORDS**

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

## INTRODUCTION

Species coexistence is one of the most studied topics in ecology (Vellend, 2016); however, some have observed that competitive exclusion is the norm rather than the exception in nature (Blowes et al., 2019; Goldford et al., 2018; Hardin, 1960). Indeed, coexisting species within ecological communities are usually a fraction of all the species available in a local species pool (Odum et al., 1971; Sigmund, 1995). Exclusion as a ubiquitous feature of ecological communities has been demonstrated empirically across a wide range of life forms, including algae (Narwani et al., 2013), annual plants (Godoy & Levine, 2014), microbiomes (Friedman et al., 2017), bacteria (Tan et al., 2017), and nectar-colonising yeasts (Grainger et al., 2019). Importantly, due to the inherent stochasticity in community assembly, competitive exclusion can be broadly classified into two ecologically different categories (Fukami, 2015; 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. Knowing whether competitive exclusion is deterministic or contingent is fundamental to understanding the role of predictability and randomness in community assembly (Fukami, 2015; Lawton, 1999). For example, it has direct implications for conservation management: depending on whether the exclusion of native species is deterministic or contingent, we should adopt different strategies to restore biodiversity resulting after exotic species invasion (Bøhn et al., 2008; McGeoch et al., 2016).

Since the 1930s, theoretical and empirical research has systematically documented and expanded our understanding of competitive exclusion between two competing species (Ayala, 1969; Brown, 1971; Gause, 1932; Gilpin & Justice, 1972). Moreover, in recent decades, theoretical studies have started to provide an overarching framework to synthesise data across different competition systems (Johnson & Bronstein, 2019; Ke &Wan, 2020; Mordecai, 2013). This theoretical development started by focusing on the conditions leading to deterministic exclusion (Adler et al., 2007; Chesson, 2000), and then it was extended to investigate the conditions for contingent exclusion (Fukami et al., 2016; Ke & Letten, 2018; Mordecai, 2011). Similarly, extensive empirical research started to examine the sources of deterministic exclusion (Adler et al., 2010; Mayfield & Levine, 2010; Violle et al., 2011), and more recently it has moved to the analysis of contingent exclusion (Grainger et al., 2018, 2019; Song et al., 2020a). Focusing on competition between two species, 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 negative intraspecific interactions are stronger than interspecific interactions. By contrast, greater similarity in species intrinsic growth rates and stronger interspecific relative to intraspecific interactions promote contingent exclusion (Ke & Letten, 2018; Song et al., 2020a).

However, it remains unclear whether these clear conditions at the *two-species* level also operate in *multispecies* communities of three or more species. First, the aforementioned body of work has been mainly executed under a theoretical formalism for two-species communities, which does not have a counterpart for multispecies communities. Specifically, the standard formalism for two-species communities is incompatible with the current canonical formalism for multispecies communities (Song et al., 2019). While the formalism for two-species communities can easily distinguish competitive exclusion into deterministic exclusion and contingent exclusion, the formalism for multispecies communities cannot distinguish them as easily (Barabás et al., 2018). Second, the patterns of contingent and deterministic exclusion are inherently more complicated in multispecies communities. For example, multispecies communities may exhibit a mixed outcome of competitive exclusion: 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 in multispecies communities, which is typically done in two-species communities. Instead, competitive exclusion in multispecies communities should be analysed at the species level. Specifically, for a community with $S$ interacting species, there are in total $S!$ possibilities of species arrival orders, for which the outcome can be classified as follows: if a species is competitively excluded in all possible arrival orders, then the species is deterministically excluded; if a species is competitively excluded in some but not all possible arrival orders, then the species is contingently excluded. Thus, we still lack a full understanding of competitive exclusion in species-rich ecological communities, where more complex dynamics, including non-hierarchical competition and higher-order interactions, can occur (Levine et al., 2017; Saavedra et al., 2017).

The complexity of competitive exclusion in multispecies communities calls for further developing the existing theory or establishing new approaches. Along these lines, the *structural approach* in ecology has provided an alternative theoretical perspective to study competitive exclusion in multispecies communities (Saavedra et al., 2017; Song et al., 2018b). 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 (contexts) 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), it can also be extended to study competitive exclusion (Song et al., 2020a). 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 of our framework, we use data on five grass species from California grasslands. The invasion of exotic annual species presumably has, together with human-induced habitat shifts, competitively excluded native perennial species in many regions. This has been described as 'one of the most dramatic ecological invasions worldwide" (Seabloom et al., 2003). Indeed, empirical evidence suggests that long-term, stable coexistence of multiple annual and perennial species is unlikely (Uricchio et al., 2019). However, most theoretical (Crawley & May, 1987; Kisdi & Geritz, 2003; Rees & Long, 1992; Uricchio et al., 2019) and empirical studies (Corbin & D'Antonio, 2004; Hamilton et al., 1999; Mordecai et al., 2015; Seabloom et al., 2003), have primarily focused on the competitive exclusion between two species (i.e. one annual species and one perennial species). Thus, it remains unclear how these ecological dynamics are expected to play out among multiple competing annual and perennial species. To this end, we apply our investigation to data from previously published 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, we integrate a structural approach with numerical simulations to systemically disentangle the contributions of life-history traits (as components of intrinsic growth rates), community size, and competition structure to deterministic and contingent exclusion in California grasslands.

