**RESEARCH ARTICLE**

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# When can competition and dispersal lead to checkerboard distributions?

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## Abstract

1. Checkerboard distributions—mutually exclusive species co-occurrences—are a common observation in community ecology and biogeography. While the underlying causes of checkerboard distributions have remained elusive, a long-standing argument is that they are representative of strong competitive interactions and/or dispersal limitation.

2. We explore this using a stochastic two-patch metacommunity model combined with an experimental two-patch system of competing *Tribolium* species, quantifying checkerboard distributions using the abundance-based index $A_{st}$.

3. We find that maintenance of checkerboard distributions is possible in a limited parameter space consisting of low dispersal rates, low population growth rates and high interspecific competition. Checkerboards were not maintained in experimental metacommunities.

4. Our model, parameterized using independent data, echoed this finding, providing a clear link between model and experiment, and suggested that only small regions of parameter space would allow for checkerboard distributions between patches with equally hospitable environments. These findings may provide insight into when interspecific competition and dispersal limitation would promote checkerboard distributions.

**KEYWORDS**
community assembly, co-occurrence, multispecies communities, mutual exclusion, *Tribolium*

## 1 | INTRODUCTION

Co-occurrence studies are common in the ecological literature, with the broad goal of providing insight into community assembly processes (Connor & Simberloff, 1983; Weiher, Clarke, & Keddy, 1998). However, this overall goal is in contrast with the multiple interpretations of co-occurrence patterns (Barner, Coblentz, Hacker, & Menge, 2018; Connor, Collins, & Simberloff, 2013). For instance, two species that occupy many of the same habitats (i.e. positively co-occur) may do so as a result of mutualistic interactions, dispersal limitation or similar environmental tolerances. Further, nonrandom co-occurrence patterns can result from neutral processes (Bell, 2005). The range of potential explanations for the pattern limits any potential insight into community assembly processes. While it is useful to identify how common nonrandom species co-occurrence patterns may be, the lack of theoretical development and experimental testing has stymied the understanding of what nonrandom species co-occurrences actually mean for ecological communities. Focusing on negative species co-occurrence patterns, the pervasive view that mutually exclusive species co-occurrences are a signature of competition has continued to persist in the ecological literature (Berry & Widder, 2014; He, Bertness, & Altieri, 2013; Sfenthourakis, Tzanatos, & Giokas, 2006), despite sound theory indicating that other processes can lead to the same pattern (Cazelles, Araújo, Mouquet, & Gravel, 2016; Ulrich, Jabot, & Gotelli, 2017).

Negative co-occurrence patterns are often referred to as *checkerboard distributions*, suggesting perfect reciprocal exclusion of species among sites, resulting in an alternating pattern of habitat patches occupied by one species and patches occupied by the other. The search for checkerboard distributions has lead to the development of many statistical measures (Griffith, Veech, & Marsh, 2016; Hastings, 1987; Stone & Roberts, 1990; Veech, 2014) and null model randomization approaches (Gotelli, 2000; Sanderson & Pimm, 2015), along with a multitude of observational studies using these statistical tools (Barner et al., 2018; Boschilia, Oliveira, & Thomaz, 2008; Gotelli & Rohde, 2002; Horner-Devine et al., 2007; Sfenthourakis et al., 2006). The idea that negative species co-occurrences infer competitive interactions—that observing a checkerboard indicates interspecific competition—has a historical legacy over 40 years old (Diamond, 1975). A nearly equally old objection to this idea is that environmental filtering could result in a checkerboard distribution in the absence of any species interactions (Connor & Simberloff, 1979). This suggests that checkerboard distributions can be the result of at least two different mechanisms. First, environmental differences could exist, and species are responding to unmeasured climatic or environmental variation (i.e. environmental filtering). Second, competition between species is strong enough to outweigh the effect of dispersal, such that colonization does not occur or colonists are kept at low frequency (Levin, 1974). Distinguishing between these two structuring mechanisms could provide insight into when checkerboard distributions would be expected or even be possible (Barner et al., 2018).

