RESEARCH ARTICLE

Initial abundance and stochasticity influence competitive outcome in communities

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Abstract

1. Predicting competitive outcomes in communities frequently involves inferences based on deterministic population models since these provide clear criteria for exclusion (e.g. R* rule) or long-term coexistence (e.g. mutual invasibility).

2. However, incorporating stochasticity into population- or community-level processes into models is necessary if the goal is to explain variation in natural systems, which are inherently stochastic.

3. Similarly, in systems with demographic or environmental stochasticity, weaker competitors have the potential to exclude superior competitors, contributing to what is known as 'competitive indeterminacy'. The importance of such effects for natural communities is unknown, in part because it is difficult to demonstrate that multiple forms of stochasticity are present in these communities. Moreover, the effects of multiple forms of stochasticity on competitive outcomes are largely untested, even in theory.

4. Here, we address these issues by examining the role of stochasticity in replicated communities of flour beetles (*Tribolium* sp.). To do so, we developed a set of two-species stochastic Ricker models incorporating four distinct forms of stochasticity: environmental stochasticity, demographic stochasticity, demographic heterogeneity and stochastic sex determination.

5. By fitting models to experimental data, and simulating fit models to examine long-term behaviour, we found that both the duration of transient coexistence and the degree of competitive indeterminacy were sensitive to the forms of stochasticity included in our models. These findings suggest the current estimates of extinction risk, coexistence and time until competitive exclusion in communities may not be accurate when based on models that exclude relevant forms of stochasticity.

KEYWORDS
competition, extinction risk, priority effects, stochasticity, *Tribolium*

1 | INTRODUCTION

Stochasticity—either intrinsic (demographic) or extrinsic (environmental)—can strongly influence population dynamics of single species (Desharnais et al., 2006; Lande, 1993; Neubert & Caswell, 2000). Demographic stochasticity, in particular, occurs when similar individuals exhibit random or unexplained variation in their demographic rates, which can be caused by a number of different processes. As such, demographic stochasticity can take multiple forms. For example, demographic heterogeneity, the intraspecific variation in demographic rates among individuals due to (in principle) measurable differences between individuals (e.g. stage structure, genetic

variation), is a form of stochasticity largely unmeasured or unaccounted for in descriptive models. This contrasts with the more traditional conception of demographic stochasticity, generally assumed to reflect cases where birth and death occurs probabilistically or effectively so, even within populations of identical individuals. A third form of demographic stochasticity arises as a result of variability in the production of male and female offspring (i.e. stochastic sex determination), which influences future mating opportunities and population growth rates. In addition to these forms of demographic stochasticity, demography may be also affected by extrinsic stochasticity from random or unpredictable changes to environmental conditions (e.g. temperature), hereafter referred to as environmental stochasticity.

Whether arising from 'true' randomness in demographic rates or simply unmeasured differences between individuals/environments, stochastic variation is known to strongly affect population-level outcomes. Theoreticians (Ovaskainen & Meerson, 2010) and experimentalists (Drake, 2005) alike have investigated how both demographic and environmental stochasticity influence population extinction risk (Lande, 1993). On the one hand, environmental stochasticity can increase extinction risk by exposing populations to suboptimal or lethal conditions. On the other hand, certain forms of environmental variation can also benefit species that overcompensate to changing conditions (Lawson et al., 2015; Petchey et al., 1997). Similarly, demographic stochasticity can both increase extinction risk at the local scale (Lande, 1993) and decrease extinction in larger metapopulations by reducing synchrony between patches (Simonis, 2012). Thus, both environmental and demographic stochasticity can have opposing—and potentially neutralizing—effects, depending on population responses to each form of stochasticity. In all cases, population size is an important consideration since it determines the relative importance of environmental and demographic stochasticity on population dynamics (Feller, 1939; May, 1973; Purvis et al., 2000).

While the effects of stochasticity on single-species population dynamics are well-established (Lande et al., 2003; Melbourne & Hastings, 2008; Ovaskainen & Meerson, 2010), a smaller—yet still considerable—body of research has focused on the effect of stochasticity on the outcomes of interspecific competition, specifically on how it influences coexistence between species consuming a single limiting resource (Chesson, 1986; Gravel et al., 2011; Hart et al., 2016). In the absence of stochasticity (i.e. all individuals have identical demographic rates), 'weaker' species will always be excluded by 'superior' competitors (Hardin, 1960). However, when there is stochasticity and considering population dynamics in infinite time, theory predicts extinction for all competitors, including both weak and superior competitors. Transient competitive coexistence may still be possible on shorter time-scales, especially if fitness differences between competing species are small (Okuyama, 2015; Pedruski et al., 2015), or as a result of temporal (Ellner et al., 2016) or spatial (Sears & Chesson, 2007) storage effects. Stochasticity can also cause superior competitors to go extinct before weaker

competitors, introducing uncertainty in competitive outcomes (Okuyama, 2015; Orrock & Watling, 2010; Pedruski et al., 2015), a phenomenon referred to as *competitive indeterminacy* (Mertz et al., 1976). Here, the initial abundance of competitors is also important (Edmunds et al., 2003; Leslie, 1962; Leslie et al., 1968; Park, 1957).