# MATERIALS AND METHODS

## Structural approach to competitive exclusion

The structural approach in ecology is built on a systematic and probabilistic understanding of how likely a given type of qualitative dynamics is to occur (Saavedra et al., 2020; Song, 2020). Here, the qualitative dynamics of interest are deterministic exclusion and contingent exclusion. The structural approach simplifies ecological dynamics as a function of internal and external conditions (Saavedra et al., 2017). External 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 conditions. Internal 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 (see Appendix B for an in-depth discussion). This characterisation and set of assumptions allows us to calculate the domain of external conditions (the context) compatible with a given qualitative outcome as a function of a given set of internal conditions. The larger this domain is, the higher the probability that the observed external conditions match with one inside the domain, leading to the realisation of the corresponding qualitative outcome.

Formally, the structural approach uses the *feasibility domain* as the domain of external 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., 2018b, 2020a; 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). When the community is outside of the feasibility domain, the community is expected to be driven by deterministic exclusion. To further understand the qualitative dynamics when the community is inside the feasibility domain, we need to consider the *orientation* of the feasibility domain in addition to its shape. 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., 2020a). In sum, following the structural approach, whether competitive exclusion is deterministic or contingent should be expected to be mainly driven by the match between the observed intrinsic growth rates (mainly constrained by life-history processes) with the shape and the orientation of the feasibility domain (both of which are determined by the observed competition structure). Note that our framework is only an expectation given that multispecies dynamics is a function of the underlying complexity of a system (AlAdwani & Saavedra, 2020).

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., 2020a): (1) 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). (2) The larger the intrinsic growth rate of the competitively inferior species, the more likely contingent exclusion is to occur. (3) The larger the feasibility domain, the more likely contingent exclusion is to occur. The opposite holds for deterministic exclusion. 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). We hypothesise these three intuitions operate in multispecies communities as heuristic rules, which we test in the empirical dataset. 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., 2018b). Thus, following these premises, contingent exclusion should be more likely to occur in ecological communities (1) with species that more strongly depress their competitor's growth rate relative to their self-regulation, (2) where life-history processes increase the intrinsic growth rates of competitively inferior species, and (iii) with a fewer number of species.

