








## ARTICLE

# Environmental context, parameter sensitivity, and structural sensitivity impact predictions of annual-plant coexistence

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**Abstract**

Predicting the outcome of interactions between species is central to our current understanding of diversity maintenance. However, we have limited information about the robustness of many model-based predictions of species coexistence. This limitation is partly because several sources of uncertainty are often ignored when making predictions. Here, we introduce a framework to simultaneously explore how different mathematical models, different environmental contexts, and parameter uncertainty impact the probability of predicting species coexistence. Using a set of pairwise competition experiments on annual plants, we provide direct evidence that subtle differences between models lead to contrasting predictions of both coexistence and competitive exclusion. We also show that the effects of environmental context dependency and parameter uncertainty on predictions of species coexistence are not independent of the model used to describe population dynamics. Our work suggests that predictions of species coexistence and extrapolations thereof may be particularly vulnerable to these underappreciated founts of uncertainty.

**KEYWORDS**

competition, competitive exclusion, density dependence, phenomenological models, population dynamics, structural stability

**INTRODUCTION**

The effects species have on one another are the result of multiple processes that often act simultaneously. In the case of competition between plants, examples include

the depletion of local resources in the soil (Craine & Dybzinski, 2013; Dybzinski & Tilman, 2007), visits from shared pollinators (Lanuza et al., 2018), and the frequency and intensity of disturbance events (Pickett, 1980; Villarreal-Barajas & Martorell, 2009). Notwithstanding

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their importance, fully including all such phenomena in the study of plant dynamics is often impractical. Hence, it is more straightforward to treat these processes implicitly and model the relationship between interacting species phenomenologically, for example by fitting models that describe how the densities of intraspecific and interspecific neighbors change plant fitness and growth (Adler et al., 2018; Case, 1999; Connell, 1990; Goldberg, 1990; Hart et al., 2018).

Despite their “necessary incompleteness,” phenomenological models can accurately reproduce data observed in various natural systems and contexts (Bolker, 2008; Hilborn & Mangel, 1997; Houlihan et al., 2015). Perhaps more importantly, they are useful tools with which to make predictions that extend beyond the phenomena they describe (Broekman et al., 2019). Such predictions are possible because of the implicit assumption that models that reproduce the observed data faithfully also capture how the studied system operates (Klir, 1985; Marquet et al., 2015; Stouffer, 2022; Zeigler et al., 2000). For example, models that describe the effects neighboring plants have on each other can be used to make quantitative predictions about changes of biomass in the system (Godoy et al., 2020; Lai et al., 2022) or qualitative predictions such as whether or not co-occurring plant species can coexist (Levine & HilleRisLambers, 2009; Zepeda & Martorell, 2019).

Model-based predictions are subject to uncertainty arising from many distinct sources (Shoemaker et al., 2020). One such source is environmental context dependency, or the extent to which outcomes change as a function of the abiotic conditions species experience (Bimler et al., 2018; Chamberlain et al., 2014). Many abiotic factors vary across both temporal and spatial scales in ecologically meaningful ways (Craine & Dybzinski, 2013; Pake & Venable, 1996; Soliveres et al., 2010). For example, previous studies found substantial evidence that interaction strengths between plants varied along environmental gradients (Bimler et al., 2018; Lanuza et al., 2018; Villarreal-Barajas & Martorell, 2009), and interspecific interactions in particular could switch from competitive to facilitative when moving from favorable to harsh environments (Brooker et al., 2008; Callaway et al., 2002; Maestre et al., 2005, 2009). This environment-driven variation can even lead to the identity of the competitively superior plant species changing, depending on local abiotic conditions (Dybzinski & Tilman, 2007; Poorter & Lambers, 1986). Extrapolations from phenomenological models of plant competition can therefore be highly specific to the set of conditions under which data were collected and for which models were parameterized (Bimler et al., 2018).

Model-based predictions are also subject to two forms of uncertainty that arise from the use of models

themselves: parameter sensitivity and structural sensitivity. Parameter sensitivity refers to the sensitivity of model outputs to variation in parameter values, and exploring it constitutes a routine analysis in the domain of the biological sciences (Jørgensen & Bendoricchio, 2001; Terry et al., 2021). On the other hand, structural sensitivity characterizes how mathematical expressions that have similar phenomenological behavior can produce qualitatively different outcomes (Aldebert & Stouffer, 2018; Cordoleani et al., 2011; Myerscough et al., 1996). Parameter and structural sensitivity are often intertwined (Wood & Thomas, 1999), and both have been shown to drastically change model predictions in a vast array of biological systems (Aldebert et al., 2016; Aldebert & Stouffer, 2018; Cordoleani et al., 2011; Fussmann & Blasius, 2005; Poggiale et al., 2010; Wood & Thomas, 1999).

The interplay between environmental context dependency, parameter sensitivity, and structural sensitivity is rarely explored simultaneously and, to the best of our knowledge, has never been explicitly explored for the case of models of annual-plant population dynamics. In this study, we therefore aim to understand how these three sources of uncertainty change predictions of a widely studied and vastly important ecological process: species coexistence. We focused our analysis on annual plants, which is a common natural system used to study species coexistence (Godoy & Levine, 2014; Levine & HilleRisLambers, 2009; Wainwright et al., 2019; Zepeda & Martorell, 2019). We assessed the empirical relevance of these three sources of uncertainty by making coexistence predictions based around data from competition experiments between two annual-plant species conducted in two contrasting abiotic conditions. Our analyses provide evidence that uncertainty can radically change predictions made from a simple competition experiment and add to the growing literature on the importance of incorporating uncertainty from as many sources as possible when making model-based predictions (Bowler et al., 2022; Shoemaker et al., 2020).

## METHODS

We will first provide a mathematical description of how to make and interpret coexistence predictions made with a population-dynamics model for two annual-plant species growing in close proximity to each other. We then expand our framework to introduce alternative phenomenological models of density-dependent seed production and show how our framework can be used to make predictions using a different model for each species. Second, we describe how to use a Bayesian framework to parameterize the aforementioned phenomenological models to

data from a set of competition experiments between two annual-plant species growing under two distinct abiotic conditions. Finally, we describe how we simultaneously explored how environmental context dependency, parameter sensitivity, and structural sensitivity impact predictions of species coexistence.

### Model-based predictions of species coexistence

We used the Cohen model (Cohen, 1966; Watkinson, 1980) to describe annual-plant population dynamics and as the starting point for our model-based predictions of species coexistence. This model predicts the density of seeds  $N_{i,t+1}$  from species  $i$  in year  $t + 1$  with

$$N_{i,t+1} = (1 - g_i)s_iN_{i,t} + g_iN_{i,t}F_{i,t}, \tag{1}$$

which is a function of (1) the density of seeds in the seed bank from the previous year ( $N_{i,t}$ ) that do not germinate yet remain viable in the seed bank (as weighted by  $s_i$ , the annual rate of seed survival in the seed bank) and (2) the density of seeds that germinate (determined by the germination rate  $g_i$ ) multiplied by the number of viable seeds produced per seed germinated, often called the “realized fecundity” ( $F_{i,t}$ ). The realized fecundity of species  $i$  can be accurately described by many different phenomenological forms (Godwin et al., 2020; Hart et al., 2018; Law & Watkinson, 1987; Stouffer, 2022). These phenomenological descriptions of  $F_{i,t}$  generally try to capture the relationship between plant reproductive output and the densities of conspecific and heterospecific neighbors but do not necessarily imply a hypothesis about the mechanisms underpinning this density dependence (Stouffer, 2022).

For example,  $F_{i,t}$  can be given by the Beverton–Holt (also known as a reciprocal or inverse) model (Beverton & Holt, 1957), which in a two-species context equals

$$F_{i,t} = \frac{\lambda_i}{1 + \alpha_{ii}g_iN_{i,t} + \alpha_{ij}g_jN_{j,t}}. \tag{2}$$

In this model, the per-germinant fecundity of species  $i$  in the absence of density dependence is described by the parameter  $\lambda_i$ , while the numbers of germinants of species  $i$  and  $j$  in year  $t$  are given by  $g_iN_{i,t}$  and  $g_jN_{j,t}$ , respectively. The density-dependent effects are captured by the interaction coefficients  $\alpha_{ii}$  and  $\alpha_{ij}$ , which describe the interaction strengths of conspecifics and heterospecifics, respectively. The Beverton–Holt model is the most commonly used phenomenological model to make coexistence predictions and can be easily parameterized with empirical observations of annual plants growing in proximity to

each other (Godoy et al., 2014; Godoy & Levine, 2014; Hart et al., 2018; Levine & HilleRisLambers, 2009).