Both transient coexistence and competitive indeterminacy have been observed previously in laboratory populations of two competing *Tribolium* species more than 70 years ago (Park, 1948; Park & Frank, 1948). These findings resulted in a series of important papers related to the mathematics of competition and coexistence (Costantino & Desharnais, 1991; Desharnais et al., 2005; Leslie, 1962; Mertz et al., 1976). While this generated interesting insight into coexistence in stage structured cannibalistic populations, most of the subsequent studies of the effects of stochasticity on competitive coexistence have largely been theoretical (Leslie, 1962; Okuyama, 2015; Pedruski et al., 2015). Empirical studies have been limited to, for example, studying the effects of demographic stochasticity on coexistence (Legault et al., 2019), one of many forms of stochasticity affecting populations. To our knowledge, no empirical studies have examined the combined effects of the multiple forms of stochasticity (e.g. demographic, environmental) and initial species abundances on competitive indeterminacy.

Here, we explore the effects of initial competitor abundance and stochasticity on competitive indeterminacy and extinction dynamics in two-species communities, combining laboratory experiments with stochastic models, which include environmental and demographic stochasticity, but also demographic heterogeneity and stochastic sex determination. To do so, we established short-term experimental communities of competing *Tribolium* species along a gradient of initial abundances. We then defined a set of stochastic Ricker models incorporating multiple forms of stochasticity and fit these models to data from these communities. Finally, we simulated our fitted models to examine the long-term behaviour of two-species communities affected by different forms of stochasticity. With these fitted stochastic models, we were able make biologically informed predictions about how competitive outcomes could be affected by differences in initial abundances and the presence of different forms of demographic or environmental stochasticity.

2 | MATERIALS AND METHODS

2.1 | Two-species *Tribolium* competition experiment

Flour beetles (*Tribolium castaneum* and *Tribolium confusum*; *S* and *F* in the modelling framework below) were obtained from long-running laboratory populations maintained in $4 \times 4 \times 6$ cm enclosures partly filled with 30 ml of flour and yeast medium (95% wheat flour and 5% brewer's yeast by volume). Stock populations were maintained at 30°C and ≈50% relative humidity. We enforced non-overlapping generations in accordance with the previous *Tribolium*

experiments (Dallas et al., 2020; Hufbauer et al., 2015; Legault et al., 2020; Melbourne & Hastings, 2008, 2009; Weiss-Lehman et al., 2017). This serves not only to simplify the interactions by limiting the multi-stage cannibalistic effects that have been suggested to yield complex dynamics (Costantino & Desharnais, 1991; Desharnais et al., 2005), but also increases the potential generality of our model and findings to other systems with non-overlapping generations.

We manipulated initial species abundance along a gradient from 0 to 256 individuals per patch (0, 2, 4, 8, 16, 32, 64, 128, 256). We considered all two-species (*T. castaneum* and *T. confusum*) abundance combinations for abundances between 0 and 64 individuals, and additional combinations of 0, 128 and 256 individuals per species to capture high density effects (Supporting Information Figure A1). The high abundance populations (128, 256) were replicated eight times each, while lower abundance combinations were replicated 15 times each, for a total of 768 populations. The single-species combinations—zero *T. castaneum* or zero *T. confusum*—allowed us to quantify intraspecific competition along a gradient of initial abundances. One experimental population—consisting of 64 *T. castaneum* and 0 *T. confusum*—was discarded due to experimental error. Populations were monitored for a single generation, and were established by placing adult beetles of each species at their experimental abundances, allowing them to lay eggs for 24 hr and then discarding adults. We were unable to determine sex of the beetles at the start of the experiment, such that small populations could feasibly consist of all males or all females. During these 24 hr, adults both produce and consume eggs, so cannibalism is still present in the system, but only during this 24-hr period. After a 5-week generation period, adult beetles were identified to species, counted and weighed. Competition in this experimental system is a combined function of adult cannibalism on eggs during egg laying (Park, 1954, 1957), larval crowding during development, production of allelopathic chemicals (Bullock et al., 2020) and other species interactions that may influence demographic rates to a lesser degree (e.g. reproductive interference).

At least four kinds of stochasticity have the potential to influence our experimental results. First, since we did not determine the sex of beetles before or after they were (randomly) added to enclosures to lay eggs, there is uncertainty in the sex ratio of the starting generation, which is equivalent to there being stochastic sex determination. Second, while both *T. confusum* and *T. castaneum* came from laboratory cultures with presumably low genetic diversity, there could nevertheless be genetic differences among beetles that affect intrinsic demographic rates such as egg-laying or cannibalism. In principle, such differences could be measured (with great difficulty), but since we did not do so, demographic heterogeneity represents another form of stochasticity that could affect our system. Finally, both traditional demographic stochasticity, that is randomness in demographic processes from otherwise similar individuals, and environmental stochasticity in the form of random differences in temperature, humidity or medium may also be present.

