Habitat-mediated carry-over effects lead to context-dependent outcomes of species interactions

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Summary

1. When individuals disperse, their performance in newly colonized habitats can be influenced by the conditions they experienced in the past, leading to environmental carry-over effects. While carry-over effects are ubiquitous in animal and plant systems, their impact on species interactions and coexistence are largely ignored in traditional coexistence theory.

2. Here we used a combination of modelling and experiments with two competing species to examine when and how such environmental carry-over effects influence community dynamics and competitive exclusions.

3. We found that variation in the natal habitat quality of colonizing individuals created carry-over effects which altered competitive coefficients, fecundity and mortality rates, and extinction probabilities of both species. As a consequence, the dynamics of competitive exclusion within and across habitat types was contingent on the natal habitat of colonizing individuals, indicating that spatial carry-over effects can fundamentally alter the dynamics and outcome of interspecific competition.

4. Interestingly, carry-over effects persistently influenced dynamics in systems with interspecific competition for the entire duration of the experiment while carry-over effects were transient and only influenced initial dynamics in single-species populations. Thus carry-over effects can be enhanced by species interactions, suggesting that their long-term effects may often not be accurately predicted by single-species studies.

5. Given that carry-over effects are ubiquitous in heterogeneous landscapes, our results provide a novel mechanism that could help explain variation in the structure of natural communities.

Key-words: carry-over effects, community structure, competition, competition model, condition dependence, demography, natal habitat effect, parental effects, phase plane, *Tribolium*

Introduction

Identifying which factors determine the coexistence or exclusion of interacting species has been a perennial challenge in ecology (Elton 1946; Chesson 2000). Classical theory typically assumes that species traits are fixed in a given environment (MacArthur 1955; Hutchinson 1959). While this framework suggests that community structure within a given environment should be constant, this prediction is at odds with the empirical data indicating that community structure can differ substantially within a given environment (Chase 2003). Traditionally, this discrepancy has been attributed to differences in the timing or density of species arriving to an environment, that is to variation in the history of community assembly (Chase 2003; Fukami 2004; Melbourne *et al.* 2007; Hufbauer *et al.* 2013; Rasmussen, Van Allen & Rudolf 2014). However, differences in coexistence could instead arise due to differences in the phenotype of colonizing individuals. Phenotypic variation within species is increasingly recognized as having the potential to alter population dynamics and species interactions (Prout & McChesney 1985; Miner *et al.* 2005; Conrad *et al.* 2011; Bolnick *et al.* 2011; Pruitt 2012; Dibble, Hall & Rudolf 2014), but how it affects community assembly and coexistence is poorly understood (Agrawal *et al.* 2007).

The phenotype of individuals can be shaped in large part by the conditions they experienced during development (Pechenik 2006; Monaghan 2008; Burton & Metcalfe 2014). When these individuals move to a new location, they carry over some portion of these traits (Benard & McCauley 2008). Such environmental

carry-over effects can arise through constraints on development, for example those caused by nutrient stress, or through adaptive plasticity, such as behaviours for making the best of a particular environment (Monaghan 2008; Harrison *et al.* 2010). An important distinction between carry-over effects and other sources of phenotypic variation is that they are specific to the case when phenotypic variation is caused by past experiences in another location, and thus, carry-over effects have a distinct spatial and temporal component (Benard & McCauley 2008; O'Conner *et al.* 2014). Carry-over effects are ubiquitous across taxa, ranging from bryozoans (Burgess & Marshall 2011) to birds (Duckworth 2009), and frogs (Van Allen *et al.* 2010) to elephants (Lee *et al.* 2013), and continue to affect performance, and sometimes the performance of offspring through parental or maternal effects, in novel environments through lifetimes (Harrison *et al.* 2010; O'Conner *et al.* 2014).

Increasing evidence indicates that carry-over effects can alter population dynamics by affecting traits such as fecundity, survival, dispersal behaviour and intraspecific interactions (Lindstrom & Kokko 2002; Plaistow, Lapsley & Benton 2006; Van Allen & Rudolf 2013; Van Allen & Bhavsar 2014), but little is known about how they affect species interactions and community assembly (Benard & McCauley 2008). Many of these traits which carry-over effects frequently alter are also important for species interactions such as competition, suggesting that carry-over effects could alter the dynamics and outcomes of competitive interactions and thereby change the conditions for coexistence or exclusion of interacting species (Rossiter 1996; Pechenik 2006; Duckworth, Belloni & Anderson 2015).

We tested the hypothesis that carry-over effects can alter the dynamics and outcome of competition with a multi-generational experiment manipulating the natal (past) and current habitats of two species of flour beetle (*Tribolium* spp.). The two species, *Tribolium castaneum* and *Tribolium confusum,* are a classic pair of competing species for which competitive dominance for any two given strains is determined by both environmental quality and initial density (Park, Leslie & Mertz 1964; Leslie, Park & Mertz 1968). We specifically predicted that environmental carry-over effects could alter this relationship between initial density and competitive dominance within a given environment. Consistent with our predictions, we found that carry-over effects of natal habitat quality dramatically altered competitive dominance and that the direction and strength of effects were driven by the interplay between natal and current habitats. Furthermore, we generate phase planes using competition models parameterized with single-species data and our competition experiments to show how carry-over effects introduced context dependence into competitive dominance within environments. Given that carry-over effects are ubiquitous in heterogeneous landscapes, our results provide a

mechanism that could help explain variation in the structure of natural communities.

Materials and methods

STUDY ORGANISMS

The flour beetles *T. castaneum* and *T. confusum* are cosmopolitan pests of stored grains and dry goods. *Tribolium* develop from egg to adult in approximately 1 month in high-quality habitat. *Tribolium* species can live and continuously reproduce for months after reaching adulthood (Walter 1990). In addition to dry goods, adults and larvae of both species readily consume conspecific and heterospecific eggs and pupae (Park *et al.* 1965).