### Coexistence predictions

From the population dynamics that result from using Equation (1) and estimates of the relevant parameters of Equations (1) and (2), it is possible to predict whether a pair of species can coexist. Multiple approaches exist to predict species coexistence (Barabás et al., 2018; Chesson, 2000, 2018; Letten et al., 2017; Saavedra et al., 2017). One of them is to directly evaluate, given the competitive constraints each species experiences, whether the set of species’ intrinsic growth rates is feasible (i.e., if there exists an equilibrium point under which both species have positive densities; Rohr et al., 2014; Saavedra et al., 2017). To do so, it is necessary to derive the equations determining the equilibrium density for each species, which for species  $i$  is found at

$$\frac{N_{i,t+1}}{N_{i,t}} = (1 - g_i)s_i + \frac{g_i\lambda_i}{1 + \alpha_{ii}g_iN_i^* + \alpha_{ij}g_jN_j^*} = 1. \tag{3}$$

This equilibrium condition can be arranged to provide a linear equation in terms of densities:

$$-1 + \left( \frac{g_i\lambda_i}{1 - (1 - g_i)s_i} \right) = \alpha_{ii}g_iN_i^* + \alpha_{ij}g_jN_j^*. \tag{4}$$

For simplicity, Equation (4) can be rewritten as

$$\nu_i = \alpha_{ii}g_iN_i^* + \alpha_{ij}g_jN_j^*, \tag{5}$$

where  $\nu_i$  is the vital rate of species  $i$  that, at equilibrium, is compensated for by species interactions. Note that this vital rate  $\nu_i$  is a composite parameter that depends on the values of  $s_i$ ,  $g_i$ , and  $\lambda_i$ . As we will discuss later, different models of density-dependent fecundity have different mathematical expressions for the composite vital rate  $\nu_i$ , and these differences can be relevant when making inferences regarding coexistence.

Equivalent expressions for species  $j$  can be derived from its equilibrium condition. The combined two-species equilibrium condition is

$$\begin{bmatrix} \nu_i \\ \nu_j \end{bmatrix} = \begin{bmatrix} \alpha_{ii} & \alpha_{ij} \\ \alpha_{ji} & \alpha_{jj} \end{bmatrix} \begin{bmatrix} g_iN_i^* \\ g_jN_j^* \end{bmatrix}. \tag{6}$$

Given estimates of  $\nu_i$ ,  $\nu_j$ , and the  $2 \times 2$  matrix of interaction coefficients, predicted species densities at equilibrium can be determined by rearranging Equation (6) to

$$\begin{bmatrix} g_i N_i^* \\ g_j N_j^* \end{bmatrix} = \begin{bmatrix} \alpha_{ii} & \alpha_{ij} \\ \alpha_{ji} & \alpha_{jj} \end{bmatrix}^{-1} \begin{bmatrix} \nu_i \\ \nu_j \end{bmatrix}. \quad (7)$$

When predicted equilibrium densities for both species are positive, then the model-based prediction is that they can coexist (Rohr et al., 2014; Saavedra et al., 2017). In contrast, if one of the predicted equilibrium densities is less or equal to zero, then the model-based prediction is that one of the species will competitively exclude the other.

In practice, it is useful not only to determine whether some particular values of  $\nu_i$  and  $\nu_j$  allow species to coexist but to explore the full set of values of species' vital rates that are compatible with species coexistence. This is often referred to as the structural approach and is easily applicable to models of annual-plant population dynamics (Saavedra et al., 2017). The region of vital-rate parameter space where both species can have positive densities at equilibrium, given the constraints imposed through the interaction matrix, is called the feasibility domain (Rohr et al., 2014; Saavedra et al., 2017; Song et al., 2018, 2020). Biologically, a large feasibility domain means that competitive constraints are lax, and species can grow at different combinations of rates without excluding each other. In contrast, a small feasibility domain means that competitive constraints are rigid, and only a handful of vital rates allow their coexistence.

## Biologically constrained feasibility domain

Importantly, locations in the vital-rate parameter space carry direct biological interpretations with them beyond whether or not equilibrium densities are feasible. Consider, for example, a vital-rate vector  $\tilde{\nu}$  that allows for a vector of positive equilibrium densities  $\tilde{N}^*$ . For any scalar value  $x$ , the proportional vector  $x\tilde{\nu}$  will also produce  $x\tilde{N}^*$  as a solution to Equation (7). However, it is reasonable to assume that there is an upper limit to species' densities in nature (i.e., we do not expect species to achieve infinite local abundances). If a vital-rate vector leads to predicted densities beyond a particular species' observable limit, we argue that vector may be mathematically possible but should not be considered biologically sensible. The imposition of an abundance constraint such as this one will tend to create an upper bound on the vital rates that define the feasibility domain.

In addition, the Beverton–Holt model implicitly imposes further biological constraints on the values species' vital rates can take. Recall that a species' composite vital rate  $\nu_i$  is a product of three biologically meaningful parameters. Those parameters have bounds themselves

and when combined together they can further impact the values species' composite vital rates can take. Specifically,  $s_i$  and  $g_i$  are proportions and can only have values between zero and one, while the per-germinant fecundity in the absence of interaction effects  $\lambda_i$  can only have positive values. If it is assumed that the density dependence for a given species follows the Beverton–Holt model, these parameter constraints together imply that vital rates  $\nu_i < -1$  are not biologically achievable. Indeed, all values of  $\nu_i < -1$  correspond to

$$\left( \frac{g_i \lambda_i}{1 - (1 - g_i) s_i} \right) < 0,$$

but for this inequality to be true we require either  $1 - (1 - g_i) s_i < 0$  or  $g_i \lambda_i < 0$ . Since  $s_i$  and  $g_i$  are both proportions,  $1 - (1 - g_i) s_i$  can never be lower than zero. Thus, the only way to obtain  $\nu_i < -1$  is for species  $i$  to have a negative intrinsic fecundity (i.e.,  $\lambda_i < 0$ ), which is also not biologically sensible. In contrast, the Beverton–Holt model itself imposes no upper bound to species' composite vital rates. Note that the lower bound of  $-1$  and lack of an upper bound are specific to the Beverton–Holt model (Table 1). As we will discuss later, different models of density-dependent fecundity will have different implicit model-based constraints on  $\nu_i$ .

Building upon the feasibility domain defined within the structural approach, we define the biologically constrained feasibility domain as the region of parameter space where both species can have positive abundances given (1) intraspecific and interspecific interactions, (2) constraints on maximum species abundances, and (3) vital-rate constraints imposed by each phenomenological fecundity model. In the two-species case, the biologically constrained feasibility domain can also be thought of as a region that we denote by the symbol  $\beta$ . We estimated  $A_\beta$ —the size of  $\beta$ —using Monte Carlo integration methods, as described in Appendix S1, and show a visual example in Figure 1.

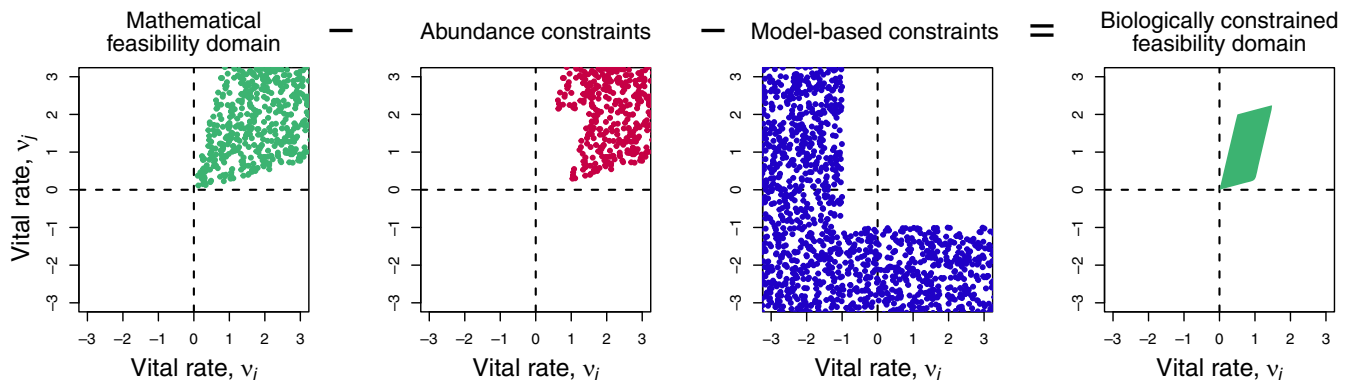
## Relative coexistence ratio

As a basis of comparison, it is also useful to quantify the parameter space that allows both species to grow in monoculture (i.e., when they have no niche overlap). Importantly, this parameter space can also be expressed as an area, and for reasons equivalent to those described earlier, this area is also subject to both abundance- and model-based constraints. We denote this region with the symbol  $\gamma$ , and the mathematical details of how we calculate its size ( $A_\gamma$ ) are described in Appendix S2. By comparing the size of the parameter space where both species

**TABLE 1** Equilibrium vital rates and model-based constraints thereof for the two models of density-dependent fecundity we used to make coexistence predictions.