## 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 & Saavedra, 2018).

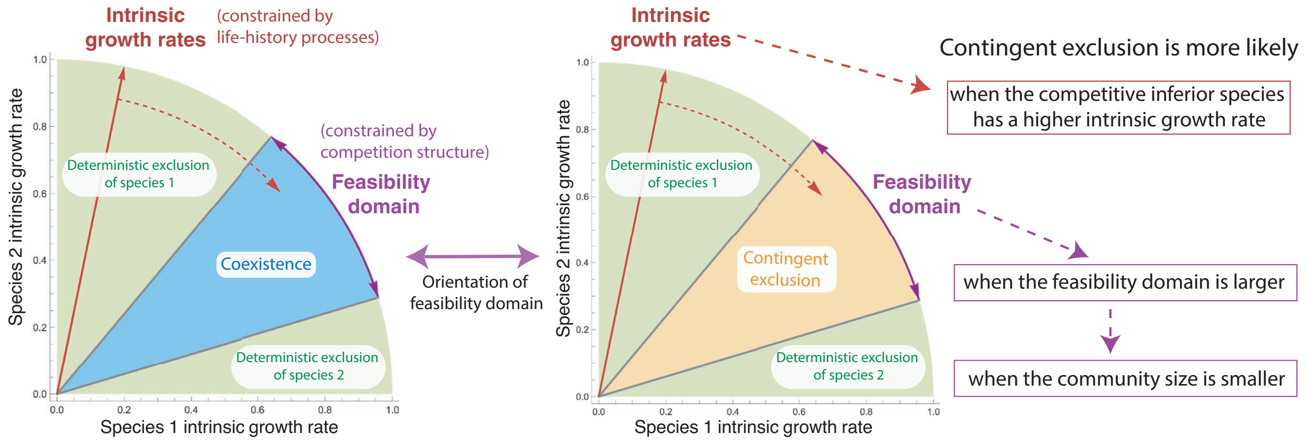

**FIGURE 1** Three key intuitions on competitive exclusion following a structural approach. For a hypothetical community with two competing species, the figure shows the parameter space defined by the intrinsic growth rates (phenomenological abiotic conditions) of the two species. The feasibility domain (middle blue or orange region) is the set of all directions of intrinsic growth rates compatible with a feasible equilibrium. If the feasible equilibrium is dynamically unstable (i.e. intraspecific competition is weaker than interspecific competition), the region corresponds to parameters that are compatible with contingent exclusion (right panel: orange region); if the feasible equilibrium is dynamically stable (i.e. intraspecific competition is stronger than interspecific competition), the region is compatible with stable coexistence (left panel: blue region). The complement of the feasibility domain regardless of dynamical stability (green region) corresponds to the directions of intrinsic growth rates associated with deterministic exclusion: species 1 is deterministically excluded in the upper region while species 2 is deterministically excluded in the lower region. The dashed, red arrows shows the direction where the community can move from deterministic exclusion of species 1 into either coexistence or contingent exclusion. Following the structural approach in ecology, we can derive three key intuitions: (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. As a corollary of (iii), contingent exclusion is less likely in species-rich communities because adding a new species generally further constrains the feasibility domain to be smaller. The opposite intuitions operate for deterministic exclusion

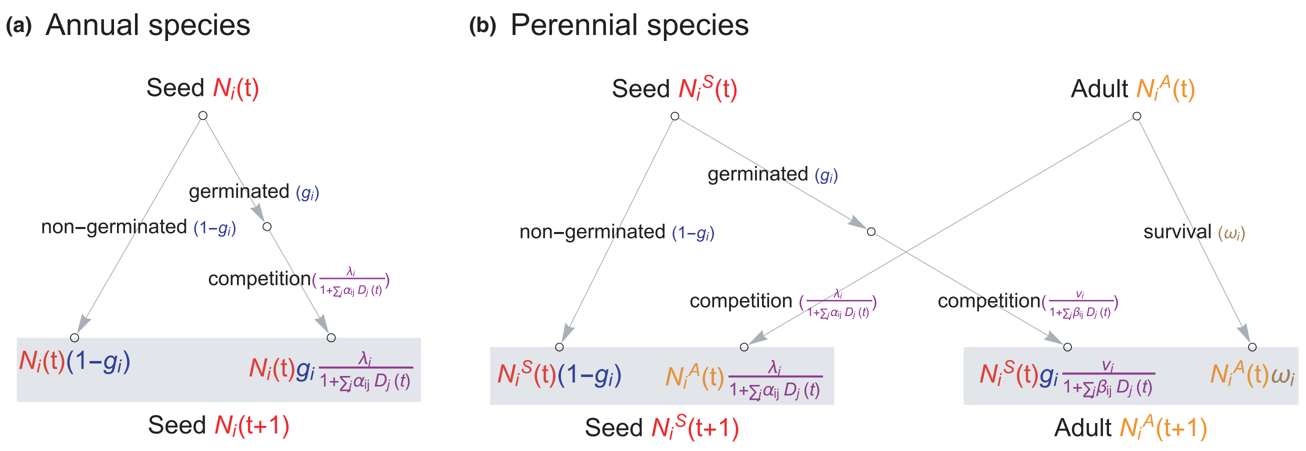

**FIGURE 2** Population dynamics of annual and perennial plant species. Panel (a) illustrates the population dynamics of an annual plant species (Equation 1). Annual plant dynamics are tracked as seeds entering each growing season. Some annual seeds germinate, and the germinated seeds produce seeds at a rate reduced by competition from other plant species. Panel (b) illustrates the dynamics of a perennial plant species (Equations 3 and 4). The perennial plant has two life stages, seed and adult. Some perennial seeds germinate, and the germinated seeds would produce adults at a rate reduced by competition from other plant species. Perennial life history: some perennial adults survive as perennials, while some perennial adults produce seeds and are decreased by competition from other plant species. Note that the dynamics of perennial plants can be be modeled with or without these perennial life-history processes (Figure S1)

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 (Godoy & Levine, 2014; Levine & HilleRisLambers, 2009). 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, $\lambda_i$ is per-capita seed production in the absence of competition, and $\alpha_{ij}$ 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 Equation 3) and the survival of non-germinating perennial seeds (second term in Equation 3). The competition coefficients $\alpha_{ij}$ and densities $D_j$ are defined as above (Equation 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 $\omega_i$ 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 Equation 4) and seeds $S_i$ that germinate and survive over the summer to become adults. Again, the abundance of perennial adults is reduced by species competition (second term in Equation 4), with per-capita effect $\beta_{ij}$ of species $j$ on species $i$.