The type (quality) of flour habitat in which larvae develop strongly influences larval development and the phenotypes of adults (Van Allen & Rudolf 2013). Following previous studies (Van Allen & Rudolf 2013), we used wheat media (94·5% organic white flour, 5% brewer's yeast) as high-quality habitat and oat media (99·5% organic oat flour) as low-quality habitat for both species of flour beetle. Oat flour is a very challenging habitat for *T. castaneum* (Via 1999), while *T. confusum* copes relatively well with low-quality habitat, but its population performance in oat flour has not been assessed to our knowledge. Both media contained 0·5% Fumagillin B to prevent epidemics of pathogenic fungal parasites. Recent studies indicate that the phenotypic changes caused by development on wheat or oat can lead to long lasting carry-over effects which alter the population dynamics of flour beetles in the same or the other flour type (Van Allen & Rudolf 2013; Van Allen & Bhavsar 2014). In *T. castaneum,* oat flour natal habitat reduces larval survival, development rates and size at metamorphosis, but increases adult cannibalism rates and adult longevity in oat flour (but shortens it in wheat flour; Van Allen & Rudolf 2013). In addition, these changes appear to carry over into the next generation as offspring of females who developed in oat flour appear to show some of these same feature even when developing in wheat flour (Van Allen & Rudolf 2013).

We acquired *T. confusum* from the United States Department of Agriculture (USDA) Agricultural Research Service station at Kansas State University and *T. castaneum* from B. Melbourne at the University of Colorado (RR strain). We kept beetle stocks on 60–70 g of wheat flour in environmental chambers (28–31°C and 10–30% humidity) for at least two generations, with each generation started by approximately 500 randomly selected eggs in a new container. To create populations that differed in natal habitats for each species for the experiment, we collected eggs from these stock colonies to start new laboratory stock colonies (with the same methods) in both wheat and oat flour. We collected adults under 1-month old from these colonies to initiate our experiments.

EXPERIMENTAL DESIGN

To explore the implications of carry-over effects for competitive interactions, we conducted a factorial experiment that manipulated the natal (past) and current habitat quality for both of our study species. Both single- and two-species current habitat venues consisted of clear plastic vials filled with 6 g. of either oat or wheat flour held in environmental chambers (29–31°C and 25–30% humidity, constant darkness).

SINGLE-SPECIES TREATMENT

We set up single-species populations for each species to quantify population performance in the absence of interspecific competition. We added two males and two females, from either wheat or oat flour stock colonies, into either wheat or oat flour to produce 2 (natal habitat quality, oat vs. wheat) × 2 (current habitat quality, oat vs. wheat) factorial single-species treatments. We replicated each single-species treatment four times, for 32 total experimental populations (16 per species).

INTERSPECIFIC COMPETITION TREATMENT

We estimated how carry-over effects changed each species competitive performance and coexistence conditions for *T. castaneum* and *T. confusum* by independently manipulating the current habitat (i.e. habitat in which competition took place, oat or wheat) and natal habitat (i.e. habitat in which individuals developed, oat or wheat) for both species. We generated carry-over effects by performing the same cross between oat and wheat flour as in the single-species treatment, but for both species resulting in a 2 × 2 × 2 set of natal and current habitat combinations (2 natal habitats for *T. castaneum* × 2 natal habitats for *T. confusum* × 2 current habitat patch qualities). This design allowed us to examine how carry-over effects in two species influence competitive dynamics across two contexts of current environmental quality.

Because relative initial densities of both species are known to determine which species is competitively excluded in this system (Leslie, Park & Mertz 1968), we varied initial densities for each species within these eight factorial habitat combinations to better infer changes to coexistence in our model (Inouye 2001). Previous work suggests that *T. confusum* can become competitively dominant to *T. castaneum* when *T. castaneum* initial density is four and *T. confusum* initial density is between 32 and 40. However, this pattern has only been established in wheat and from wheat habitat, and it was unknown how this pattern will change in our other seven natal:current treatment combinations. Thus, to examine where the switch in competitive dominance occurs in different habitat combinations, we established two gradients: first, *T. confusum* density varied across 4, 8, 16, 24, 32, 40 and 64 adult beetles while *T. castaneum* density constant was held constant at four individuals. The second gradient held *T. confusum* density constant at eight, but varied *T. castaneum* density across 4, 8 and 16 beetles. The gradient varying *T. castaneum* density was established because *T. confusum* performance declines more slowly in low-quality habitat than it does for *T. castaneum*, though by how much in oat flour we did not know, meaning it could be a superior competitor in oat (Sokoloff *et al.* 1966; Nathanson 1975). Note that one initial density combination, four *T. castaneum* and eight *T. confusum*, exists in both gradients leaving nine total density combinations. To reduce stochastic variation in sex ratio at low initial densities, up to the first eight beetles of each species entering an experimental replicate were an even mix of male and female beetles with the remainder randomly selected. The natural sex ration of flour beetle populations is 50–50 (Van Allen & Rudolf 2013). In total, this resulted in 2 current habitat qualities × 2 natal habitat qualities for *T. castaneum* × 2 natal habitat qualities *T. confusum* × two gradients of 9 total density combinations, with 18 replicates of each factor combination and doubled replicates of each density combination for a total of 144 populations. Note that our density gradients are treated as continuous covariates in all analyses, making this experiment a replicated regression design (Cottingham, Lennon & Brown 2005). Both single-species and interspecific competition treatments were set up simultaneously.