Model	Vital rate, $v_i$	Lower bound	Upper bound
Beverton–Holt	$-1 + \left(\frac{g_i \lambda_i}{1 - (1 - g_i) s_i}\right)$	-1	$\infty$
Ricker	$\ln\left(\frac{g_i \lambda_i}{1 - (1 - g_i) s_i}\right)$	$-\infty$	$\infty$

Note: Vital rates are given by solving each model’s equilibrium conditions. Upper and lower bounds are the result of how bounds on  $g_i$ ,  $s_i$ , and  $\lambda_i$  come together to impact the values the vital rate can take while maintaining biological sensibility.



**FIGURE 1** Estimation of biologically constrained feasibility domain. (A) We show the mathematical feasibility domain (green points) given a hypothetical competition matrix with intraspecific competition coefficients  $\alpha_{ii} = \alpha_{jj} = 1$  and interspecific competition coefficients  $\alpha_{ij} = \alpha_{ji} = 0.5$ . Points sampled in this region of parameter space lead to both species having positive equilibrium densities. Note that, mathematically, this region extends infinitely in the positive quadrant. (B) Some of these mathematically feasible points, however, may correspond to equilibrium abundances that are greater than empirically informed abundance constraints (red points). For this visual example, we restrict biologically sensible equilibria to have  $g_i N_i^* \leq 1$  and  $g_j N_j^* \leq 2$ . (C) Part of the parameter space may also fall outside model-based constraints (blue points); for example, when both species’ density dependence is described by the Beverton–Holt model  $v_i \geq -1$  and  $v_j \geq -1$ . (D) The space of the mathematical feasibility domain that does not overlap with any abundance- or model-based constraints gives the biologically constrained feasibility domain (green area).

can feasibly coexist ( $A_\beta$ ) to the size of the space where species can grow in monoculture ( $A_\gamma$ ), we can quantify the importance of interspecific interactions relative to intraspecific interactions in determining the vital rates consistent with biologically plausible coexistence. This comparison can be expressed as a ratio  $\rho = A_\beta/A_\gamma$  that we call the relative coexistence ratio. When  $\rho = 1$ , then species coexistence is as achievable as species growing in monoculture; when  $\rho < 1$ , then the parameter space where the two species can coexist is smaller than the parameter space where each species can grow in monoculture, and it is harder for them to coexist because of their interspecific interactions; finally,  $\rho > 1$  implies that species facilitate each other, and it is easier for them to coexist because of their interspecific interactions.

### An alternative model of density dependence

The Beverton–Holt model is only one of many phenomenological models used to describe density-dependent

performance of annual plants. There is no hard and fast rule for how to choose the appropriate phenomenological model to describe the effect of species interactions, and it is often a choice governed by mathematical convenience (Stouffer, 2022), the type of study system (Godwin et al., 2020), the governing paradigm around species interactions (Martyn et al., 2021), or statistical fit to data (Martorell & Freckleton, 2014). One common alternative to the Beverton–Holt model is the Ricker model:

$$F_{i,t} = \lambda_i e^{(-\alpha_{ii} g_i N_{i,t} - \alpha_{ij} g_j N_{j,t})}, \tag{8}$$

where the interpretation of the parameters remains the same as previously described (Ricker, 1954a, 1954b). The Ricker model is known to be a biologically plausible and versatile model to quantify density dependence in annual-plant communities, plus it has the virtue of being better than the Beverton–Holt model at capturing both competitive and facilitative interactions (Bimler et al., 2018; Hart et al., 2018; Levine & HilleRisLambers, 2009;

Martyn et al., 2021; Mayfield & Stouffer, 2017; Stouffer, 2022). When discrete response variables like fecundities are modeled as Poisson or negative-binomial random variates, for example within a generalized linear model, the default log link function also implicitly imposes a Ricker function on the model being fit (Mayfield & Stouffer, 2017; O'Hara & Kotze, 2010; Rao et al., 2010; Stouffer et al., 2018).

Similar to the process we followed from Equations (4)–(7), the Ricker model has its own composite vital rate at equilibrium. For species  $i$ , this is given by

$$\nu_i = \ln\left(\frac{g_i \lambda_i}{1 - (1 - g_i) s_i}\right). \quad (9)$$

The fact that this expression is different than Equation (5) necessarily implies that the model-based constraints on vital rates are different when using the Ricker model than when using the Beverton–Holt model. Indeed, the Ricker model has no model-based constraints on the lower and upper bounds of a species' vital rate  $\nu_i$  (Table 1).

## Multimodel predictions of species coexistence

By parameterizing a phenomenological model of plant competition, like the Beverton–Holt model (Equation 2) or Ricker model (Equation 8), we get a description of how seed set varies with neighbor density. Perhaps more importantly, by linking these models to Equation (1) we can make predictions about whether or not two species are able to coexist. So far, we have been working with the implicit assumption that the same model describes the density dependence of the two species. However, given the lack of a clear mechanistic underpinning with which to justify using one model over another (Stouffer, 2022), there is no a priori reason to assume this is the case. This is particularly true when the models are parameterized with experimental data and from a statistical perspective appear to provide comparable fits (Hart et al., 2018).

To predict coexistence using a different density-dependence model for each species, we still must solve for species equilibrium abundances as a function of vital rates and competition (Equation 7). Unlike the single-model approach, each species' vital rate has its own formulation based on the model used to describe each species' realized fecundity (Table 1). As in the previous approach, if Equation (7) predicts positive abundances for both species within the bounds of each species' model-based and abundance constraints, it is predicted that species can coexist.

## Interplay of different forms of uncertainty

### Data

To assess the relevance of different sources of uncertainty in an explicit empirical context, we made coexistence predictions using parameter estimates inferred directly from a set of competition experiments. During 2017, we conducted pairwise competition experiments between two annual-plant species, *Goodenia rosea* and *Trachymene cyanopetala*. These experiments took place in the West Perenjori Nature Reserve in Western Australia (−29.479° S, 116.199° E). The reserve is dominated by York gum-jam woodlands, which support an understory of mixed native and exotic annual grasses and forbs (Dwyer et al., 2015).

Using locally collected seeds, we conducted competition experiments using a response–surface experimental design, which has the advantage of being able to accurately distinguish intraspecific and interspecific competition (Hart et al., 2018; Inouye, 2001). Within this design, we varied the densities of both species independently by using treatments that combined the two species at two or more densities. To also allow us to examine how abiotic conditions changed coexistence predictions, the experiments took place in two contrasting environments: an open environment, where plants interacted at least 1 m from woody debris, and a woody environment, where plants interacted within 30 cm of woody debris.

To implement our response–surface experiments, in October 2017 we first weeded out all aboveground biomass of plants inside circular plots with a 7.5-cm radius. This neighborhood radius has been shown to be sufficiently large to capture local plant–plant interactions within the study system (Martyn et al., 2021). Each plot was then sown at one of four different densities of each species as a focal species: an invasion density where only five seeds were sown (thinned to one individual after germination), low density (15 seeds in total), medium density (30 seeds in total), and high density (60 seeds in total). We varied the densities with which the nonfocal species was sown across three treatments: absent (0 seeds in total), medium (30 seeds in total), or high (60 seeds in total). Treatments therefore consisted of combinations of the density of each species sown as a focal species, the density of each species sown as a neighbor, and the environment where interactions took place. We had eight replicates per treatment, which yielded 256 total plots. Seeds were allowed to germinate, and we thinned plots in composition in July 2018 (i.e., we weeded out neighboring plants from species that were not shown) and counted the abundance of neighbors removed during weeding. We then collected the seeds produced after the growing season in October 2018 and also counted

the number of conspecific plant individuals and heterospecific plant individuals in the plot at the time of peak biomass.