## Empirical data and patterns of competitive exclusion

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 sampled 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 joint posterior distribution of these parameters to conduct our study.

Given the timescale of competitive exclusion in natural grassland communities, the empirical study did not perform experiments on competitive exclusion. Thus, we employ the experimentally parameterised population dynamics of annual and perennial species to simulate the patterns of competitive exclusion. Specifically, for a community with $S$ interacting species, we simulate all $S!$ possible species arrival orders. Each species arrives into the community when the community has already reached its stationary state, and we focus on the final stationary state. Using the final stationary states across all arrival orders, we can classify a species as either contingently excluded (excluded in some arrival orders), deterministically excluded (excluded in all arrival orders) or persistent (not excluded in any arrival orders). Importantly, note that the classification of species is based solely on the dynamical outcomes derived from numerical simulations, which is not directly related to whether the community is feasible or dynamically stable (AlAdwani & Saavedra, 2020). This also prevents a tautological link between the classification scheme and the structural approach.

## 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 & Des Marais, 2020)—as we have exemplified in our population dynamics model. 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.

To consider the effects of perenniality, we propose a null model that treats perennial species essentially as annual species by theoretically removing the life-history difference between annual and perennial species (Lundgren & DesMarais, 2020; Uricchio et al., 2019). Specifically, we remove the over-summer survival of adult perennials, the over-summer maturation from perennial seedlings into adults, and competition during this transition, while the germinated seeds transition directly into seeds in the next year (illustrated in Figure S1). Note that we have completely removed the perenniality of perennial species in the population dynamics as it is unclear how to remove some of these processes related to perenniality but not the others. Under this null model where the perenniality of the perennial species is not considered, the feasibility condition of a multispecies community reduces to

$$\begin{cases} \lambda_i - 1 = \sum_{j \in \mathscr{A}} \alpha_{ij} g_j N_j^* + \sum_{j \in \mathscr{P}} \alpha_{ij} g_j N_j^{S*}, \ \forall i \\ N_i^* > 0, \ \forall i, \end{cases} \tag{5}$$

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

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

$$\begin{cases} \lambda_i - 1 = \sum_{j \in \mathscr{A}} \alpha_{ij} g_j N_j^* + \sum_{j \in \mathscr{P}} \alpha_{ij} g_j \left(1 + \sqrt{\frac{v_j}{\lambda_j (1-\omega_j)}}\right) N_j^{S*}, \\ \text{if species } i \text{ is annual} \\ \sqrt{\frac{\lambda_i v_i}{1-\omega_i}} - 1 = \sum_{j \in \mathscr{A}} \alpha_{ij} g_j N_j^* + \sum_{j \in \mathscr{P}} \alpha_{ij} g_j \left(1 + \sqrt{\frac{v_j}{\lambda_j (1-\omega_j)}}\right) N_j^{S*}, \\ \text{if species } i \text{ is perennial} \\ N_i^* > 0, \ \forall i, \end{cases} \tag{6}$$

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

Importantly, the feasibility domain of the multispecies community is the same excluding (Equation 5) or including (Equation 6) perennial life-history processes. The mathematical rationale of this identity comes from the column scaling invariance of the feasibility domain (Song et al., 2020b) TREE (Appendix E). 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). Thus, for the assumed population dynamics, the feasibility domain of the multispecies community is uniquely determined by the competition structure $\{a_{ij}\}$ summarised in the interaction matrix, but not by any other parameter (see Appendix C for a description of our assumptions). 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 perennial species from $(\lambda_i - 1)$ to $(\sqrt{\frac{\lambda_i v_i}{1-\omega_i}} - 1)$ (see Appendix C for variations of assumptions).

We test the effects of life history differences on competitive exclusion in the species present in our empirically parameterised California grassland system. 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 perennial species empirically.

## Community size

As described above, following a structural approach, the deterministic exclusion is hypothesised to dominate over contingent exclusion in species-rich communities (see section *Structural approach on competitive exclusion*, Figure 1). In order to investigate the contribution of community size to the patterns of competitive exclusion, we need to analyse 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 the California grassland system.