2.2 | Ricker model development

We developed a family of eight stochastic Ricker models that account for the effect of various forms of stochasticity on two-species competitive communities. These two-species models are direct extensions of models previously developed for single-species populations of *Tribolium castaneum* (Melbourne & Hastings, 2008), one of the species included in the experiments. The models incorporate stochasticity by describing the population sizes of the two species (S and F) at time $t + 1$, S_{t+1} and F_{t+1}, as mixtures of random variables representing biological processes such as offspring production and density-dependent cannibalism. For example, the simplest Ricker model (Poisson Ricker) incorporates demographic stochasticity by assuming that the number of eggs produced by each adult from generation t is a Poisson random variable with mean β_i, and that the number of eggs that survive to generation $t + 1$ is a binomial random variable with probability determined by the number of adults of both species and their rates of egg cannibalism (αij), as well as a density-independent death rate while eggs mature to adulthood (d_i); specifically $e^{-(\alpha SS\ St\ +\ \alpha SF\ Ft)}\ (1 - d_S)$ for species S and $e^{-(\alpha FF\ Ft\ +\ \alpha FS\ St)}$ $(1 - d_F)$ for species F. Thus, the number of beetles that form the next generation of adults is the convolution of St or Ft binomial random variable conditioned on Poisson random variables, which reduce to the Poisson random variables:

$$
\begin{aligned}
S_{t+1} &\sim \text{Poisson}\left(S_t R_S e^{-(\alpha_{SS} S_t + \alpha_{SF} F_t)}\right) \\
F_{t+1} &\sim \text{Poisson}\left(F_t R_F e^{-(\alpha_{FF} F_t + \alpha_{FS} S_t)}\right),
\end{aligned}
\tag{1}
$$

where $R_i = \beta_i (1 - d_i)$. Further details on the derivation of single-species stochastic Ricker models are provided in the Supporting Information of Melbourne and Hastings (2008). As described above, competition in this system (α terms) is largely assumed to be due to egg cannibalism by adults, based on foundational work in this system (Park, 1948; Park & Frank, 1948). Smaller effects of larval crowding leading to the development of chemical cues that hinder development (Kotaki & Fujii, 1995) may be present, but are certainly much less important than cannibalistic effects. Further, when fitting the model to experimental data, any effects of larval crowding or other density-dependent interactions will be absorbed into the α terms.

To this basic model with demographic stochasticity only, we add the three remaining sources of stochasticity in various combinations (Table 1; Figure 1). Stochastic demographic heterogeneity and environmental stochasticity are incorporated by allowing birth rate, β_i to itself be a random variable with a gamma distributions, with shape parameters k_D for demographic heterogeneity and k_E for environmental stochasticity. Under the assumption that the number of offspring produced by an individual is a Poisson random variable (see, Akçakaya, 1991 for a discussion), the gamma mixture of Poisson random variables is equivalent to the negative binomial distribution where the population size in the next generation is a negative binomial random variable with variance inversely proportional to k_E for environmental stochasticity, or inversely proportional to $k_D Ft$ or $k_D St$ for demographic heterogeneity. This

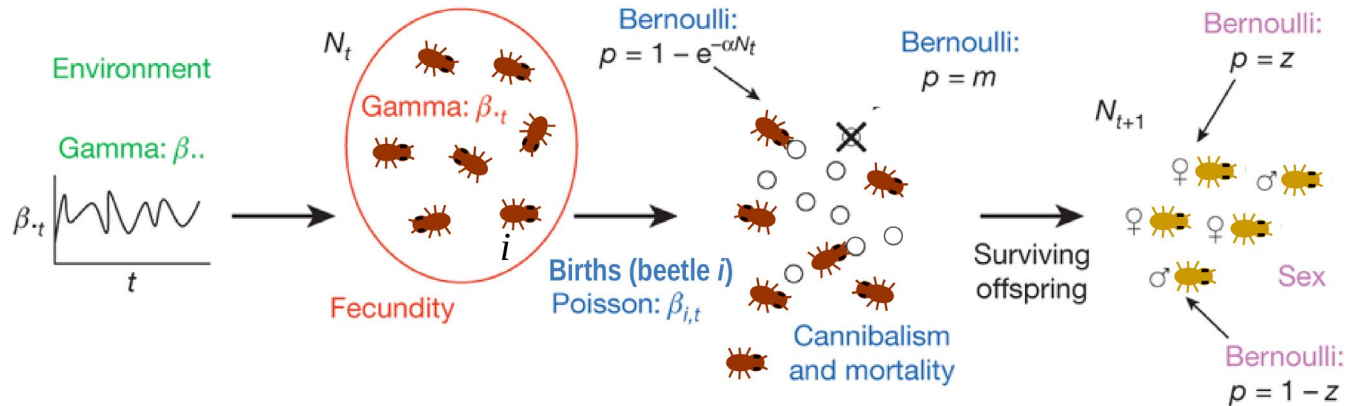| Model	Abbrev	Dem	Env	Dem Het	Sex
Poisson	P	+			
NB (demographic)	NBd	+		+	
NB (environmental)	NBe	+	+		
NB-gamma	NBg	+	+	+	
Poisson-binomial	PB	+			+
NB-binomial (demographic)	NBBd	+		+	+
NB-binomial (environmental)	NBBe	+	+		+
NB-binomial-gamma	NBBg	+	+	+	+