We determined the maximum local abundance of seeds each species could achieve based on empirical observations of individual plants within a 7.5-cm radius. Both *G. rosea* and *T. cyanopetala* rarely exceed abundances of more than 100 plant individuals within a 7.5-cm radius (T. E. Martyn, personal communication). Finally, we obtained estimates of the survival and germination rates in the field for both of our focal species from a separate study (Towers et al., 2022). Using these germination rates, we can convert maximum observed numbers of plants to corresponding maximum potential numbers of seeds in the seed bank. We then decided to use a threshold that was five times larger than these empirically informed estimates so that the abundance constraints we imposed would be as conservative as possible. We show these values of seed survival rate, germination rate, and maximum abundance for each species in Appendix S3: Table S1.

### Statistical inference

We fit Equations (2) and (8) separately for both of our focal species in order to get the relevant parameter estimates necessary to make coexistence predictions. As an additional basis of comparison, we also fit a “null” model where all interaction coefficients were fixed to zero. This helps to serve as a demonstration that the models were capturing meaningful signals of density dependence in the empirical data. For both species, we fit these nonlinear models with a Bayesian framework using Hamiltonian Monte Carlo (HMC) methods. We used Bayesian inference to explicitly incorporate the uncertainty surrounding model parameters in probability distributions (McElreath, 2018). Across all models, we explicitly accounted for the environment where seeds were sown in our parameter estimates. For all of the parameters across all models, we did this by treating the woody treatment as a dummy variable  $W$  that takes the value  $W = 0$  in the open conditions and  $W = 1$  in the woody conditions.

For all models and all environmental conditions, we constrained the fecundity in the absence of density dependence ( $\lambda_i$ ) to be positive in order to keep our predictions biologically plausible. Across all model fits, we included an extra interaction coefficient ( $\alpha_{ik}$ ) to account for the effects of the nonfocal neighbor plants that were weeded out in the experiment. We fit this extra interaction term to improve the parameter estimates related to our focal species, but because we do not know those species’ other parameter values, we could not model their corresponding coexistence outcomes. To ease later

interpretation, we constrained all focal–focal interaction coefficients to be positive (i.e., competitive). This only led to minor variation in inferred parameter values as only the posterior distributions of the “other” interaction coefficients showed a strong tendency toward values  $\leq 0$  (Appendix S4: Figures S2 and S4).

Since seeds produced per focal individual is a discrete count response variable, we modeled these outcomes as negative-binomial variates. We used a negative binomial instead of a Poisson model because the former provided significantly improved model fit, indicating a degree of overdispersion in the empirical data. To ensure consistency across our different linear and nonlinear models, we fit all models using the negative-binomial family and an identity link function.

We fit all models using the function “brm” from the brms package (Bürkner, 2017) in the statistical program R version 4.0.2 (R Core Team, 2013). For nonlinear models, brms required explicit specification of the prior distributions for all parameters except the dispersion parameter in the negative-binomial distribution (for which we used the default prior). Intrinsic fecundities could vary over multiple orders of magnitude between species; we therefore used vague priors for these parameters (Banner et al., 2020). In contrast, we expected interaction coefficients to vary over a more restricted range and hence gave them weakly informative priors (Banner et al., 2020). As a representative example, the full Bayesian description of the Beverton–Holt model for species  $i$  is

$$F_{i,d} \sim \text{Negative Binomial}(\mu_{i,d}, \phi_i), \tag{10}$$

$$\mu_{i,d} = \frac{\lambda_{i,d}}{1 + \alpha_{ii,d}n_{i,d} + \alpha_{ij,d}n_{j,d} + \alpha_{ik,d}n_{k,d}}, \tag{11}$$

$$\lambda_{i,d} = (1 - W_d)\lambda_{i,o} + W_d\lambda_{i,w}, \tag{12}$$

$$\alpha_{ii,d} = (1 - W_d)\alpha_{ii,o} + W_d\alpha_{ii,w}, \tag{13}$$

$$\alpha_{ij,d} = (1 - W_d)\alpha_{ij,o} + W_d\alpha_{ij,w}, \tag{14}$$

$$\alpha_{ik,d} = (1 - W_d)\alpha_{ik,o} + W_d\alpha_{ik,w}, \tag{15}$$

$$\{\lambda_{i,o}, \lambda_{i,w}\} \sim \text{Cauchy}^+(0, 5), \tag{16}$$

$$\{\alpha_{ii,o}, \alpha_{ii,w}, \alpha_{ij,o}, \alpha_{ij,w}\} \sim \text{Normal}^+(0, 1), \tag{17}$$

$$\{\alpha_{ik,o}, \alpha_{ik,w}\} \sim \text{Normal}(0, 1), \tag{18}$$

$$\phi_i \sim \text{Gamma}(0.01, 0.01), \tag{19}$$

where the subscript  $d$  indicates each focal observation, the subscript  $o$  indicates parameters applicable in the open environment, the subscript  $w$  indicates parameters applicable in the woody environment, and  $n_{i,d}$  is the count of species  $i$  in the plot corresponding to focal observation  $d$ . Only Equation (11) changes when moving from the Beverton–Holt to the Ricker model.

For each focal species–fecundity model combination, we ran four chains with a warmup of 50,000 iterations and 1000 sampling iterations. We determined convergence when trace plots were well mixed and stationary and when the Gelman–Rubin convergence diagnostic (Rhat) was less than 1.05 for all parameters (Vehtari et al., 2021). We conducted posterior predictive checks of converged models to verify our model assumptions, and overall our model predicted values of seed production that matched our observations (Appendix S4: Figures S1 and S3). After performing these preliminary checks, we compared the fits of the models for each focal species using the leave-one-out cross-validation information criterion (LOOIC). This goodness-of-fit measure is used to estimate the out-of-sample prediction accuracy of Bayesian models and provides a measure of model fit that is penalized for the number of model parameters. As with other information criteria, lower values of LOOIC correspond to better supported models. Additionally, LOOIC is more robust for models with weak priors or influential observations compared to other information criteria (Vehtari et al., 2017). We calculated out-of-sample deviance separately for models in open and woody environments because LOOIC is calculated additively over observations. We also calculated Akaike weights for each model in each environmental condition, which can be interpreted as an estimate of the probability that the model will make the best predictions of new data, based on the set of models considered (McElreath, 2018). It is worth noting that Akaike weights computed from LOOIC implicitly assume that the prior probability of preferring each model is equal, and model weights are attributable to differences in model fit and out-of-sample prediction. Though we do not explore the possibility here, a fully Bayesian approach that created model-averaged predictions could potentially also include prior knowledge across models, for example when there are biological reasons to prefer one mathematical form over another (e.g., Freckleton & Watkinson, 1999; Stouffer, 2022).

## Predictions incorporating uncertainty

As a first test of how model formulation changes predictions of species coexistence, we used our framework to make predictions using median parameter estimates and

a different model per species (Equations 2 and 8). We examined all the possible combinations of each species' density dependence as defined by a different model. Furthermore, we also explored how abiotic conditions changed predicted coexistence outcomes by making predictions using median parameter estimates in the open and woody conditions. Within our approach, there are  $E \times (M^S)$  sets of model combinations to explore, where  $E$  is the number of distinct environments,  $M$  is the number of candidate models, and  $S$  is the number of species. In our study, we have  $E = 2$  environments,  $M = 2$  models, and  $S = 2$  species, yielding a total of eight different sets of median parameter estimates with which to predict the pairwise coexistence outcome and with which to calculate the size of  $\beta$ , size of  $\gamma$ , and value of  $\rho$ .

To incorporate parameter uncertainty, we also made predictions using each of the  $D = 4000$  draws from the parameters' joint posterior distributions. Posterior distributions of parameters contain the relative plausibility of different parameter values, conditional on the data and the model used (McElreath, 2018). By sampling from the joint posterior distribution, any covariance between parameters that arises during the HMC sampling process is automatically preserved (McElreath, 2018). Recall that models were fit separately across observations for each focal species; therefore, we randomly paired together posterior draws from models fit separately to each species in order to generate multimodel predictions. For each of the eight predicted coexistence outcomes made using median parameter values, this gives us a full posterior distribution of 4000 additional predictions. We therefore had a total of eight different sets of posterior distributions of predicted coexistence outcomes, as well as posterior distributions of the size of  $\beta$ , the size of  $\gamma$ , and the value of  $\rho$ .

For each model combination in each environmental condition, we lastly determined the proportion of posterior draws that predicted coexistence and competitive exclusion driven by *G. rosea* or *T. cyanopetala*. When the predicted outcome was competitive exclusion, this implies that the empirical expectation is a monoculture of the “dominant” species. Therefore, we also qualified these single-species dominant equilibria with whether or not the species was expected to be present at densities below or above the abundance-based constraints we considered elsewhere.