## Competition structure

Ecological communities are characterised by non-random competition structures (Thébault & Fontaine, 2010; Song et al., 2018a; Song & 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 system. 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 (Barabás et al., 2017; Gallien et al., 2017; Kinlock, 2019; Soliveres et al., 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 is more prevalent in multispecies communities with larger feasibility domains. We compute numerically the size of the feasibility domain from Equation (6) (Song et al., 2018b). 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: (1) communities with either weak (intraspecific<interspecific) or strong (intraspecific>interspecific) intraspecific competition, and (2) 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 first generate a Erdös-Rényi structure as an instrumental initiation where each competition strength is independently sampled from a uniform distribution [0, 1] (Song & 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 tested other parameterisations to evaluate the robustness (Appendix F).

# RESULTS

We first analysed the effects of perennial life-history processes on whether a community is dominated by deterministic or contingent exclusion. The structural approach postulates that contingent exclusion is more likely when competitively inferior species have higher intrinsic growth rates (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 that perennial life-history processes promote contingent exclusion. To illustrate this effect, we used a standard graphical representation of ecological dynamics for two species: the niche-overlap-fitness-ratio space (Adler et al., 2007; Chesson & Kuang, 2008). Specifically, Figure 3 shows that by adding perennial life-history processes to the model, the species average fitness of perennial species increases, which leads to an increase in contingent exclusion (as well as in the probability of coexistence, which remains an unlikely outcome) and a decrease in 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., 2020a). That is, we found that communities exhibit robustness to perturbations acting on intrinsic growth rates but not on competition strength when perennial life-history is excluded, while they exhibit robustness to perturbations acting on competition strength but not on intrinsic growth rates when perennial life-history is incorporated (Appendix D). Importantly, multispecies communities exhibit qualitatively identical patterns (see Figure 4).

Next, we analysed the effects of community size on the patterns of competitive exclusion. The structural approach argues that contingent exclusion is less likely—and deterministic exclusion is more likely—when the community size is larger. Figure 4 confirms this expectation in the empirical data. By summing across the bars in each panel in Figure 4, we found that the percentage of deterministically excluded species rises from 23% in two-species communities to 85% in five-species communities. By contrast, the percentage of contingently excluded species falls from 31% in two-species communities to 9% in five-species communities. In addition, we found that the effect of community size acts more strongly on annual than perennial species (Appendix F). The effect of community size remained consistent with and without incorporating perennial life-history processes (Appendix F). Note that Figure 4 shows the patterns of competitive exclusion on a species level here (i.e. whether a

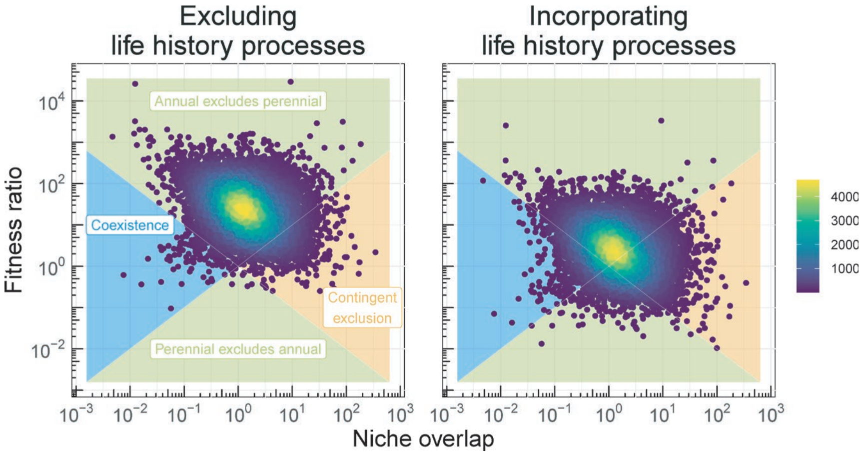

**FIGURE 3** Perennial life-history processes increase the frequency of contingent exclusion by increasing the effective intrinsic growth rates of perennials. Plots represent two-species dynamics based on niche overlap (horizontal axis) and species average fitness ratio (vertical axis) between a pair 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 species average fitness ratio and niche overlap computed from 2000 posterior samples from the posterior distribution of parameter values (the color map represents the density of the points). We use all possible annual-perennial pairings. Note that the species average fitness ratio here refers to the ratio of annual fitness to the perennial fitness, so that the upper green regions correspond to annual-dominated deterministic exclusion and the lower green regions to perennial dominance. 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 increases the proportion of the posterior distribution that falls into the contingent exclusion region (orange region). Note that including perennial life-history processes also increases the frequency of coexistence (blue region) and deterministic exclusion of annuals by perennials (lower green region). The details of computing fitness ratio and niche overlap can be found in Appendices A and C, and plots for individual pairs can be found in Appendix E

species persists, is deterministically excluded, or is contingently excluded). The patterns on a community level can be different. For example, a roughly constant proportion of communities with different community sizes has at least one species exhibiting contingent exclusion (Figure S7).