FIGURE 1 Flour beetle population dynamics are influenced by numerous forms of stochasticity. Demographic stochasticity (blue text) is incorporated by treating the number of offspring produced as a Poisson random variable, and mortality (including cannibalism) as a Bernoulli random variable. Environmental stochasticity (green; density independent) and demographic heterogeneity (red; density dependent) treat the Poisson number of offspring as a random variable. Lastly, stochastic sex determination (purple) treats the sex of an individual as a Bernoulli random variable

dependence of the variance due to demographic heterogeneity on density in the previous generation means that, at low population sizes, there is greater variance in population size in the next generation. The final source of stochasticity is stochastic sex determination, which we include by assuming that some fraction of a population is female, and that the number of females in the population controls the number of offspring possible. To do so, we replace S_T with a Bernoulli random variables representing the number of females in the population. Here, there is no mate-finding Allee effect, and all females are considered to be reproductively able.

2.3 | Fitting models to data

The joint probability mass functions of all eight stochastic two-species models were derived following Melbourne and Hastings (2008), making it possible to fit the two-species Ricker models described above, incorporating different combinations of stochastic processes, to our experimental data. Models were fit using maximum likelihood estimation in the stats4 R package (R Core Team, 2015) and compared using model selection criteria, specifically AICc. Associated data and R code, including the probability mass

functions, are available on figshare (https://dx.doi.org/10.6084/m9.figshare.5593633). We also fit single-species Ricker models to the single-species treatments to compare parameter estimates and fitted models as a function of competitor presence.

2.4 | Coexistence and competitive indeterminacy

Using the fitted values for each model, we explored extinction dynamics and competitive indeterminacy by simulating each of the Ricker models for 1,000 generations. We did this 1,000 times for each initial abundance combination to determine both the probability of transient coexistence, and the probability that *T. castaneum* excludes *T. confusum* given that coexistence is not observed (competitive indeterminacy). Transient coexistence probabilities were measured as the fraction of coexisting populations after 10, 100 and 1,000 generations, capturing both short- and long-term dynamics. This measure was used instead of mean extinction time, as mean extinction times are sensitive to the number of simulated generations. This simulation duration was much greater than previous experimental examinations of coexistence (e.g. 27 generations, Leslie et al., 1968), allowing us to consider the influence of stochasticity on community dynamics over the long term. Competitive indeterminacy

was defined as the probability that one competing species persisted longer than the other species, provided that at least one species had gone extinct during the simulation (i.e. coexistence was not observed). A probability of 0.5 indicates the highest degree of indeterminacy, as this suggests that species have equal chances of being excluded.

3 | RESULTS

3.1 | Sources of stochasticity

The Poisson Ricker model, incorporating only demographic stochasticity, fit poorly to both single-species (Supporting Information Tables A4) and two-species (Table 2) experimental populations, relative to other models. In contrast, the best-fit models for single-species dynamics of *T. castaneum* included demographic stochasticity, environmental stochasticity and stochastic sex determination (NBBe). It is important to note that the model incorporating all forms of stochasticity (NBBg) had the same likelihood as the model without demographic heterogeneity (NBBe) since the NBBe model is nested within the NBBg model. That is, the NBBg model can have an estimate of ∞ for demographic heterogeneity (k_D), which would indicate a lack of effect of demographic heterogeneity and demonstrates the nested structure of the fitted models. The best-fit model for single-species dynamics of *T. confusum* and two-species competition dynamics (Table 2), included demographic stochasticity, demographic heterogeneity and stochastic sex determination (NBBd; Supporting Information Table A4). Meanwhile, the full model (NBBg) incorporating all forms of stochasticity was the best-fit model to two-species communities. However, if the effects of environmental stochasticity (k_E) and demographic heterogeneity (k_D) were fit to each species instead of taking a single value corresponding to both species, demographic heterogeneity was no longer included in the best-fit two-species model (NBBe is the best fit; Supporting Information Table A3). All models were simulated to explore co-occurrence and competitive outcome, and

further simulation results and more information on the best-fit models are provided in the Supplemental Materials.