The theory behind the appearance of checkerboard patterns in uniform environments has basically taken two forms, with one using colonization and extinction dynamics and the other based on assuming that in any local patch there is contingent competition and dispersal is weak (Levin, 1974). Earlier work (Hastings, 1987) using patch occupancy models has convincingly shown that with the colonization—extinction mechanism even very strong competition will not lead to strong checkerboard patterns; in fact, the patterns produced are very difficult to distinguish from random. The other explanation based on weak dispersal (Levin, 1974) has been shown to lead to strong checkerboard patterns in a deterministic setting in the limit as the connectivity approaches zero, but both the role of stochasticity and how small connectivity really needs to be to sustain checkerboard distributions are much more difficult issues. Further, the theory underlying the maintenance of checkerboard distributions in heterogeneous environments is not well-developed. Incorporating existing theory on competition–colonization trade-offs may provide insight into so-called "supertramp" species—efficient dispersers but poor competitors—which may promote the formation and maintenance of checkerboard distributions (Sanderson & Pimm, 2015).

While many studies have investigated checkerboard distributions from observational data, it is impossible to distinguish between the two mechanisms listed above based solely on observational data. Further, observational studies testing for the existence of checkerboard distributions have greatly outpaced the development of theory aimed at determining when checkerboard distributions

would likely be observed. The lack of theoretical development and the inability for observational studies to distinguish between the two main putative causes of checkerboard distributions clearly identify an obtrusive knowledge gap. This gap is addressable through (a) the development of transparent multispecies models that account for dispersal and competitive processes, and (b) experimental examinations of species distributions in simplified landscapes (Schamp, Arnott, & Joslin, 2015), allowing for direct tests of each of the two main putative mechanisms. That is, observing checkerboard formation in a set of homogeneous habitat patches would suggest that environmental filtering did not strongly influence species distributions. On the other hand, manipulating species abundance among habitat patches could test the effects of competitive pressure on species colonization and the formation of checkerboard distributions.

Here, we address the potential for dispersal and interspecific competition to result in checkerboard distributions by pairing a theoretical model where we examine the effect of different levels of connectivity and competition with controlled and replicated experimental metacommunities. The development of the theoretical model permits an investigation into when checkerboard patterns would be expected, and how they are influenced by dispersal rates, competition and species abundance in each local habitat patch. The use of experimental metacommunities provides a demonstration of checkerboard formation, or the lack thereof, in a homogeneous landscape. We developed a stochastic two-patch Ricker model to investigate how checkerboard distributions are influenced by dispersal, population size, intraspecific/interspecific competition and population growth rates. We then test model predictions using an experimental system of two competing *Tribolium* species, finding clear agreement between model predictions and experimental metacommunities. Together, our findings suggest that the necessary strength of interspecific competition and limitation of dispersal may underlie the limited number of cases where empirical checkerboards can be observed in systems with equally hospitable habitats. Considering the rarity of equivalent intraspecific competitive forces, growth rates and dispersal probabilities between competing species in natural systems, it is unlikely that observed checkerboard distributions are maintained through interspecific competition, but perhaps more likely that historical contingency, strong dispersal limitation and habitat differences play a dominant role.

## 2 | MATERIALS AND METHODS

### 2.1 | Two-patch metacommunity model

We developed a spatially explicit, two-patch stochastic Ricker model to determine the conditions under which checkerboard distributions are possible. Specifically, we investigated the influence of dispersal, competition and initial population sizes on resulting spatial distribution and formation of checkerboard distributions. The discrete time model was broken into two phases—growth and dispersal— separated by a small unit of time *h*. During the growth phase, populations of species *S* and *F* grow according to growth

rate ($R_S$ and $R_F$), where population size in the next generation is constrained by intraspecific ($\alpha_{SS}$ and $\alpha_{FF}$) and interspecific ($\alpha_{SF}$ and $\alpha_{FS}$) competition.

$$S_{i,t+h} = S_{i,t}R_S e^{-(\alpha_{SS}S_t + \alpha_{SF}F_t)}$$
$$F_{i,t+h} = F_{i,t}R_F e^{-(\alpha_{FF}F_t + \alpha_{FS}S_t)} \tag{1}$$

During the dispersal phase, individuals of each species emigrate from their resident patch at a density-dependent rate $d_S$ or $d_F$.