Lastly, we analysed 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 system: 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 the feasibility domain decreases as a function of community size, and coexistence (middle blue histograms) is only observed in two-species communities (Figure 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 (i.e. comparing the left vs. right sides of panel C), regardless of being intransitive or hierarchical (Figure 5c). These results are robust to different parameterisations in simulations (Appendix G).

## DISCUSSION

Despite the recent research focus on understanding the mechanisms underlying stable coexistence (Adler et al., 2007; Chesson, 2000; Godoy et al., 2014; Kraft et al., 2015; Levine & HilleRisLambers, 2009), competitive exclusion occurs frequently in nature, and the drivers of deterministic versus contingent exclusion remain poorly understood in multispecies communities (Fukami, 2015; Fukami et al., 2016; Mordecai, 2013; Mordecai et al., 2015; Uricchio et al., 2019). Indeed, 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 in multispecies communities derived from our theoretical framework: (1) 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. (2) The larger the intrinsic growth rates of competitively inferior species, the more likely that contingent exclusion occurs. (3) The larger the feasibility domain of a community, the more likely

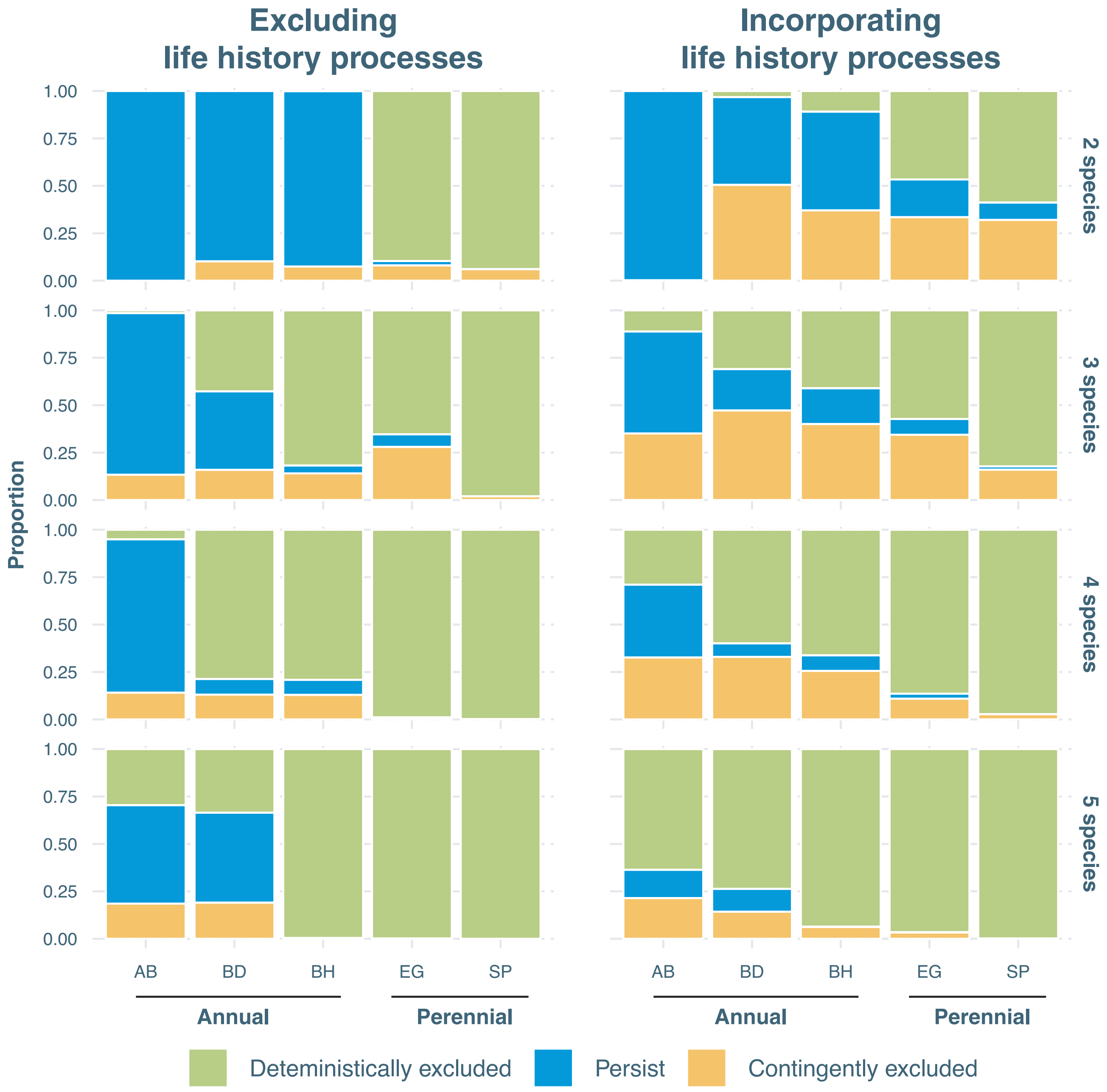

**FIGURE 4** Contingent exclusion is less likely when the community size is larger. We show how the proportions of contingent exclusion, deterministic exclusion and persistence for each of the five focal species change with community size. The horizontal axis denotes the plant species, where AB stands 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. We tested all the possible *n*-species combinations with both annual and perennial species present using 2000 posterior parameter samples. The vertical axis denotes the average proportion of occurrences of deterministic exclusion (green), persistence (blue) or contingent exclusion (orange) in all these combinations. 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, while the proportions of contingent exclusion and persistence decrease

that 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 on the dynamics of competitive exclusion in this system using the structural approach, which applies to communities larger than two species.