3.2 | Competition coefficients and predicted deterministic outcome

In the absence of a competing species, both species had similar estimated intraspecific competition coefficients in all model fits (Supporting Information Tables A4), with best-fit estimates of $\alpha_{SS} = 0.007$ and $\alpha_{FF} = 0.003$. In two-species communities, intraspecific competition coefficients were only slightly different—$\alpha_{SS} = 0.011$ and $\alpha_{FF} = 0.002$—suggesting that *T. castaneum* has a stronger intraspecific effect when in competition with *T. confusum* (Table 2). Further, *T. castaneum* had a threefold larger effect on *T. confusum* (best fit, $\alpha_{FS} = 0.006$) compared to the competitive effect of *T. confusum* on *T. castaneum* (best fit, $\alpha_{SF} = 0.002$). Model fits to experimental populations are visualized in the Supplemental Materials (Supporting Information Figures A6–A10).

For deterministic Ricker models, the equilibrium abundances for *T. castaneum* (S^*) and *T. confusum* (F^*) are functions of population growth rates and competitive effects. Previous studies have examined mutual invasibility and the criteria for coexistence in the two-species Ricker model (Högnäs, 2012; Luís et al., 2011), demonstrating that coexistence is possible and depends on population growth rates and species interaction terms (α coefficients). Luís et al. (2011) identified four potential equilibria for the two-species Ricker model (S, F); no species persist (0, 0), one species excludes the other—either (S^*, 0) or (0, F^*)—or both species coexist (S^*, F^*). Coexistence is stable if.

$$\frac{\alpha_{FS}}{\alpha_{SS}}\ln(R_S) < \ln(R_F) < \frac{\ln(R_S)\alpha_{FF}}{\alpha_{SF}}, \quad (2)$$

whereas exclusion of either species occurs if the above inequality (Equation 2) is violated. Given our best-fit model parameters (Table 2), the long-term coexistence criteria of equation 2 are met, suggesting that long-term coexistence is a stable equilibrium in the deterministic

TABLE 2 Two-species Ricker models were fitted to the data by maximizing the negative log likelihood (*NLL*), calculated from the probability mass function of each stochastic Ricker model. Population growth rates (R_S and R_F) and competition coefficients (α_{SS}, αFF, αFS, αSF) were estimated for each model, as well as model-specific parameters for demographic (kD) and environmental (kE) stochasticity. Differences in the Akaike information criterion (AIC) were used to compare models

Model	R_S	R_F	α_{SS}	α_{FF}	α_{FS}	α_{SF}	k_D	k_E	*NLL*	AIC	ΔAIC
Poisson	4.70	2.61	0.010	0.003	0.005	0.002			−9535.4	19,082.8	9,641.6
NBd	4.53	2.50	0.010	0.002	0.005	0.002	0.16		−4970.8	9,955.6	514.3
NBe	4.85	2.81	0.011	0.001	0.007	0.001		2.72	−4829.0	9,672.0	230.7
NBg	4.97	2.68	0.011	0.002	0.006	0.002	0.63	4.63	−4784.4	9,584.9	143.6
PB	4.78	2.87	0.010	0.003	0.005	0.002			−5591.7	11,195.3	1754.0
NBBd	4.40	2.48	0.009	0.001	0.005	0.003	0.45		−4951.1	9,916.1	474.8
NBBe	4.83	2.78	0.011	0.002	0.006	0.002		4.84	−4716.2	9,446.4	5.1
NBBg	4.82	2.77	0.011	0.002	0.006	0.002	3,255.82	4.84	−4712.6	9,441.3	0.0

sense. However, this stable equilibrium stands in contrast to our simulations of models containing the different forms of stochasticity.

3.3 | Transient coexistence

Based on the coexistence criteria (Equation 2) and the parameters of the best-fit two-species model (*NBBg*), long-term coexistence of both species is predicted to be stable given deterministic dynamics. However, model simulations suggest that coexistence depends on initial abundance (Figure 2), is sensitive to various forms of stochasticity (Figure 2) and is strongly reduced over time (Supporting Information Figures A3 and A4). In general, long-term co-occurrence was markedly reduced in the model incorporating demographic and environmental stochasticity (Figure 2).

3.4 | Competitive indeterminacy

Competitive indeterminacy was calculated after removing those populations where coexistence was observed. Regions of parameter space corresponding to the most indeterminate competitive outcome are those with exclusion probabilities of 0.5, which means

species exclude one another equally often, and values less than 0.5 indicate *T. confusum* tends to exclude *T. castaneum*. High competitive indeterminacy was observed in simulations of the best-fit two-species model (*NBBg*), highlighting the effect of stochasticity on competitive outcome (Figure 3). Further, models incorporating fewer forms of stochasticity tended not to capture competitive indeterminacy, but the exclusion of one or the other species (Figure 3). In the most extreme case, the Poisson Ricker model—incorporating only demographic stochasticity—predicted that *T. castaneum* would nearly universally exclude *T. confusum* (Supporting Information Figure A5). Environmental stochasticity, in particular, enhances indeterminacy in competitive outcomes, as seen by comparing *NBd* and *NBBd* models—which incorporate demographic stochasticity and demographic heterogeneity—to *NBe* and *NBBe* models, which contain demographic and environmental stochasticity (Figure 3).