EXPERIMENTAL METHODS

All single-species and competition populations were checked every 30 days. During each check, we used sifters to separate the conditioned flour from all stages of the *Tribolium* life cycle, which were then examined to ensure that no parasites were affecting the population. We counted mature adults of each species since larvae, pupae and eggs are difficult to identify to species. Dead adults were counted and removed and all other individuals, including juveniles and eggs, were returned to their containers with fresh flour. This census protocol follows previous studies (Park 1948; Leslie, Park & Mertz 1968) and allowed us to quantify adult population sizes, recruitment rates into the adult stage and death rates of adult flour beetles of both species. For example, if we counted ten living adults and eight dead adults, then 18 total adults were alive between this check and the previous check. Therefore, the death rate was $8/18 = 0.444$. Six checks were performed after the competition, and single-species experiments were initiated, allowing for roughly six egg to adult development times in wheat flour and four in oat flour.

ANALYSIS

We used two approaches to examine how carry-over effects influence population dynamics and competitive performance of species across our two current habitat types. First, we used generalized linear models (GLMs) to determine whether carry-over effects significantly changed long-term population dynamics. For this, we examined mean population abundances across the last 4 months of both single-species and competition experiments. We also examined how carry-over effects altered differences in the risk of extinction during the experiment. Secondly, we used our full experiment population time series of six monthly checks to parameterize a dynamic model of flour beetle competition with and without carry-over effects, which allowed us to generate phase planes to visually inspect the long-term impacts of carry-over effects on competitive dominance.

SINGLE-SPECIES POPULATION PERFORMANCE

While we performed the single-species population experiments for each species primarily to model single-species growth and limitation terms (see Model Fitting), we also examined whether carry-over effects had a lasting influence on population size by comparing the log-transformed mean of the final 4 months of adult abundance for each species separately using GLMs with Gaussian errors. For each model, we fit fixed effects of natal habitat quality (two levels) and current habitat quality (two levels).

OVERALL COMPETITIVE PERFORMANCE

For each species, we first tested how carry-over effects influence their mean population size over the last 4 months of the

competition experiment. We used GLMs with Gaussian errors, fit separately for each species, with fixed effects of the natal habitat, the current habitat type and continuous covariates of initial density of *T. confusum* (along the gradient holding *T. castaneum* density constant at four), and the initial density of *T. castaneum* (along the gradient holding *T. confusum* density constant at eight) and all possible interactions except for the interaction between both density gradients as they were not factorially implemented. Both density gradients were treated as continuous variables. Because we were interested in persistent and not transient effects, we used the log-transformed mean of the last 4 months of adult density measurements within a replicate as dependent variable in our GLMs to test whether different treatments led to long-term changes in mean population size. For all statistical tests, we removed non-significant higher order interactions until at least one significant effect remained at that order of interaction. Significant differences in the intercepts or slope across a density gradient between treatments with different natal habitats of either species indicate a significant influence of carry-over effects on competitive dynamics.

EXTINCTION RISK

During the course of the experiment, several extinctions (adult population counts of 0) were observed when both species were present in oat flour. *Tribolium castaneum* was the species that went extinct in all of these cases, and only when starting at a density of four adults. To determine whether carry-over effects and/or the competitor's initial density influenced the probability of extinction during the experiment, we performed logistic regression on the status (zero or >zero adults?) of *T. castaneum* populations in oat with each species' natal habitat and the initial density of *T. confusum* as fixed effects.

DYNAMIC MODEL

To generate phase planes and gain insights into how carry-over effects altered coexistence conditions, we used the experimental data to parameterize a two-species competition version of a modified Ricker model previously used in Van Allen & Rudolf (2013):

$$N_{it+1} = (N_{it} + b_i N_{it} e^{(-c_{ii}N_{it} - c_{ij}N_{jt})})(1 - \mu_{it}) \qquad \text{eqn 1a}$$

$$N_{jt+1} = (N_{jt} + b_j N_{jt} e^{(-c_{jj}N_{jt} - c_{ji}N_{it})})(1 - \mu_{jt}) \qquad \text{eqn 1b}$$

Here, the adult population size (N) at time step t_{+1} (for species i) is determined by (i) the recruitment rate b_i of species i, which is reduced by (ii) cannibalism (c_{ii}) by species i, (iii) predation (c_{ij}) by species j and (iv) mortality ($1 - \mu_{it}$) of species i. b_i represents the emergent product of fecundity, juvenile growth rate and density independent juvenile survival probability, none of which are directly quantifiable using our methods. ($1 - \mu_{it}$) is the survival probability of adults. Adult mortality increases as cohorts of individuals age and was directly quantified during the experiment, so we used a separate mortality term (μ_{it}) in the model. We fit adult mortality (μ_{it}) using a Cox hazards type model (Andersen & Gill 1982):

$$\mu_t = h e^{\beta t} \qquad \text{eqn 2}$$

Here, the mean adult mortality rate at a given time step (μ_t) starts at rate h which increases exponentially by the factor β with time. Importantly, μ_{it} represents the mean mortality rate of all adults of a species present at a given time, as adult beetles cannot be reliably aged. Fitting this model for each combination of species' past and present habitats allows us to explore how carry-over effects could alter competitive dominance.

MODEL FITTING

We fitted eqn 1 first with our single-species population sizes over 6 months for single-species model coefficients (b_i) and (c_{ii}). Starting single-species population with four adults allowed us to estimate both growth and limitation as they grew towards carrying capacity. Then, using these coefficients from the single-species populations, we fit the model to our 6 months of competition experiment population data to fit interspecific competition coefficients (c_{ij}). We fit the competition and single-species models using a log-link and normally distributed maximum likelihood. All model fitting was performed across the entire time series of the single-species and competition experiments. Fitting competition models using a combination of single-species and competition experiment time series follows previous approaches (Leslie, Park & Mertz 1968; Fox 2007; Hunt & Bonsall 2009). Since we had exact counts of adult mortality in all replicates, we were able to estimate b and c terms independently from adult mortality by fitting models using the observed mortality from each individual population. Instead of multiplying N_{it} by ($1 - \mu_{it}$), we subtracted the count of observed dead adults from N_{it} for each population at each time step. We fit eqn 1 to the population data from each of the four single-species and eight competition experiment factorial combinations of natal and current habitat quality separately since the model could not converge with multiple additional parameters. Fitting each habitat treatment provided good fits to our time series data (Table 1, R^2 values), but the exact parameter estimates should be treated cautiously since with multiple free parameters many similar sets of parameters could fit the same data fairly well (Fox 2007).