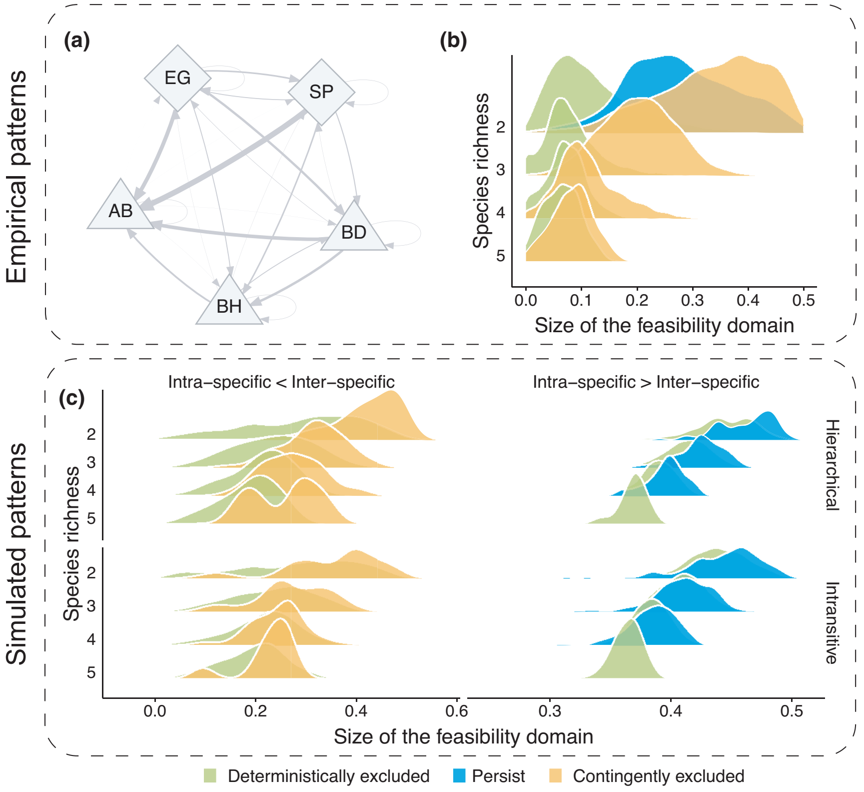

**FIGURE 5** Weak intraspecific and not intransitive competition drives the patterns of competitive exclusion. Panel (a) shows the competition structure among annuals and perennials in the empirical data from California grassland plant species. Each node represents a plant species, where the triangles (*Avena barbata* (AB), *Bromus hordeaceus* (BH) and *Bromus diandrus* (BD)) are annuals and the diamonds (*Elymus glaucus* (EG) and *Stipa pulchra* (SP)) are perennials. The direction and width of the links represent the direction 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—deterministically excluded, persist, or contingently excluded—for each empirically derived parameter set, grouped into histograms by qualitative outcome. We characterise the competition structure of a community across different community sizes using the normalised size of the feasibility domain (horizontal axis). The empirical data show that deterministic exclusion (green histograms) is mostly characterised by structures with a relatively small feasibility domain. Contingent exclusion (orange histograms) has opposite patterns. Coexistence (blue histograms) is characterised by structures with a medium-sized (in between the characteristic sizes for deterministic exclusion and contingent exclusion) in two-species communities and is almost impossible for communities with three or more species. 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)

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, perennial 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 population persistence of inferior competitors. A caveat is that we have only studied the joint contribution of all life-history processes. Future work can explore the relative contribution of each life-history process (Lundgren & Des Marais, 2020).