4 | DISCUSSION

Models containing multiple forms of stochasticity fit best to the experimental data, suggesting that multiple forms of stochasticity influence dynamics in our two-species communities. Further, both co-occurrence and competitive indeterminacy were sensitive to the
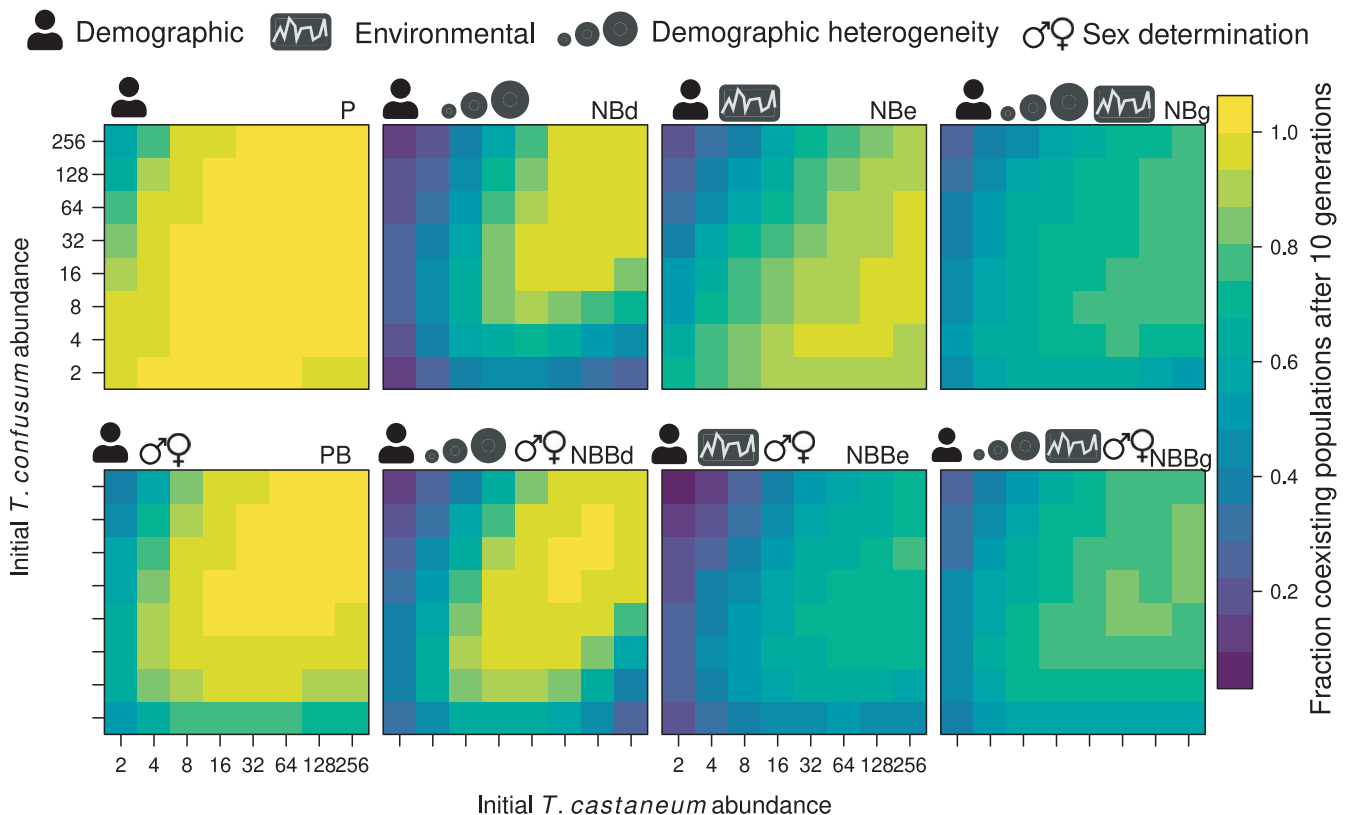