$$S_{i,t+1} = S_{i,t+h} - S_{i,t+h}d_{S,i} + S_{j,t+h}d_{S,j}$$
$$F_{i,t+1} = F_{i,t+h} - F_{i,t+h}d_{F,i} + F_{j,t+h}d_{F,j} \tag{2}$$

Stochasticity was incorporated as pure demographic stochasticity (number of births as a Poisson random variable, number of deaths as binomial process), environmental stochasticity (gamma distribution of birth rates among patches and times representing density-independent variation), demographic heterogeneity (gamma distribution of birth rates among individuals, representing intrinsic variation among individuals) and stochastic sex determination (number of female offspring is a binomial random variable with probability 0.5). This corresponds to the full model (referred to as the NBBg model in Dallas, Melbourne, and Hastings (in review); Melbourne and Hastings (2008)). Further information about model development is provided in Dallas et al. (in review) and Melbourne and Hastings (2008), which focus on local population and community dynamics as a function of stochasticity.

For a perfect checkerboard distribution to be maintained, the force of dispersal must be countered by the inhibitory effects of intraspecific and interspecific competition. That is, the reproductive potential of individuals of species $S$ into patch $i$ (immigration from patch $j$ minus emigration from patch $i$) must be less than or equal to the force of intraspecific ($\alpha_{SS}$ and $\alpha_{FF}$) and interspecific ($\alpha_{SF}$ and $\alpha_{FS}$) competition present in patch $i$ (Equation 3).

$$S_{j,t+h}d_{S,j} - S_{i,t+h}d_{S,i} \leq \alpha_{SS}S_t + \alpha_{SF}F_t$$
$$F_{j,t+h}d_{F,j} - F_{i,t+h}d_{F,i} \leq \alpha_{FF}F_t + \alpha_{FS}S_t \tag{3}$$

While dispersal in our simulations is not a function of species density, future experimental work will help estimate the shape of the likely density-dependent dispersal rate, though it is unlikely that this will strongly influence our results.

## 2.2 | Checkerboard statistic calculation

For each two-patch metacommunity, we calculated the probability of adult dispersal and the abundance-based checkerboard statistic. Metacommunities can be represented as a 2 × 2 square matrix (Equation 4), in which matrix rows represent local habitat patches, and matrix columns represent abundances of each species at each site. The two species ($F$ and $S$) can exist in either site (subscripts 1 or 2 in Equation 4).

$$\begin{bmatrix} F_{1,t} & S_{1,t} \\ F_{2,t} & S_{2,t} \end{bmatrix} \tag{4}$$

From this representation of species abundances in the metacommunity, we can calculate a statistic that captures to what extent species are partitioning the landscape as a result of the combined effects of dispersal and competition. We used the abundance-based checkerboard statistic $A_{st}$ (Ulrich & Gotelli, 2010), which in the two-patch, two-species case is

$$A_{st} = \sqrt{\frac{(F_{1,t} - F_{2,t})^2 + (S_{1,t} - S_{2,t})^2}{F_{1,t}^2 + S_{1,t}^2 + F_{2,t}^2 + S_{2,t}^2}} \tag{5}$$

This statistic is bounded between 0 and 1, where values of 0 indicate a completely even and mixed distribution of species abundances across the landscape, where both species coexist in one or both habitat patches (e.g. one habitat patch could contain zero individuals of either species), and values of 1 indicate perfect mutual exclusion, where each species inhabits one habitat patch exclusively.

## 2.3 | The effect of dispersal and competition on checkerboard distributions

To explore the maintenance of checkerboard distributions, we simulated our two-species stochastic Ricker model 1,000 times for each combination of interspecific competitive effect ($\alpha_{SF}$ and $\alpha_{FS}$) between 0.001 and 0.1. This was performed for four different dispersal rates, where we consider dispersal rates of both species to be equal ($d_S = d_F = 0.01, 0.05, 0.1$ and $0.15$), representative of dispersal rates seen in natural populations of plant (Pakeman, 2001) and animal (Ibrahim, Nichols, & Hewitt, 1996) species. For this exercise, we considered species to be equivalent in density-independent population growth rates ($R_S = R_F = 2$), intraspecific competition ($\alpha_{SS} = \alpha_{FF} = 0.001$) and initial abundance ($S_t = F_t = 20$). Simulations began from a perfect checkerboard—equivalent to our experimental landscapes—with each habitat patch containing individuals of one species. Simulations in which long-term co-occurrence was observed—defined here as both species persisting past 10 generations—were considered here, as the checkerboard statistic ($A_{st}$) is interpretable only with two or more coexisting species. However, extinction of either species was rare, occurring in <2% of model simulations on average.