## RESULTS

### Model fits

Model comparison using LOOIC showed that the Ricker model was the preferred model overall for density

dependence of *G. rosea* and the Beverton–Holt model was the preferred model overall for *T. cyanopetala* since they had the lowest respective LOOIC scores (Table 2). However, Akaike weights showed that there was support for both models depending on whether focal plants were in open or woody environmental conditions. Likely owing to the particularly weak interactions experienced by *T. cyanopetala* in the woody environment (Appendix S4: Figure S4), the null model attained nontrivial model weight; however, the null model received limited Akaike weight across all the data, supporting the notion that the Ricker and Beverton–Holt models do indeed capture meaningful signals of density-dependent fecundity for both focal species.

### Structural sensitivity and environmental context dependency

As a starting point, we focus on predictions made using median parameter values but while varying the models used for density dependence and the environment in which the species were competing. Here, we found that inferences related to the biologically constrained feasibility domain, and how it varied across environments, were clearly contingent on the model formulation used for both species. The location of the biologically constrained feasibility domain showed clear shifts when moving from the open to woody environment (Figure 2). Effectively all model combinations indicated that interactions allowed for greater variation in the vital rate of *G. rosea* in the open environment and for greater variation in the vital rate of *T. cyanopetala* in the woody environment while still maintaining coexistence. Three out of four model combinations also gave strong indications that the sizes of the biologically constrained feasibility domain ( $A_\beta$ ) and area of monoculture ( $A_\gamma$ ) were larger in the woody

environment than in the open environment (Figure 3 and Appendix S5: Figure S3). All model combinations indicated that the size of the biologically constrained feasibility domain was (1) larger than the size of the area in monoculture in the open environment but (2) smaller than the size of the area in monoculture in the woody environment (Figure 4).

Predictions of species coexistence using median parameter estimates were also contingent on the model formulation used for both species in both environments (Figure 5). In the open environment, the model used for *G. rosea* did not impact these predictions; however, we predicted *T. cyanopetala* would outcompete *G. rosea* when using the Beverton–Holt model for *T. cyanopetala* and predicted coexistence when using the Ricker model for *T. cyanopetala*. In the woody environment, the prediction using median parameter values was that *G. rosea* would outcompete *T. cyanopetala* as long as the Ricker model was used for *G. rosea* or when both species were modeled with the Beverton–Holt model; when the Beverton–Holt model was used for *G. rosea* but the Ricker model was used for *T. cyanopetala*, the prediction using median parameter values was that the two species would coexist.

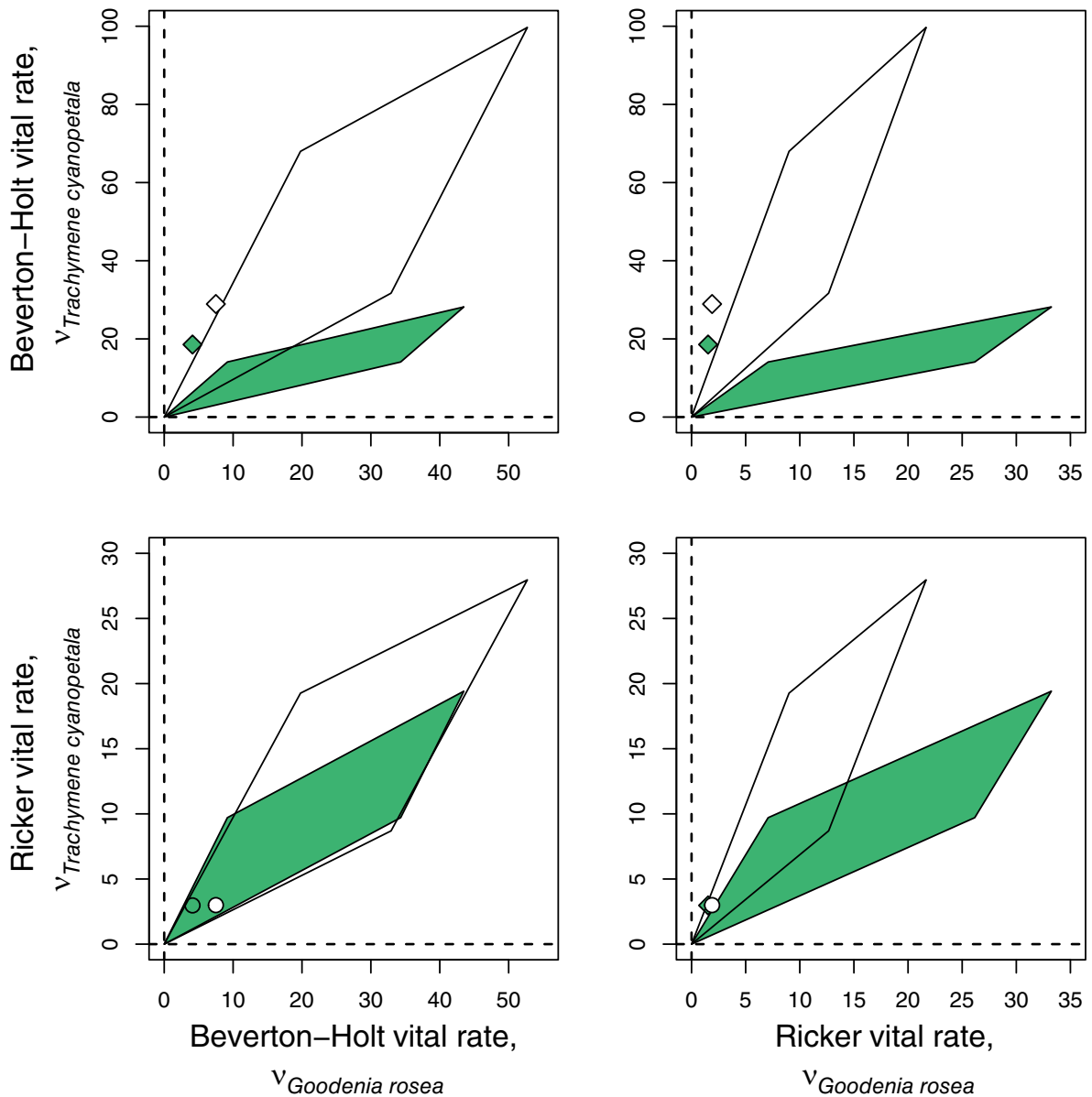
### Structural sensitivity, environmental context dependency, and parameter sensitivity

Predictions made with the full posterior distributions of parameter values could be quantitatively and qualitatively very different than predictions made with median parameter values (Figures 3–5). Some model combinations appeared to induce greater variation in the location of the biologically constrained feasibility domain, whereas other model combinations appeared to induce greater variation in the species’ inferred vital rates (Appendix S5: Figures S1

**TABLE 2** Model comparison for data collected in open environment, woody environment, and for all data together.

Species	Model	Open		Woody		All	
		LOOIC	Weight	LOOIC	Weight	LOOIC	Weight
<i>Goodenia rosea</i>	Null	691.96	0.01	693.45	0.00	692.70	0.00
<i>G. rosea</i>	Beverton–Holt	682.73	0.55	682.95	0.39	682.84	0.47
<i>G. rosea</i>	Ricker	683.18	0.44	682.10	0.60	682.64	0.52
<i>Trachymene cyanopetala</i>	Null	946.47	0.00	943.19	0.06	944.83	0.01
<i>T. cyanopetala</i>	Beverton–Holt	934.95	0.66	937.60	0.92	936.28	0.88
<i>T. cyanopetala</i>	Ricker	936.33	0.33	944.52	0.03	940.42	0.11

Note: LOOIC (leave-one-out cross-validation information criterion) penalizes models for the number of parameters, and the lowest value reflects the best-performing model. The resulting Akaike weight for each model is an estimate of the probability that the model will make the best predictions of new data across the set of models considered.