To estimate μ_{it}, we fit the proportional mortality of adults for each species in each treatment of both the single-species and competition experiments to eqn 2. Despite using raw mortality counts to fit eqn 1, we fit μ_{it} so that we could project eqn 1 to construct phase planes. Fitting mortality terms also allowed us to compare mortality between treatments. We used maximum likelihood with a binomial distribution and a log-link to fit mortality rates to eqn 2. All *T. castaneum* populations in the single-species and competitive experiments exhibited increasing mortality for the first 4 months and then reached an equilibrium mortality rate (Fig. S1, Supporting information). To account for this clear change in mortality (increasing vs. constant) with time, we fitted the mortality function twice: first for the initial four time steps while mortality increased, then for the fourth to sixth time steps where mortality did not increase. The same parameters were estimated at each side of this mortality rate threshold resulting in two parameterization of the mortality function for *T. castaneum* populations (Fig. S1). *Tribolium confusum* mortality rates followed a single pattern during the course of the experiment, so we only fit the mortality model once across all time steps. We discuss the implications of our modelling of dynamic mortality rates in the Supporting information in more detail.

Table 1. Parameters for eqns 1 estimated using maximum likelihood. Letters for the natal (past habitat in which colonizers developed) and current habitat indicate O for oat (low quality) and W for wheat (high quality). Parameters b and c_{ii} were estimated from single-species treatments, so values will not change with natal habitat of the competitor. R^2 values are for eqn 1 compared to actual mean experimental competitive dynamics. Confidence intervals for parameter estimates are shown in Table S1

Tribolium castaneum natal	O	O	W	W	O	O	W	W
Tribolium confusum natal	O	W	O	W	O	W	O	W
Current:	O	O	O	O	W	W	W	W
T. castaneum								
b	2·625	2·625	4·434	4·434	11·45	11·45	14·93	14·93
c_{ii}	0·146	0·146	0·148	0·148	0·041	0·041	0·051	0·051
c_{ji}	0·312	0·267	0·369	0·339	1·37	1·494	1·307	1·192
R^2	0·844	0·774	0·634	0·659	0·737	0·421	0·619	0·601
T. confusum								
b	4·16	4·342	4·16	4·342	15·27	18·46	15·27	18·46
c_{ii}	0·067	0·062	0·067	0·062	0·056	0·051	0·056	0·051
c_{ji}	0·11	0·054	0·089	0·07	0·074	0·108	0·078	0·118
R^2	0·894	0·911	0·919	0·93	0·697	0·811	0·729	0·834
T. castaneum								
Early h	0·028	0·007	0·027	0·02	0·005	0·008	0·013	0·011
Early β	0·529	0·907	0·537	0·699	1·009	0·931	0·792	0·827
Late h	0·275	0·127	0·086	0·159	0·191	0·436	0·241	0·41
Late β	−0·02	0·189	0·231	0·175	0·1	−0·062	0·056	−0·076
T. confusum								
h	0·006	0·004	0·006	0·007	0·003	0·003	0·005	0·003
β	0·414	0·53	0·447	0·433	0·568	0·573	0·491	0·589

T. cas, *Tribolium castaneum*; *T. con*, *Tribolium confusum*.

PHASE PLANE ANALYSIS

To visually explore our model results and see how carry-over effects altered competitive exclusion in our experiment, we used eqn 1 to generate phase planes of the outcome of simulated competition across initial density combinations for each species. A detailed description of the methods for generating these phase planes is given in the Supporting information. All analyses were performed in ʀ (Version 3.1.3, R Core Team 2015). We used the functions 'mle2' and 'confint' in the ʀ package 'bbmle' (Bolker & R Development Core Team 2014), for maximum likelihood estimation of the parameters and the ʀ package 'lattice' (Sarkar 2008), for phase planes.

Results

SINGLE-SPECIES POPULATION EXPERIMENT

In the absence of interspecific competition, both species reached on average higher population sizes in wheat than in oat (4·1 times more for *T. castaneum* and 2·2 times more for *T. confusum*) during the last 4 months of the experiment (Fig. S2), but *T. confusum* reached 2·9 times higher density in oat than *T. castaneum*. Current habitat quality was the only factor still affecting *T. castaneum* population dynamics (Natal habitat: LR $\chi^2 = 0.0$, $P = 0.998$; Current habitat: LR $\chi^2 = 270.152$, $P < 0.001$; Natal × Current: LR $\chi^2 = 1.539$, $P = 0.215$) and *T. confusum* population dynamics (Natal: LR $\chi^2 = 1.313$, $P = 0.252$; Current: LR $\chi^2 = 68.675$, $P < 0.001$; Natal × Current LR $\chi^2 = 0.103$, $P = 0.748$) beyond the first 3 months. The lack of any significant effects of natal habitat for either species indicates that there is no

evidence that carry-over effects influenced single-species dynamics during the last 4 months of the experiment.

COMPETITION EXPERIMENT

Similar to our single-species treatment, we examined the mean population size over the final 4 months of dynamics for each species in the competition experiment to see whether carry-over effects influenced their mean densities. Significant effects of natal habitat quality in GLM results are evidence for an influence of carry-over effects on competitive dynamics. The full population dynamics for each species across all time steps are given in the Supporting information (Figs S5–S7).