## 2.4 | The effect of initial abundance and species growth rates on checkerboard distributions

Next, we investigated the effect of species abundance and density-independent growth rates on the maintenance of checkerboard distributions, maintaining the same dispersal rate and intraspecific competition coefficients used above, and setting interspecific competition equal to intraspecific competition (i.e. species have the same effect on one another as they do on a competitor). We simulated this model 1000 times for every possible combination of initial abundance for the two species from one to 200 individuals, for a set of three different density-independent growth rates ($R_S = R_F = 0.9, 3$, and 6). Simulations lasted 10 generations and began from a perfect checkerboard—equivalent to our experimental landscapes—with each habitat patch containing either

species. We examine the effect of initial species abundance distributions in the Supplemental Materials by simulating metacommunities with both species initially in the same patch.

## 2.5 | Experimental metacommunities

Flour beetles (*Tribolium* species) are a classic model system to examine species interactions, competitive exclusion and coexistence (Edmunds et al., 2003; Jillson & Costantino, 1980; Leslie, Park, & Mertz, 1968; Park, 1948, 1954). As an experimental system, flour beetles provide an ideal test of the maintenance of checkerboard distributions, as their resource and habitat are the same (flour media), age effects can be controlled for by enforcing nonoverlapping generations, and habitats can be replicated extensively. Furthermore, life history and competition parameters are well known in this system based on both foundational (Leslie et al., 1968; Park, 1948) and contemporary (Szűcs et al., 2017; Weiss-Lehman, Hufbauer, & Melbourne, 2017) experiments, demonstrating the potential for both competitive exclusion and competitive indeterminacy (Edmunds et al., 2003). Lastly, the Ricker modelling framework discussed above has been previously applied to single species *Tribolium* populations, establishing a link between theoretical model and experimental data (Melbourne & Hastings, 2008).

Two flour beetle species (*Tribolium castaneum* and *T. confusum*) were obtained from laboratory populations maintained in $4 \times 4 \times 6\,cm$ enclosures partly filled with 30 ml of flour medium (95% enriched white flour and 5% brewer's yeast). Stock populations were maintained at 30°C and approximately 50% relative humidity. Nonoverlapping generations were enforced by allowing adults to lay eggs in fresh standard medium for 24 hr. After this period, adults were removed and discarded while eggs and flour were kept and allowed to develop to adulthood. Species could be readily identified by colour, as *T. castaneum* are black and *T. confusum* are rust red in colour.

Two-patch landscapes were connected by a smaller hole (around 2 mm diameter) connected to a slightly larger hole (3 mm diameter) to ensure alignment of patches. Adults were censused before and after being allowed to disperse and lay eggs for 24 hr, allowing us to estimate adult dispersal probability. After this period, adult beetles were sieved and discarded, and resulting eggs were kept at 30°C and allowed to develop for a 5 week generation period. Experimental trials were started by placing 20, 40 or 80 *T. castaneum* or *T. confusum* individuals in either side of the two-patch landscape. Ten replicate landscapes per initial abundance combination were established, giving a total of 90 two-patch landscapes.