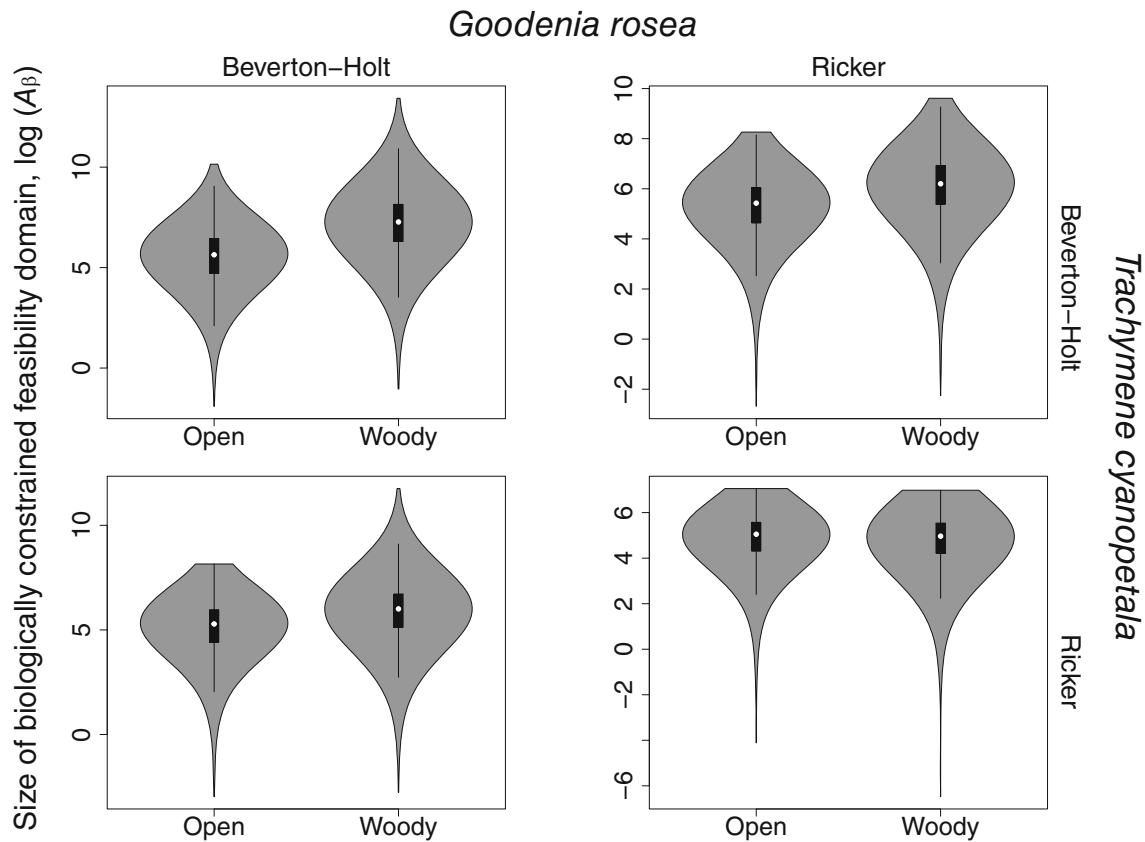


**FIGURE 2** Biologically constrained feasibility domains and species' inferred vital rates in the open and woody environments for different model combinations. For each combination of models used to quantify species' density-dependent fecundity, we show the inferred feasibility domain and species' vital rates using the median parameter values inferred from the experimental data. In each panel, the white area is the biologically constrained feasibility domain in the open environment and the green shaded area is the same in the woody environment. The white point corresponds to the inferred vital rates in the open environment and the green point the same in the woody environment. Points that are circles imply predicted coexistence (i.e., the vital rates fall inside the biologically constrained feasibility domain); points that are diamonds correspond to a prediction of competitive exclusion (i.e., the vital rates fall outside the biologically constrained feasibility domain).

and S2). The extent of parameter sensitivity depended on the models used and the environment where interactions took place. Importantly, we also noticed that the prediction made using median parameter values did not always correspond to the outcome that was predicted to be most likely across the full posterior distribution of parameter values (Figure 5). There was a slightly higher tendency for model combinations, including the Beverton-Holt model, to

predict monospecies dominance at a density greater than that given by our abundance-based constraints; however, these predictions were rare overall.

When the two species interacted in the open environment, the most common prediction across posterior draws was that the two plant species would coexist (49% of all posterior draws). That said, the proportion of posterior draws that predicted coexistence ranged from 25% to



**FIGURE 3** Estimated size of biologically constrained feasibility domain ( $A_\beta$ ) in open and woody environments for different model combinations. Each column corresponds to a different model used to capture the density-dependent fecundity of *Goodenia rosea*, whereas each row corresponds to a different model used to capture the density-dependent fecundity of *Trachymene cyanopetala*, as indicated on top and at right. Within each panel, we show box-and-whisker plots for  $A_\beta$  estimated from each draw from the parameters' joint posterior distribution. In all cases, the box covers the 25th–75th percentiles, the middle line marks the median, and the maximum length of the whiskers is 1.5 times the interquartile range. Underneath the box-and-whisker plots, we show violin plots that demonstrate the full posterior distributions of the quantities in question. Owing to their large underlying variation, we logarithmically transformed the values of  $A_\beta$  prior to plotting.

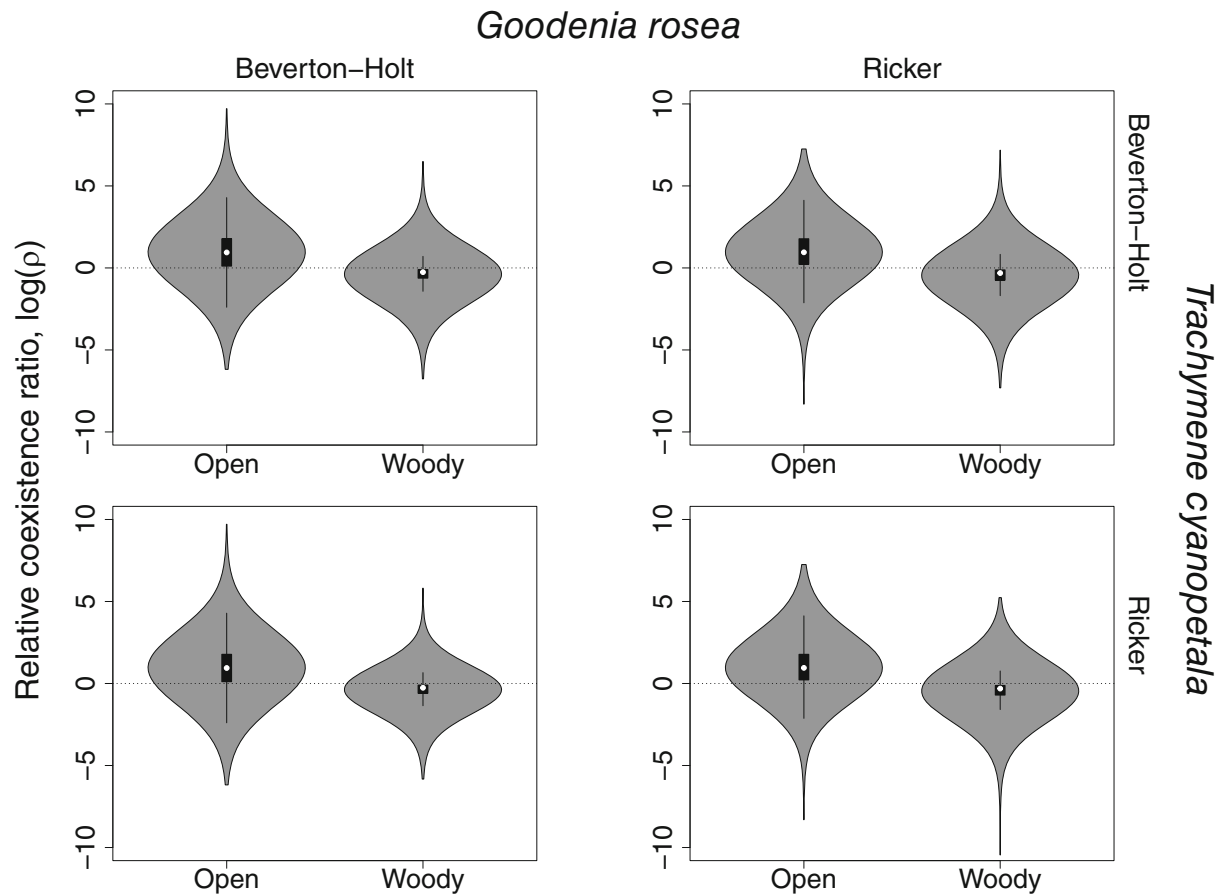
67% depending on the models used to capture density dependence. In the open environment and across all model combinations, 34% (range: 12%–58%) of posterior draws predicted that *T. cyanopetala* would competitively exclude *G. rosea*, whereas 14% (range: 11%–19%) predicted the reverse. The open environment, therefore, was the environment in which *T. cyanopetala* appeared to have a competitive advantage.

When the two species interact in the woody environment, the most common prediction across posterior draws and model combinations was that *G. rosea* would competitively exclude *T. cyanopetala* (mean: 64%; range 32%–88%). The next most likely predicted outcome was coexistence (mean: 29%), though this varied substantially across model combinations, from a low of 7% to a high of 59%. Competitive exclusion of *G. rosea* by *T. cyanopetala* was predicted to be rare across posterior draws (mean: 3%); however, it was predicted to occur for >7% of posterior draws when the

Beverton–Holt model was used for *G. rosea* and the Ricker model was used for *T. cyanopetala*. The woody environment therefore was the environment in which *G. rosea* appeared to have a competitive advantage.