Carry-over effects significantly influenced densities of both species over the last 4 months of the experiment (Table 2, Fig. 1). For instance, *T. castaneum* from wheat natal habitat caused a one-third reduction in *T. confusum* density in both current habitats at the lowest initial densities (i.e. four vs. four, Table 2, Fig. 1b,d). Partially mirroring this result, *T. castaneum* reached on average 2·5 times higher densities in oat flour when either itself or *T. confusum* came from wheat natal habitat and *T. confusum* initial density was low (Table 2, Fig. 1a). The effects of each species natal habitat, when both species initial density was lowest, combined to lead to the highest *T. castaneum* population size when both species came from wheat, which was 3·3 times higher than when both came from oat (Fig. 1a). Together, these results in oat current habitat suggest that coming from wheat increased *T. castaneum* competitive ability, while the opposite was true for *T. confusum* (at lower initial densities at least).

Table 2. Generalized linear model of the relationship between the time-averaged abundance of adult *Tribolium castaneum* (left columns) and *Tribolium confusum* (right columns) during the competition experiment and the natal habitats of both *T. castaneum* and *T. confusum* as well as their initial densities and the current habitat type. Analyses were done separately for each species. NS for *T. confusum* indicate non-significant three-way interactions which were dropped from the model for the final analysis (see Materials and methods)

Factor	*T. castaneum*		*T. confusum*	
	LR χ^2	*P*	LR χ^2	*P*
T. cas natal habitat	5·559	0·018*	6·648	0·01*
T. con natal habitat	5·096	0·024*	0·198	0·656
Current habitat	42·37	<0·001*	3·330	0·068
Initial *T. con* density (DenCon)	3·170	0·075	26·25	<0·001*
Initial *T. cas* density (DenCas)	8·157	0·004*	13·35	<0·001*
T. cas natal: *T. con* natal	0·048	0·826	0·263	0·608
T. cas natal: current	3·400	0·065	0·224	0·635
T. con natal: current	7·558	0·006*	3·703	0·054
T. cas natal: DenCon	4·632	0·031*	3·42	0·064
T. con natal: DenCon	2·663	0·103	0·157	0·692
Current: DenCon	0·160	0·690	0·11	0·74
T. cas Natal: DenCas	0·885	0·347	1·77	0·183
T. con natal: DenCas	1·431	0·231	0·795	0·373
Current: DenCas	2·193	0·139	7·828	0·005*
T. cas: *T. con* natal: current	2·181	0·140	NS	NS
T. cas: *T. con* natal: DenCon	0·558	0·455	NS	NS
T. cas natal: current: DenCon	3·250	0·071	NS	NS
T. con natal: current: DenCon	6·421	0·011*	NS	NS
T. cas: *T. con* natal: DenCas	0·312	0·577	NS	NS
T. cas natal: current: DenCas	0·148	0·701	NS	NS
T. con natal: current: DenCas	1·921	0·166	NS	NS
N = 144				

T. cas, *Tribolium castaneum*; *T. con*, *Tribolium confusum*.
Analysis of deviance table using type three sums of squares. Starred *P*-values indicate significance at the 0·05 level.

In wheat current habitat, *T. castaneum* followed its single-species performance by exhibiting higher densities than in oat current habitat (Table 2, Fig. 1). In contrast, *T. confusum* performed only marginally better in wheat flour than oat flour (Table 2, Fig. 1). Increasing densities of *T. castaneum* had a much stronger negative effect on *T. confusum* density in wheat flour than in oat flour (Fig. S3b vs. d) and *T. confusum* initial density was generally not as important (Fig. 1c). Along the density gradient varying the initial number of *T. castaneum*, there were no significant interactions with the natal habitat of either species, indicating that carry-over effects operated in a similar fashion regardless of whether *T. castaneum* was initially at low or high densities (Table 2, Fig. S3).

Otherwise, the general patterns were similar to the patterns observed in oat habitat, except that carry-over effects were somewhat weaker in the high-quality (wheat) habitat. Thus, regardless of the current habitat quality, the density of each species changed if the natal habitat of the other species changed. This demonstrates that carry-over effects can significantly alter interspecific interactions. Interestingly, in contrast to single-species treatments, carry-over effects persisted in competition treatments throughout the experiment, indicating that carry-over effects impacts were amplified in a community context.
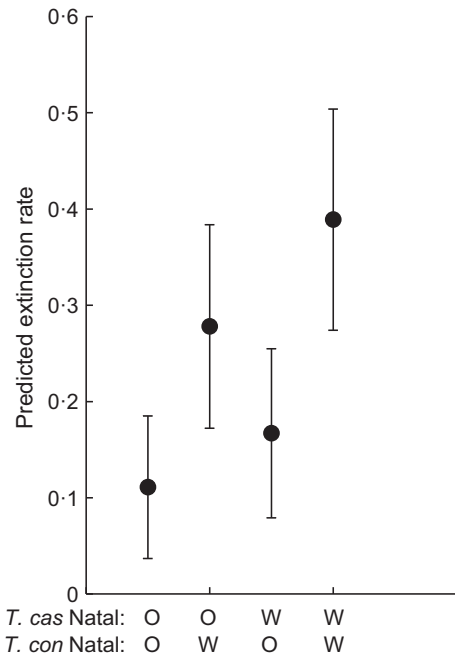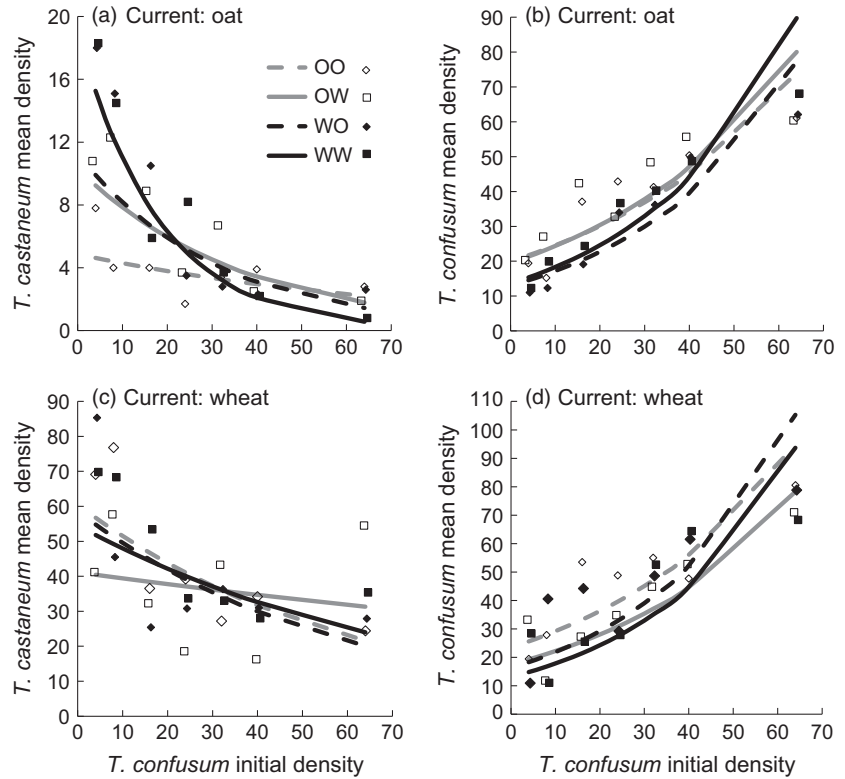
EXTINCTION RISK