To link our stochastic two-patch Ricker model with our experimental trials, we simulated the model for 10 generations using parameter estimates from previous experiments in the laboratory (Dallas et al. (in review); Melbourne and Hastings (2008); Supporting information Table S1). Dispersal was estimated from the current experiment, as dispersal rate could be reliably estimated since we counted beetles both before and after the dispersal phase of each generation. Model parameters are provided in Supporting information Table S1.
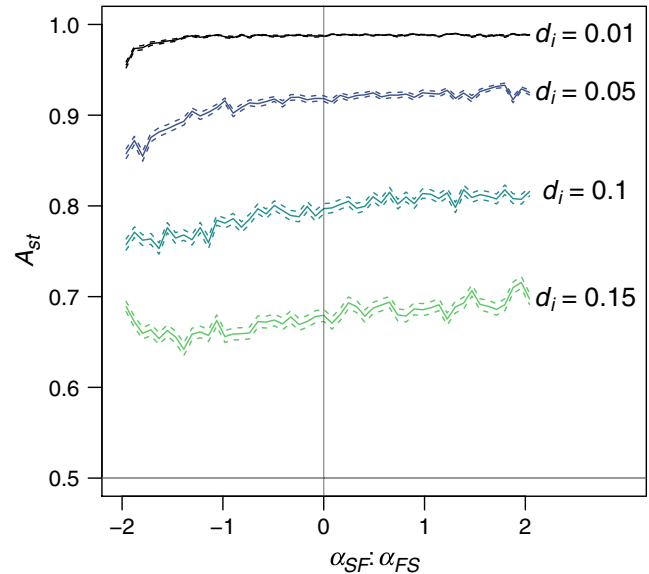


**FIGURE 1** The balance of interspecific competition ($\alpha_{SF}$:$\alpha_{FS}$) did not strongly influence the checkerboard statistic ($A_{st}$; y-axis) relative to the influence of dispersal ($d_i$). Here, values of 0 correspond to equal competitive ability ($\alpha_{SF} = \alpha_{FS}$), while negative and positive values correspond to competitive dominance of either species (e.g. a value of −2 occurs when $\alpha_{FS}$ is twice that of $\alpha_{SF}$). This assumes species equivalence in intraspecific competition and growth rates. We examine a broader range of interspecific competition coefficients in the Supporting information Appendix S1

# 3 | RESULTS

## 3.1 | Model simulations

### 3.1.1 | The effect of dispersal and competition on checkerboard distributions

When dispersal was very low for competing *Tribolium* species ($d_i = 0.01$), checkerboard distributions were maintained for 10 generations at nearly all levels of interspecific competition (Figure 1, Supporting information Figure S5). However, under modest increases in dispersal rates ($d_i = 0.05$), the checkerboard statistic ($A_{st}$) quickly deteriorated, except when interspecific competition was nearly symmetric and strong ($\alpha_{SF} = \alpha_{FS} > 0.09$). Further, this is simply a test of checkerboard pattern maintenance, not formation, as checkerboards were enforced at the start of the experiment and for the simulations (but see the Supplemental Materials for exploration of the effect of different initial species distributions). Checkerboards were potentially maintained in situations of very low dispersal and strong interspecific competition as a result of initial conditions, as we artificially established species in a perfect checkerboard before allowing dispersal. However, for higher dispersal rates, we observed a rapid reduction in the checkerboard statistic ($A_{st}$) caused by dispersal of both species between habitat patches (Supporting information Figure S8). The dissolution of checkerboard distributions appears to be insensitive to differences in interspecific competitive effects and
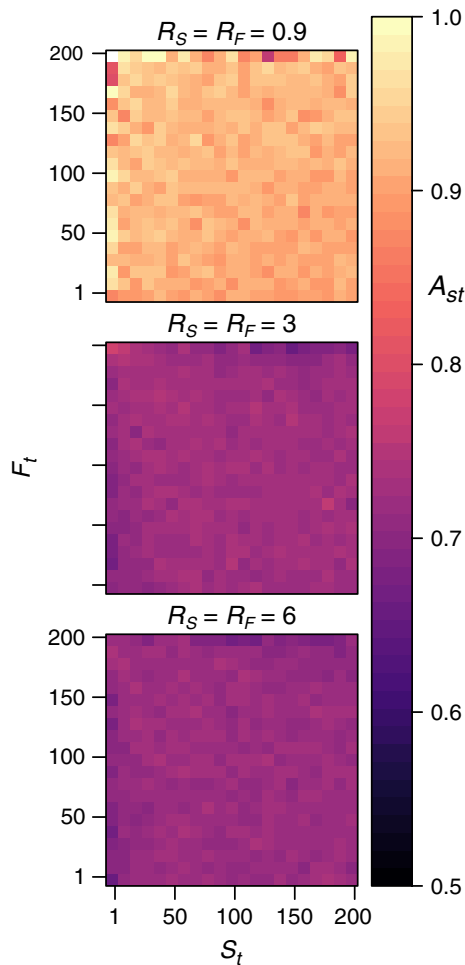
**FIGURE 2** Low population growth rates ($R_S$ and $R_F$) promoted the maintenance of checkerboard distributions, while initial species abundance of *Tribolium castaneum* ($S_t$) or *T. confusum* ($F_t$) did not strongly influence our checkerboard statistic ($A_{st}$; indicated by colours)