FIGURE 2 Model-predicted coexistence probability after 10 generations for a set of stochastic two-species Ricker models (described in Table 1), each incorporating different forms of stochasticity (identified as glyphs in the figure legend). The Poisson Ricker model, incorporating only demographic stochasticity, had the highest coexistence probability, while additional forms of stochasticity reduced coexistence probability strongly. Stochastic sex determination was incorporated for the bottom row, while the top row did not include this form of stochasticity
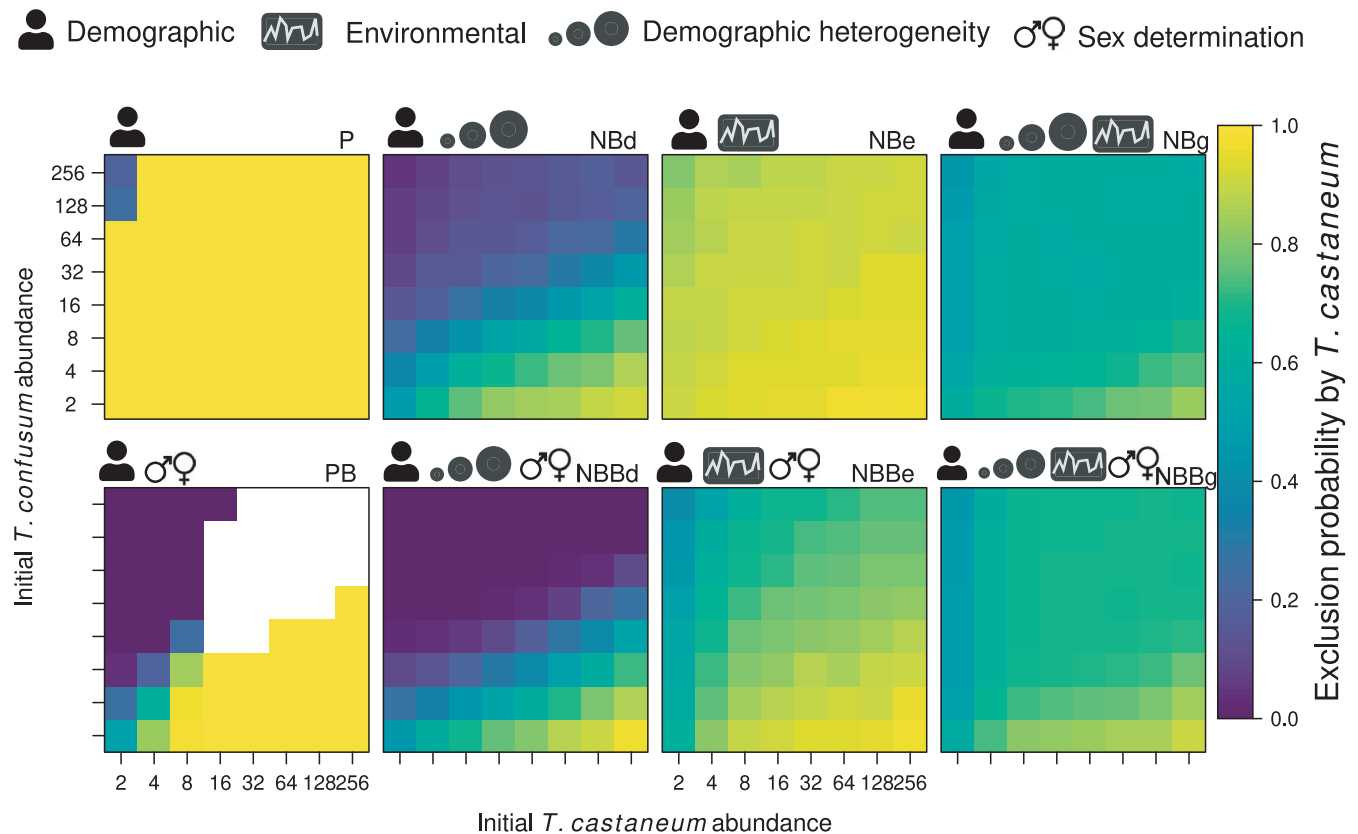
FIGURE 3 For two-species communities that did not coexist, competitive outcome depended on the combination of initial abundances and the way stochasticity was incorporated into models. Different forms of stochasticity are identified using glyphs in the figure legend. The colour gradient indicates the probability that *Triboliumcastaneum—S* in Equation1—excludes *Triboliumconfusum* (*F* in Equation 1). Areas in white correspond to situations where no competitive exclusion after 10 simulated generations across a total of 1,000 simulations. Stochastic sex determination was incorporated for the bottom row, while the top row did not include this form of stochasticity

combination of initial abundances of the competitors, suggesting that the interplay between abundance and stochasticity is especially important for understanding population and community dynamics. While the coexistence criteria for the deterministic two-species Ricker model were met, long-term coexistence in simulations of the best-fit stochastic model was rare. Further, for simulations where species did not coexist in the long term, the outcome of competition was sensitive to the initial abundance combination when stochastic processes were incorporated into the models. This work extends previous population-scale research on how various forms of stochasticity influence population dynamics and extinction to the community scale, demonstrating how multiple sources of stochasticity can reduce long-term co-occurrence and enhance competitive indeterminacy relative to a model with only demographic stochasticity incorporated in individual fecundity. Overall, our results suggest that this simple form of demographic stochasticity was insufficient to capture population and community processes, and that incorporating multiple forms of stochasticity can fundamentally change predicted competitive outcomes.