## DISCUSSION

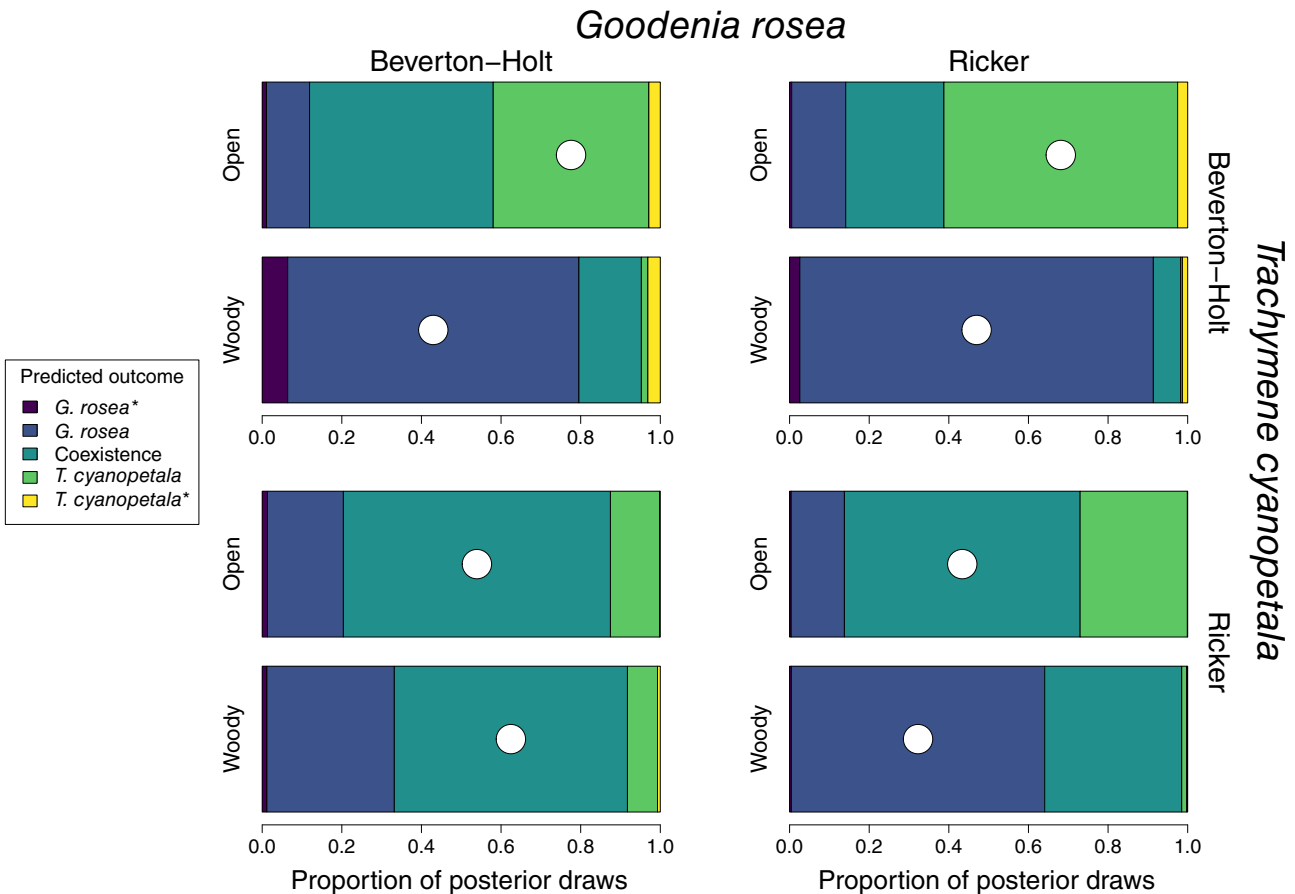
Our results show that the choice of phenomenological model can strongly influence predictions of whether or not a pair of species can coexist. Indeed, seemingly subtle differences between models led to predictions of both coexistence and competitive exclusion based on the exact same experimental data. Even in cases where we predicted the most likely outcome in a given environmental condition was competitive exclusion, which of the two species was predicted to be dominant varied depending on the models being used.



**FIGURE 4** Estimated relative coexistence ratio  $\rho$  in open and woody environments for different model combinations. Each column corresponds to a different model used to capture the density-dependent fecundity of *Goodenia rosea*, whereas each row corresponds to a different model used to capture the density-dependent fecundity of *Trachymene cyanopetala*, as indicated on top and at right. Within each panel, we show box-and-whisker plots for sizes estimated from each draw from the parameters' joint posterior distribution. In all cases, the box covers the 25th–75th percentiles, the middle line marks the median, and the maximum length of the whiskers is 1.5 times the interquartile range. Underneath the box-and-whisker plots, we show violin plots that demonstrate the full posterior distributions of the quantities in question. Owing to their large underlying variation, we logarithmically transformed the values of  $\rho$  prior to plotting. The dotted line at  $\log(\rho) = 0$  therefore indicates when the two domains have equal sizes.

Given our experimental data, both the Beverton–Holt and Ricker models received statistical support based on how they captured variation of seed sets with increasing neighbor density (Table 2). It is often the case in annual-plant studies that more than one phenomenological model has statistical support for different species or sites (Bimler et al., 2018; Levine & HilleRisLambers, 2009; Martorell & Freckleton, 2014; Martyn et al., 2021; Mayfield & Stouffer, 2017). Nonetheless, exploring predictions made by more than one model is not common practice in the study of species coexistence, unlike the study of other ecological processes like predator–prey dynamics (Aldebert & Stouffer, 2018; Fussmann & Blasius, 2005; Myerscough et al., 1996). By limiting our predictions to a single type of phenomenological model, we not only have to ignore other models that share statistical support, but we also limit our understanding of how model formulation itself changes our predictions.

We found clear indications that predictions of species coexistence using the annual-plant model are structurally sensitive. In both environments, predicted coexistence varied considerably depending on the models used to quantify density dependence (Figure 5). Our study thus provides another clear example where predictions made with different models can be quantitatively similar (e.g., in terms of their fit to data) and still have different qualitative behaviors, one of the hallmarks of structural sensitivity (Cordoleani et al., 2011). Structural sensitivity can arise because what might appear to be slight mathematical differences in model formulation can become significantly amplified (Cordoleani et al., 2011; Wood & Thomas, 1999), and the strength of structural sensitivity can depend on the model behavior being examined (Aldebert & Stouffer, 2018; Cordoleani et al., 2011). In the case of our pairwise coexistence predictions, we also made a separate model choice for each focal species,



**FIGURE 5** Predicted outcome of competition between the two focal species in the open and woody environments for different model combinations. Each paired set of horizontal bars corresponds to a different model combination; labels on the top indicate the model used for the species *Goodenia rosea*, and labels on the right show the model used for *Trachymene cyanopetala*. Horizontal bars within those panels show the proportion of posterior draws that predict competitive dominance of *G. rosea*, coexistence, or competitive dominance of *T. cyanopetala* as indicated by the color bar in the legend to the left. Outcomes highlighted with \* indicate predictions of competitive dominance but at higher than realistic abundances. In each bar, we also highlight with a white circle the prediction corresponding to the median parameter values across all posterior draws.

which means that there were two potential opportunities for structural sensitivity to crop up.

In the open environment, we predicted coexistence was the most likely outcome in three out of the four model combinations we explored (Figure 5). However, this depended most strongly on the model used to model the density dependence of *T. cyanopetala*: when using the Beverton–Holt model, competitive dominance of *G. rosea* by *T. cyanopetala* was predicted to be more likely. Overall, both the Beverton–Holt and the Ricker models predicted intraspecific interactions to be larger than interspecific interactions for both species in the open environment (Appendix S4: Figures S2 and S4), which should tend to promote coexistence since it makes species limit themselves more than they limit others (Adler et al., 2018; Chesson, 2000). However, the intrinsic fecundity of *T. cyanopetala* was also predicted to be larger given the Beverton–Holt model than given the Ricker

model (Appendix S4: Figure S4). Thus, using the Beverton–Holt model for *T. cyanopetala* led to greater predicted fitness differences between the two species; as a result, the species’ vital-rate vector more often fell outside of the biologically constrained feasibility domain and, ultimately, to an increased probability of predicting competitive exclusion of *G. rosea* by *T. cyanopetala* (Figure 5).