dispersal rates (see Supporting information Appendix S1). However, we note that at very low dispersal rates, which are perhaps representative of some species at biogeographic scales, checkerboard distributions may be maintained regardless of competitive strength or initial abundance.

### 3.1.2 | The effect of initial abundance and species growth rates on checkerboard distributions

In model simulations, the maintenance of checkerboard distributions was unaffected by species initial abundance (Figure 2). However, increasing species growth rates reduced $A_{st}$, as increasing population sizes facilitated dispersal dynamics that were unable to be countered by the force of interspecific competition. We also explored whether initial abundance and population growth rates would have a stronger affect on long-term co-occurrence dynamics if populations of species were initially placed in the same patch and allowed to colonize the empty patch. The dynamics and resulting values of $A_{st}$ were quite similar, suggesting that a stable distribution of abundance in the two

sites was reached by generation 10 (Supporting information Figure S7). Moreover, simulations with both species in the same initial patch and equal species abundance in both patches demonstrated that similar $A_{st}$ values were obtained relative to simulations where species were initially in opposing patches, further suggestive of an achieved equilibrium distribution of abundance (Supporting information Figure S8).

### 3.2 | Experimental findings

By the end of the second generation, values of $A_{st}$ had halved from their initial values, suggesting that—assuming qualitatively similar dynamics for both species—there were approximately half of the individuals of each species in the neighbouring patch as were in the initial patch (see Supporting information Figures S1–S4 for species abundances in two-patch metacommunities). The rapid decline in the checkerboard statistic over the course of two generations suggests that the forces of dispersal were much larger than the resisting force of interspecific competition. Combinations of initial abundances of species did not influence the decay in checkerboard distributions (Figure 3). Given the high dispersal rates observed, it is unlikely that checkerboard distributions would be maintained by small population sizes, as this would serve more to promote stochastic local extinction than competitive spatial co-occurrence.

The model simulations—with species dispersal rates parameterized from the first generation of the experiment—were quite similar to experimental observations (Figure 3), providing support for the ability of our theoretical model to capture real-world dynamics. Co-occurrence—both species persisting up to 10 generations—was observed for the vast majority of simulations. Matching theoretical predictions, realistic values of interspecific competition obtained from a previous experiment ($\alpha_{SF}$ = 0.011, $\alpha_{FS}$ = 0.006; Dallas et al., in review) was unable to prevent the successful invasion of both species into neighbouring patches given dispersal rates of both species estimated from experimental data ($d_S$ = 0.24, $d_F$ = 0.13). Further, the decay of the checkerboard statistic ($A_{st}$) over generation was unaffected by species abundance combination (Figure 4), echoing results from our model simulations (Figure 2).