The best two-species model fit to the experimental data contained all forms of stochasticity examined (Table 1). The importance of one form of stochasticity, environmental stochasticity, is potentially a result of either microhabitat variation due to spatial position in the incubator or small variation in habitat quality through small differences in yeast content in the flour media. Insofar as natural populations generally experience far more environmental variability than was present in our laboratory system, it is reasonable to suppose that the effects of environmental stochasticity on community dynamics are even greater in nature (Mutshinda et al., 2009). The second form of stochasticity, stochastic sex determination, creates variation in sex ratio and birth rate by incorporating stochasticity in the proportion of females in a population. This form of stochasticity is especially important for small populations whose sex ratio could be more highly variable. Demographic heterogeneity—included in the best two-species model and *T. confusum* single-species model—is likely more important to natural populations than in the flour beetle experimental system for at least two reasons. First, as laboratory populations, they are highly inbred and thus may not exhibit substantial genetically determined differences in vital rates. Second, our experimental communities consisted of non-overlapping generations, which would have largely removed effects of stage or age structure. In natural populations, we would expect that differences could exist in vital rates across size, age or stage structures, and that this variation would likely be important in estimating co-occurrence and extinction likelihoods (Noonburg et al., 2015; Vindenes et al., 2008). Previous related research has

suggested that intraspecific trait variation can mediate coexistence (Hart et al., 2016); if this trait variation is related to vital rates, intraspecific trait variation is a form of demographic heterogeneity. However, if trait variation is measured, this variation could easily be incorporated into a deterministic approach.

In addition to identifying regions of initial competitor abundance that produced moderately high transient coexistence probabilities (Figure 2), our results also support a key role of initial competitor abundance in determining competitive outcome (Legault et al., 2019; Orrock & Watling, 2010). Our estimated coexistence probabilities aligned with previous *Tribolium* competition experiments (Figure 2), in which long-term co-occurrence was observed for particular combinations of initial competitor abundance (four *T. castaneum* and 32 *T. confusum*; Leslie, 1962; Park, 1957). This initial abundance combination corresponds to a region of high competitive indeterminacy (Figure 3) in our best-fit model simulations. Previous explanations for long-term co-occurrence in competitive *Tribolium* communities include the effects of environmental conditioning (Mertz et al., 1976) or genetic founder effects (Dawson, 1970; Goodnight & Craig, 1996; Mertz et al., 1976). However, in the absence of these effects, our model identifies a region of parameter space in which long-term co-occurrence is possible, and highlights the impact of different forms of stochasticity on co-occurrence potential. Further, the co-occurrence region identified by our best-fit two-species model is closely aligned with recorded co-occurrence dynamics in previous experimental studies (Leslie, 1962). Previously, genetic founder effects were found to be unimportant relative to demographic stochasticity (Mertz et al., 1976), though Goodnight and Craig (1996) found that community-level selection could influence coexistence, while the outcome of competition was not influenced by whether the two species had coexisted in previous generations. Our experiment examines a finer gradient of initial species abundances than previous studies (Leslie et al., 1968; Mertz et al., 1976) and supports the idea that stochasticity and initial competitor abundance combined can influence the outcome of competition, thus providing a simple putative explanation for previous findings of competitive indeterminacy (Leslie et al., 1968) that does not necessitate community-level heritability (Goodnight & Craig, 1996) or the effects of environmental conditioning (Mertz et al., 1976). Further, our populations were all seeded from the same stock populations, suggesting a limited role for genetic founder effects. Park (1957) suggested that sex-specific vital rates could also promote long-term co-occurrence. Differences in demographic rates between the sexes would correspond to a form of demographic heterogeneity, a source of stochasticity found to be relatively unimportant in our models.

Stochastic processes can strongly influence population and community dynamics, and incorporating multiple forms of stochasticity into existing models can provide further insight into both population (Melbourne & Hastings, 2008) and community (Adler & Drake, 2008) processes, with large potential implications to both basic understanding of species population dynamics and to conservation, restoration and management. With respect to natural communities, understanding the roles of various forms of stochasticity

on population dynamics, extinction and competitive outcomes in natural communities is a pressing need, especially in the face of a shifting climate, where environmental stochasticity may become more prominent. The fitting of stochastic models to experimental populations and data from natural populations is a useful tool, capable of providing insight into coexistence and competitive exclusion. This combination of theory and data can provide insight not only into co-occurrence and competitive indeterminacy, but also to our understanding of priority effects, in which the order of species arrival influences competitive outcome either through the sequestration of resources or through changes to the environment itself. In their efforts to combine a stochastic model with experimental data to predict competitive outcome, Leslie et al. (1968) stated that the 'wedding of theory with fact has added a new, though preliminary, dimension to the understanding of ecological phenomena'. Nearly 50 years later, we agree with their 'extravagant claim' and encourage the combination of stochastic modelling efforts with data from controlled experiments and natural populations.

AUTHORS' CONTRIBUTIONS

All the authors contributed to experimental design, manuscript editing and approval of the final draft. T.D. performed the analyses and drafted the manuscript.

DATA AVAILABILITY STATEMENT

Data and code from this study are available on figshare https://dx.doi.org/10.6084/m9.figshare.5593633 (Dallas et al., 2018).

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SUPPORTING INFORMATION

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