The extent of structural sensitivity observed in our focal system changed in the woody environment. When we made predictions using median parameter estimates in the woody environment, three out of four model combinations predicted competitive exclusion of *T. cyanopetala* by *G. rosea* (Figure 5). Intriguingly, this occurred despite the fact that the size of the biologically constrained feasibility domain in the woody environment appeared to be larger than in the open environment (Figure 3). The increased likelihood of predicting competitive exclusion compared to the open environment seemed to be driven by several factors. One of them

is that inferred interspecific interactions were stronger than intraspecific interactions for *G. rosea* when using both models (Appendix S4: Figure S2), which resulted in a smaller  $\beta$  in the woody environment. However, since intraspecific interactions were generally inferred to be weaker in the woody environment (Appendix S4: Figures S2 and S4), the space of vital rates allowing feasible coexistence compared to the space allowing monocultures decreased (Figure 4).

Furthermore, both species in the woody environment were predicted to have lower fecundities in the absence of competition compared to the open environment, which supports observations from previous empirical studies in this system of lower plant abundances when growing under litter (Wainwright, Dwyer, & Mayfield, 2017). Of the two species, *G. rosea* was predicted to experience a sharper reduction in seed set by both models (Appendix S4: Figure S4). However, our results suggest that these two species are less likely to coexist in the woody environment due to an environmentally induced shift in interaction strengths that increased niche overlap as opposed to changes in the two species' fitness differences. This observation is similar to a study of annual grassland species in California that found that reduced rainfall also impacted niche differences more than fitness differences (Van Dyke et al., 2022).

Our results provide another example where interaction strengths, and thus coexistence predictions, change with environmental conditions, a result that was previously empirically demonstrated in this system (Bimler et al., 2018; Wainwright, Dwyer, Hobbs, & Mayfield, 2017) and in others (Matías et al., 2018; Van Dyke et al., 2022). Another study also documented that the fecundities of both focal species change while growing in coarse woody debris (Towers et al., 2020). Importantly, the extent of environmental context dependency in our experimental system is also influenced by the models used to quantify density dependence for both species. That is, the apparent effect of abiotic conditions can be enhanced or diminished in predictions of species coexistence due simply to one's choice of phenomenological model(s). It is worth noting here that our experiment was conducted during a single growing season, so we were unable to measure the extent to which temporal variability, for example between years, might also change coexistence predictions. Comparing the relative roles of spatial and temporal heterogeneity in creating structural sensitivity would be a particularly exciting avenue for future research.

In our study, we highlight the practical importance of considering the "biologically constrained feasibility domain" when operationalizing the structural approach to a real-world system. Our approach here is most similar

to those explored in two previous studies (Song et al., 2018, 2020). In the first, the authors discuss imposing constraints on growth rates in a three-species food chain depending on each species' biology (Song et al., 2018): Basal producers were required to have positive intrinsic growth rates while consumers and top predators were required to have negative intrinsic growth rates. In the second, the authors calculated the overlap between domains defined by multiple emergent model predictions, feasibility, and persistence (Song et al., 2020). Here, we focus on two additional types of constraints that, to the best of our knowledge, have never been explored. First, we emphasize that species' composite vital rates are not purely abstract mathematical quantities, even though they are dictated by one's choice of mathematical model. Since they are embedded in a population-dynamics model, they can also be used to generate predictions about observable quantities like species' densities, and not all predicted densities may be biologically sensible. Second, the mathematical specifics of the model imbues additional biological meaning in its "composite" vital rate  $\nu_i$ . In our case, it was therefore imperative to restrict ourselves to feasible values of  $\nu_i$  that were actually consistent with the biology of annual plants (e.g., intrinsic fecundities must be positive).

Using a Bayesian approach to fit our models to data also allowed us to have a better understanding of the parameter uncertainty associated with our predictions. Our results showed that estimating pairwise coexistence only using median estimates of parameter values might overlook instances where the uncertainty encompasses outcomes different from the median prediction (Figure 5). Previous studies also incorporated parameter uncertainty in coexistence predictions by propagating standard errors (Matías et al., 2018) or bootstrapping observations (García-Callejas et al., 2020). However, these approaches were only incorporated to show the robustness of predictions rather than to specifically measure the extent to which different sources of uncertainty could impact predictions of species coexistence.

Our results also show that even when we predicted competitive exclusion, the species we predicted to be competitively excluded varied across posterior draws (Figure 5). Another study that incorporated posterior distributions of parameter values in coexistence predictions also encountered this uncertainty regarding the outcome of competition (Terry et al., 2021). However, they also found that posterior predictions mostly agreed with predictions using median parameter values (i.e., species were confidently coexisting or not; Terry et al., 2021). Our results did not show as clear differences, particularly in the open environment, where species' inferred vital rates were particularly close to the coexistence boundary (Appendix S5: Figure S1).

Importantly, the effect of parameter sensitivity on predictions of species coexistence has been mostly interpreted as statements of uncertainty in the underlying data, rather than the biologically meaningful basis of a probabilistic outcome (Matías et al., 2018; Terry et al., 2021). In reality, though, it makes little sense to think that a model-based prediction of something like coexistence is really a yes-or-no, binary outcome about which we can have full confidence. Our study thus goes beyond this interpretation by calculating the posterior probabilities of the various coexistence outcomes when using different phenomenological models to quantify density dependence. Similar to Bayesian model averaging (McElreath, 2018), one could even use model weights to compute a weighted average across all model combinations, leading to what would act as a “model-independent” set of probabilities for each potential outcome. In our specific case, the combination of uncertainty across models—as captured by the different model weights—and uncertainty across parameters—as captured by their joint posterior distribution—suggests that coexistence between *G. rosea* and *T. cyanopetala* is at least plausible in the open environment but not very likely in the woody environment, which is more favorable to *G. rosea* (Figure 5).

We illustrated our approach here using an ecologically simplified context of only two focal species. Most predictions about biodiversity maintenance, however, are focused on scenarios with much higher species richness. Though coexistence outcomes with more than two species can become more fraught—for example, due to intransitivity (Godoy et al., 2017)—the structural approach has already been extended to an arbitrary number of species (Saavedra et al., 2017). Given the appropriate data, our biologically constrained feasibility domain could similarly be extended to consider the vital rates of more than two species. Operationally, the biggest constraint would likely arise from the number of models for density-dependent fecundity that a researcher is willing to consider. Recall that, in a fixed environment, there are still  $M^S$  model combinations to explore, where  $M$  is the number of candidate models and  $S$  is the number of species. We focused here on the two models of density-dependent fecundity that are most widely used in the recent literature. However, many more models have been explored elsewhere (Hart et al., 2018; Law & Watkinson, 1987; Levine & HilleRisLambers, 2009), and including them all could lead to a combinatorial explosion. On the other hand, if future studies accept that “all models are wrong but some models are useful” (Box, 1976) and thus adopt a model-averaging approach, it may be worth the effort to push past structural sensitivity and seek consensus predictions when and where possible.

## CONCLUSION

Predictions of species coexistence constitute the building blocks for many ecological studies, such as community assembly (Grainger et al., 2019; HilleRisLambers et al., 2012; Kraft et al., 2015), the evolution of competitive communities (Germain et al., 2022; Letten et al., 2021; Pastore et al., 2021), or the role of species richness in ecosystem functioning (Godoy et al., 2020). Many of these studies rely on mathematical models as the basis of their predictions. Species coexistence is determined by many processes acting simultaneously, and studying it often involves a process of abstraction from ecological reality to mathematical objects such as phenomenological models (Levins, 2006). Structural sensitivity is likely to arise when these processes are summarized into equations after adopting assumptions regarding the complexity of the biological system (Aldebert & Stouffer, 2018). This makes predictions of species coexistence made with phenomenological models particularly vulnerable, especially when the model is an extreme simplification of a much more complex phenomena (Aldebert et al., 2018; Stouffer, 2022).

Overall, our study shows that different phenomenological models can enhance or diminish the effect of environmental context dependency and parameter sensitivity and, thus, our predictions of species coexistence. We argue that the interplay between different sources of uncertainty should not be ignored when we make model-based predictions, whether for the outcome of competition between plants or any other complex and emergent ecological phenomenon. Indeed, by considering different models and accepting that there will always be uncertainty in those models' parameter estimates, we have outlined the importance of thinking of coexistence outcomes as a wide range of possibilities rather than a simple yes or no.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and novel code (Stouffer et al., 2023) are available in Zenodo at <https://doi.org/10.5281/zenodo.8271442>.


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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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