## 4 | DISCUSSION

Checkerboard distributions are a fairly common observational finding (Boschilia et al., 2008; Gotelli & Rohde, 2002; Horner-Devine et al., 2007; Sfenthourakis et al., 2006), with at least two posited—and thoroughly debated (Connor, Collins, & Simberloff, 2015; Connor et al., 2013; Diamond, Pimm, & Sanderson, 2015) —putative mechanisms. The first, conceptualized after observing bird distributions in an island system (Diamond, 1975), argued that checkerboard distributions resulted from interspecific competition and assumed that habitat patches were environmentally homogeneous. The second, in response to the potential boldness of inferring competition from observational data and assuming homogeneous environmental
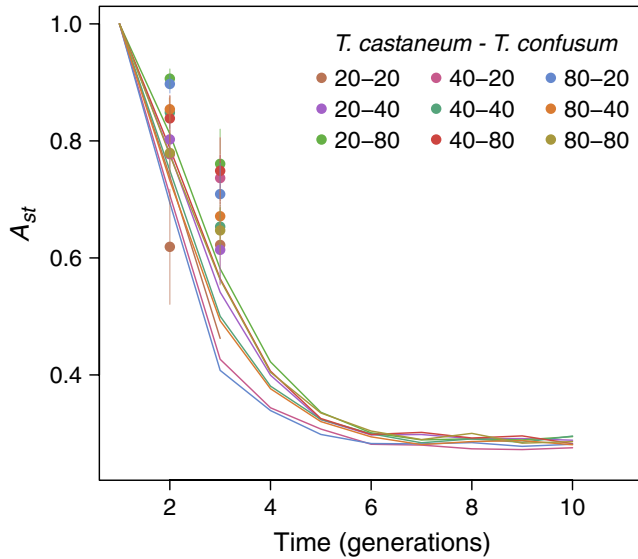
**FIGURE 3** Expected saturation of checkerboard statistic $A_{st}$ from 1,000 model simulations (lines represent mean dynamics) of each initial abundance combination (colours and legend) qualitatively agrees with our experimental findings (points and standard error bars), suggesting that both habitat patches are colonized by both species and that interspecific competition only has a weak effect in determining species abundances



**FIGURE 4** Model simulations (left column) qualitatively support the finding of experimental trials (right column) that the checkerboard statistic ($A_{st}$; indicated by colours) decays rapidly. Though initiated as a perfect checkerboard ($t = 0$; top row), values for $A_{st}$ decreased sharply by the end of the first generation ($t = 1$; middle row) and even further by the second generation ($t = 2$; third row)

conditions, argues that differences between habitats in climate, community composition and resource abundance are all equally likely to cause observed co-occurrence patterns (Connor & Simberloff, 1979). Several recent studies have failed to detect checkerboard patterns in empirical data (Barner et al., 2018; Ulrich & Gotelli, 2013), suggesting that checkerboards may be rare. Here, we demonstrate why this could be, by using a theoretical two-patch model combined with a series of replicated experimental metacommunities to characterize the dispersal and competition parameters, necessary to produce and maintain checkerboard distributions.

By controlling species interactions, dispersal dynamics and population growth rates, we provide a robust test of how an abundance-based measure of checkerboard distributions changes under a variety of conditions. It is important to note that typical examinations of checkerboard distributions search for ``true checkerboards,'' corresponding to mutually exclusive occurrence. Under this more stringent checkerboard criterion, we would have never observed checkerboard distributions given the range of species population growth rates, dispersal functions and competitive effects. Using our abundance-based measure of checkerboard tendency, we found low dispersal (1–5 dispersers out of 100 individuals) and high interspecific competition ($\alpha_{ij} > 0.05$) were key to maintain large values of the checkerboard statistic ($A_{st}$). This agrees with previous theoretical findings suggesting that mutual exclusion in two-patch metacommunities was a stable equilibrium, even with nonzero dispersal rates (Levin, 1974). Our work builds on this finding by critically examining levels of competition and connectivity that would lead to checkerboard patterns in a stochastic setting: How robust are the conclusions to varying the assumption of arbitrarily small
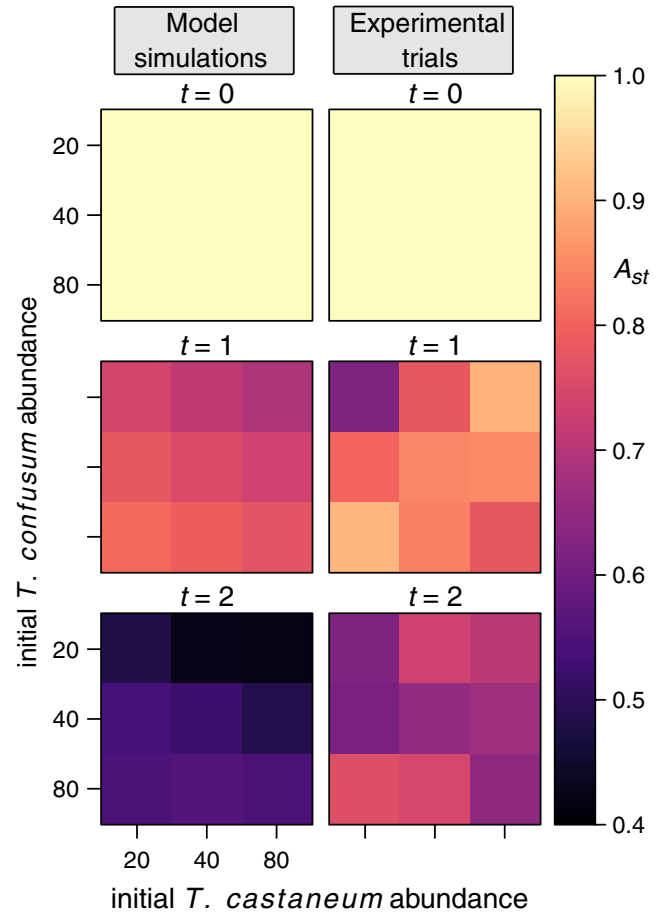
connectivity? Experimental populations of two *Tribolium* species—known to compete strongly through both resource competition and cannibalism (Park, 1948, 1954) —demonstrate both the speed at which checkerboard distributions may collapse and the utility of our model in capturing ecological dynamics. Together, our combination of experiment and model simulations suggest that interspecific competition—aside from rare scenarios—may not be generally strong enough to result in long-term mutual exclusion.