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 is more prevalent in in larger communities, derived from randomly constructed communities (Zhao et al., 2021). 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). This phenomenon is similar to the `sampling effect' in the biodiversity-ecosystem functioning research (Hector et al., 2002; Loreau & Hector, 2001).

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 the interspecific competition (Adler et al., 2018; LaManna et al., 2017), recent work has questioned the generality of the empirical evidence supporting stronger intraspecific competition (Broekman et al., 2019; Chisholm & Fung, 2018; Detto et al., 2019; Hülsmann & Hartig, 2018). 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 & Levine, 2011; Gallien et al., 2017; Soliveres et al., 2015). Thus, our findings imply that ecological mechanisms may play different roles in coexistence and competitive exclusion.

In light of an increasing rate of species invasion as a result of global anthropogenic changes in climate and land use, ecological systems are in dire need of sustainable strategies to mitigate threats to native species. Our study system of grassland plants is an ecologically important and widespread ecosystem that faces such a challenge (Myers et al., 2000). It has been suggested that exotic annual grasses have the potential to replace native perennial grasses in over 9 million hectares of California grasslands (Seabloom et al., 2003). Indeed, in our study site located in Jasper Ridge Biological Preserve, while these grasses often co-occur at the spatial scale of within ~100 m of each other, there are many patches where these grasses do not co-occur within ~10 m. However, given the long time scale for exclusion to fully play out, we cannot say for certain that competitive exclusion would dominate in the system. That is, besides the possibility of competitive exclusion, there are two other possibilities: The first possibility is that a patchwork of different environmental conditions favors different species. For example, we have observed exotic annuals in more disturbed habitats (e.g. *Avena barbata*, *Bromus hordeaceus* and *Bromus diandrus* in overgrazed and high human-impact areas), while native perennials in less disturbed habits (e.g. *Stipa pulchra* in more open grasslands with lower disturbance). The second possibility is that a patchwork of local contingent exclusion dynamics have played out such that species are maintained in local patches that are not truly stably coexisting with other species. Regardless of the specific explanation, this pressing challenge has underscored the need for systematic restoration efforts (Gea-Izquierdo et al., 2007; Seabloom, 2011; Werner et al., 2016).

Our study has also shown that the approach to restoration should be different depending on the richness of the system. According to our findings, systems with few species can be strongly driven by contingent exclusion, implying that the restoration may be facilitated by focusing on intrinsic factors, such as life-history traits, self-regulation, or population abundances. By contrast, species-rich systems can be strongly driven by deterministic exclusion, implying that the restoration may be facilitated by focusing on external factors, such as availability of resources that promote the population growth of competitively inferior species. This result, of course, needs to be taken with caution as we have not used spatio-temporal variation in our analysis (it is empirically challenging to measure local-scale variation in model parameters). This, however, can open a new perspective to restoration management since our key results are testable and generalisable to a wide range of study systems using the same study designs that investigate species coexistence (Adler et al., 2018; Godoy et al., 2014; Levine & HilleRisLambers, 2009).

Although the understanding of species coexistence has been one of the major topics in ecology for decades (Allesina & Tang, 2012; Barabás et al., 2014; Bastolla et al., 2009; Ives & Carpenter, 2007; May, 1972; McCann, 2000; Meszéna et al., 2006; Rohr et al., 2014), competitive exclusion remains the dominant—if hidden—foundation of ecological community structure. While species coexistence and competitive exclusion go hand-in-hand, our understanding about coexistence is much better than exclusion. Competitive exclusion is fundamentally different in two ways: deterministic and contingent. To understand the role of historical contingency in ecological communities, it is paramount to uncover the frequency of and mechanisms underlying deterministic versus contingent exclusion. While the classic work of modern coexistence theory takes as implicit the two distinct forms of exclusion, they are not easily separable in multispecies models, limiting our ability to understand the role of historical contingency in the formation of ecological communities. In this line, we have taken a new heuristic perspective that partitions exclusion into these two categories within multispecies communities. We hope this work can motivate future research exploring the rich and potentially predictable dynamics of competitive exclusion in multispecies communities.

## DATA AVAILABILITY STATEMENT

The data of the California grassland community have previously been archived on https://www.journals.uchicago.edu/doi/abs/10.1086/701434. The code supporting our analysis is archived on Github https://github.com/clsong/competitive_exclusion.

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## AUTHOR 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 the first version of the manuscript. All authors contributed to substantial revisions. E. M. and L. U. compiled and provided data.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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