Tribolium castaneum population size in oat flour dropped to zero in 17 replicates during the experiment. These extinctions were not random; instead, extinctions were 2·2 times more likely when the competitor, *T. confusum*, came from wheat natal habitat ($z = 2.075$, $P = 0.038$, Fig. 2). Increasing initial density of *T. confusum* coming from wheat natal habitat also contributed to a more rapid decline in *T. castaneum* population size in the final 4 months of the experiment (Table 2, Fig. 1b). Carry-over effects in one species thus were significantly associated with an increase in the extinction risk for a second species.

DYNAMIC MODELLING

Fitting the dynamic model to our experiment provides further insight into how carry-over effects influenced competitive interactions and demographic rates of species. Furthermore, it allowed us to generate phase planes estimating how carry-over effects could alter competitive dominance and create variation in community structure. As expected, cannibalism and predation rates and adult recruitment rates (estimated using eqn 1) of both species differed between habitats, and mortality rates of *T. confusum* were generally lower than in *T. castaneum* (Table 1, Fig. S4). More importantly, estimated cannibalism/predation coefficients and recruitment rates within habitats were also clearly affected by natal habitats (Table 1). Finally, mortality rates (estimated using eqn 2) revealed that death rates of *T. castaneum* in oat flour and of *T. confusum* in either habitat were generally higher in the presence of the other species than in the single-species treatment. Importantly, mortality rates of *T. castaneum* were highest when *T. confusum* came from wheat natal habitat (Table 1, Fig. S4). This increased mortality helps to explain increased extinction rates in of *T. castaneum* during the experiment in oat habitat when *T. confusum* came from wheat natal habitat. Together, these results suggest that carry-over effects can influence interspecific competitive interactions through both numerical and per-capita effects.

Fig. 1. Generalized linear models results of the time-averaged last 4 months of each species competitive dynamics. Lines are model fits across initial *Tribolium confusum* density with an initial *Tribolium castaneum* density of four. Points show raw data means of the two replicates for each treatment. The two letter codes in the key show the natal habitat for each species, first *T. castaneum* then *T. confusum*, with O for oat (low quality) and W for wheat (high quality). For *T. castaneum,* grey lines and open symbols indicate oat natal habitat while black lines and closed symbols designate wheat natal habitat. *Tribolium confusum* with a natal origin of oat are shown with a dashed line and diamond shape while wheat is shown with a solid line or square shape. Note that *y*-axis differ between species.


Fig. 2. Mean (±1 SE) *Tribolium castaneum* extinction rates in oat flour as predicted by logistic regression. Note that the predicted values are identical (to three decimal places) to the actual extinction rates in all treatments.

Phase plane analysis shows that these carry-over effects can fundamentally alter competitive dominance of species and thereby the long-term outcome of competition, that is which species will be competitively excluded within a given habitat (Fig. 3). Carry-over effects influenced whether competitive equilibria were always stable (i.e. one species always dominates) or unstable (initial density could alter which species dominates). When *T. confusum* comes from wheat while *T. castaneum* comes from oat, there is no chance of *T. castaneum* dominating at any initial density (up to approximately three times the *T. castaneum* single-species equilibrium) (Figs 3b and S2). This prediction is consistent with our experimental results where 12 of the 17 observed extinctions of *T. castaneum* populations during the experiment occurred when *T. confusum* came from wheat natal habitat (Fig. 2). The other seven treatments contain unstable equilibria allowing for whichever species has the appropriate numerical advantage to eventually exclude the other.