While interspecific competition is unlikely the underlying cause of checkerboard distributions, the fact remains that checkerboard patterns have been documented across a diverse set of systems, including communities of microbes (Koenig et al., 2011), parasites (Gotelli & Rohde, 2002), fish (Bhat & Magurran, 2007; Fernandes, Gomes, Pelicice, & Agostinho, 2009), aquatic macrophytes (Boschilia et al., 2008) and ectomycorrhizal fungi (Kennedy, 2010). Given that checkerboard distributions are commonly observed, what is the underlying mechanism that produces such distributions? Several putative explanations for the lack of colonization by competing species exist, including hypotheses related to Allee effects (Veit & Lewis,

1996), regional allopatry (Simberloff & Collins, 2009) and geological history (Simberloff & Collins, 2009). These explanations, as well as the role of founder effects, environmental filtering and interactions with other community members, are all possible mechanisms underlying the observed checkerboard distributions in natural systems. Further, while interspecific competition is unlikely to be strong enough to result in checkerboard distributions, competition may have the ability to influence geographic range limits of interacting populations (a closely related problem; Godsoe et al., 2017; Price & Kirkpatrick, 2009). This suggests that a suite of influences may lead to checkerboard distributions in natural systems, though it appears that interspecific competition is unlikely to be the root cause.

Despite the amount of observational evidence in support of checkerboard distributions, theoretical development and experimental testing of the many putative mechanisms capable of creating checkerboard distributions have lagged considerably. Large-scale patterns observed in binary site-by-species matrices, such as the checkerboard distribution, facilitated the advent of null model randomization techniques and lead to a lasting scientific debate (Harvey, Colwell, Silvertown, & May, 1983). However, null model randomizations are far from the only approach to examine distributional patterns. We provide a more mechanistic approach to understanding checkerboard distributions by combining a simple theoretical model and a controlled experiment to explore how abundance-based checkerboard statistics change under different values of competition, dispersal and population growth rates. There are numerous possible extensions to this work, including the incorporation of variability in habitat size or quality, inclusion of more than two competing species and the examination of more complex spatial structures of interconnecting patches. This work provides a theoretical basis for further explorations of checkerboard formation and suggests that small windows of parameter space may promote species mutual exclusion. Together, this provides a potential explanation for the mixed support for checkerboard distributions in sets of equally hospitable habitats and encourages further testing of when checkerboard distributions would be expected to be maintained.

## AUTHORS' CONTRIBUTIONS

All authors contributed to experimental protocol development. T.A.D. performed the simulations and statistical analyses. T.A.D. drafted the manuscript. All authors contributed to manuscript editing and approved the manuscript prior to submission.

## DATA ACCESSIBILITY

Data and R code to reproduce manuscript analyses are available on Figshare: https://doi.org/10.6084/m9.figshare.6839918 (Dallas, Melbourne, & Hastings, 2018).

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## SUPPORTING INFORMATION

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