In addition, the parameter spaces in which species were competitively dominant were changed by carry-over effects. For example, coming from wheat as opposed to oat natal habitat dramatically favoured *T. castaneum* in oat current habitat (Fig. 3c,d vs. a,b). In wheat current habitat, we found a very similar zone of competitive dominance switching between species to Leslie, Park & Mertz 1968; but only when *T. confusum* came from wheat natal habitat (Fig. 3f,h vs. e,g, see table 3 in Leslie, Park & Mertz 1968 for comparison). When *T. confusum* comes from oat instead of wheat, all of recruitment rate, cannibalism and predation rates are lower than the corresponding rate from wheat (Table 1), and this shows as the switch point of dominance to moves to a higher initial *T. confusum* density (Fig. 3e,g). *Tribolium castaneum* also appears to perform better in wheat when coming from
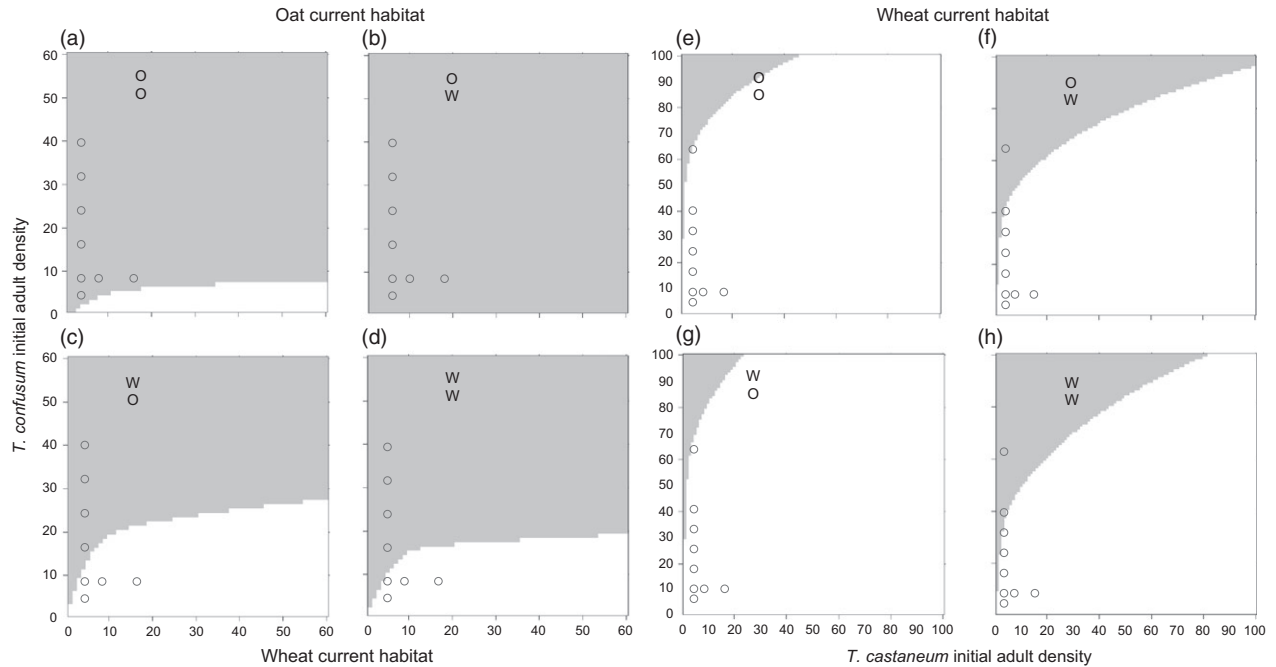
Fig. 3. Long-term carry-over effects on species coexistence as a function of initial densities of two competing flour beetle species. Predictions are based on simulations of the parameterized competition model (see Supporting information, following Rudolf *et al.* 2010). Colours of regions show which species is competitively dominant and thus persists. *Tribolium confusum* is dominant and excludes *Tribolium castaneum* in grey areas, while the opposite is true in white areas. Points indicate the initial densities of each species used in the experiment. Two letter codes within the panels indicate the natal habitat of *T. castaneum* on top, then of *T. confusum* below.

wheat, but this is a smaller effect (Fig. 3g,h vs. e,f). In general, these results suggest that within a given habitat type, differences in carry-over effects (i.e. natal habitat of colonizers) can alter the conditions which determine the presence/absence of species and thus community structure.

Discussion

Carry-over effects are ubiquitous in animals and plants, and their ability to affect population dynamics has been well documented, but their effects on competitive and community dynamics are largely unknown (O'Conner *et al.* 2014). Here we show that the natal habitat quality of colonizing individuals can carry-over to fundamentally alter the outcome of interspecific competition. In particular, we found that carry-over effects in a *Tribolium* system altered the abundance and extinction probability of competing species and the parameter space favouring persistence of a species within a given habitat type.

Current models of spatial coexistence usually assign a mean fitness/carrying capacity for a species within given habitat, which by default assumes that carry-over effects have short-term influences if any (Chesson 2000; Fox 2007). Supporting this view, we found that carry-over effects largely disappeared in single-species populations after the first generations. We did not test the first 3 months of dynamics in single-species populations, but

model parameters and empirical population dynamics suggest that carry-over effects did impact dynamics over the first 3 months (Table 1, Fig. S2). However, when two species were present carry-over effects continued to influence the dynamics of competitive communities for many generations, indicating that interspecific interactions can amplify carry-over effects. Given that carry-over effects are ubiquitous in heterogeneous landscapes, our results indicate that carry-over effects can influence the outcome of competitive interactions and the structure and dynamics of natural communities.

CARRY-OVER EFFECTS AND SPECIES INTERACTIONS

Coexistence of competing species is determined by relative differences in fecundity and mortality rates of species (numerical effects), and how these rates are affected by species interactions (per-capita effects) (Chesson 2000). We found that natal habitat quality influenced the fecundity and interspecific/intraspecific interactions of both species (Table 1). Thus, carry-over effects altered the outcome of competition through changes in numerical and per-capita effects. While the purpose of this study was to determine whether carry-over effects altered competitive dynamics and not to identify the exact mechanisms underlying these patterns, the results are consistent with previous work in this system which found that natal habitat of colonizers significantly affected survival and development rate of eggs and larva, adult body mass and

predatory behaviour in multiple generations beyond the generation experiencing carry-over effects (Van Allen & Rudolf 2013; B.G. Van Allen, unpubl. data).

Interestingly, carry-over effects varied across species and current habitats. *Tribolium castaneum* was more sensitive to low food quality in either natal or current habitat, as mean fecundity increased 1·7-fold due to wheat natal habitat in oat flour. Additionally, intraspecific competition coefficients were 3·2 times higher on average in oat rather than wheat current habitat. For *T. confusum*, wheat natal habitat increased mean fecundity by only 1·2 times in wheat habitat and had virtually no effects on intraspecific competitive coefficients and fecundity in oat. Carry-over effects therefore had notably different effects on the vital rates of our study species, but differences in the performance of these species can be partially explained by differences in their life histories. *Tribolium castaneum* is known to perform very well in high-quality habitat, but is sensitive to environmental quality, while *T. confusum* is more of a generalist, which gives it an advantage in low-quality environments (Nathanson 1975; Fig. S1). *Tribolium confusum* affected its competitor in low-quality habitat in two very different ways, either by increasing interspecific competition coefficients, or *T. castaneum* adult mortality rate. *Tribolium castaneum* mortality rates were generally increased by competition in oat flour (Fig. S4). This result is consistent with previous work indicating that interspecific competition can increase mortality rates in adult flour beetles (Lloyd & Park 1962). Intriguingly, we found very different effects of competition on mortality rates depending on *T. confusum* natal habitat (Fig. S4). These effects of one species natal habitat on the other species mortality rates, which are clearly unobservable in a single-species population, indicate that carry-over effects of natal habitat of both species were not always independent. Thus, variation in carry-over effects can lead to complex interactions among species and may lead to unanticipated outcomes.

Trait variation in response to present environmental cues (e.g. development of anti-predator morphologies or nutrient stress) frequently affects interactions between diverse taxa such as plants and herbivores (terHorst & Lau 2012), protists (DeLong, Hanley & Vasseur 2013), invertebrates (Hoverman & Relyea 2009) and vertebrates (Kishida *et al.* 2013). However, trait variation coming from previous habitats is typically neglected in spatial models of competitive coexistence (HilleRisLambers *et al.* 2012). Our study clearly shows that the influence of carry-over effects can persist for multiple generations and influence competitive outcomes.

A very interesting result of our study is that carry-over effects continued to alter competitive dynamics for the entire duration of the experiment, but they did not clearly alter the long-term dynamics of individual populations. As discussed above, flour beetle traits and offspring traits can all be influenced by natal habitat quality, but this does not fully explain why carry-over effects would persist when two species interact but not when they are alone. This discrepancy between single- and two-species systems indicates a feedback between carry-over effects and species interactions. We found the natal habitat of one species altered its interspecific predation rate and the other species' mortality in competitive populations, which clearly indicates that carry-over effects altered per-capita strength of interspecific interactions. These additional effects beyond what we can observe in single populations may strengthen the influence of carry-over effects on competition. Additionally, mothers from low-quality natal habitat have offspring who are smaller and whose development is delayed by a week or more (Van Allen & Rudolf 2013; B.G. Van Allen, unpub. data). When carry-over effects change the already different relative development rates of these two species further, this could lead to scenarios of stage structured interactions which alter competitive outcomes (Rasmussen, Van Allen & Rudolf 2014). For example, the timing of pupation for one species relative to the timing of abundant large larvae and adults (which consume pupae) of the other species could be critical for successful adult recruitment. Effects such as these could echo demographically across generations, along with parental effects on offspring traits (Beckerman *et al.* 2002). As a result, a combination of initial traits, parental effects and the demographic consequences of these effects were likely sufficient to alter dynamics for generations. Many of the carry-over effects which altered species interactions in our study (e.g. changes in behaviour, fecundity and life span) are often observed in other systems (soil mites: Beckerman *et al.* 2003; vertebrates: Harrison *et al.* 2010; bryozoans: Burgess & Marshall 2011; fruit flies: Betini *et al.* 2014), suggesting that we may not be able to safely discount their effects when predicting species coexistence across heterogeneous landscapes.

VARIATION IN COMMUNITY STRUCTURE AND CARRY-OVER EFFECTS

Differential performance across variable habitats is a cornerstone of spatial coexistence theory. It allows species to persist in some areas and be out-competed in others, thereby preventing one dominant species across all environments (Chesson 2000; Amarasekare 2003). Carry-over effects operated similarly here, by generating differential performance for a species across habitats. However, this was within habitats of the same type, depending on natal experiences. Thus, carry-over effects could prevent any one species from dominating within all of any particular environment. This suggests that carry-over effects may operate as a spatial coexistence mechanism as well as providing a mechanism to explain variation in community assembly.

Individual variation is increasingly recognized as an important driver of ecological dynamics, but the causes of variation are often not well connected to their consequences

(Agrawal *et al.* 2007). Our study shows that environmental heterogeneity can introduce intraspecific variation in dispersers and that this has important effects on species interactions with clear implications for community structure. This link between environmental and individual variation leading to changes in species interactions likely has important consequences for the dynamics of metacommunities, but more studies are needed to examine how environmental carry-over effects alter spatial community dynamics (Benard & McCauley 2008).

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.517jv (Van Allen & Rudolf 2015).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Complete methods for the phase plane analysis. We additionally provide tables and figures referred to in the main text.

Table S1. Error estimates (95% confidence interval lower and upper bounds) for model one parameters, entries of NA indicate that the high bound of the error estimate could not be retrieved.

Fig. S1. Raw mortality rate data (points) and fit (lines) of model (2) for *T. castnaeum* (a) and *T. confusum* (b) in a sample competition experiment treatment (both came from oat natal habitat and are in wheat current habitat).

Fig. S2. Mean (± 1 SE) densities in single-species control populations for *T. castaneum* and *T. confusum*.

Fig. S3. GLM results of the time-averaged last 4 months of each species competitive dynamics across the gradient of varying density of *T. castaneum*.

Fig. S4. Mean (with 95% CIs) mortality rates at the end of the experiment for both species estimated using eqn (2).

Fig. S5. Smoothed raw density data for each species in each replicate in oat current habitat across the gradient varying initial density for *T. confusum* over time during the competition experiment.

Fig. S6. Smoothed raw density data for each species in each replicate in wheat current habitat across the gradient varying initial density for *T. confusum* over time during the competition experiment.

Fig. S7. Smoothed raw density data for each species in each replicate across the gradient varying initial density for *T. castaneum* over time during the competition experiment.