

# Spatially correlated extinctions select for less emigration but larger dispersal distances in the spider mite *Tetranychus urticae*

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## Abstract

Dispersal is a central process to almost all species on earth, as it connects spatially structured populations and thereby increases population persistence. Dispersal is subject to (rapid) evolution and local patch extinctions are an important selective force in this context. In contrast to the randomly distributed local extinctions considered in most theoretical studies, habitat fragmentation or other anthropogenic interventions will lead to spatially correlated extinction patterns. Under such conditions natural selection is thought to lead to more long-distance dispersal, but this theoretical prediction has not yet been verified empirically. We test this hypothesis in experimental spatially structured populations of the spider mite *Tetranychus urticae* and supplement these empirical results with insights from an individual-based evolutionary model. We demonstrate that the spatial correlation of local extinctions changes the entire distribution of dispersal distances (dispersal kernel) and selects for overall less emigration but more long-distance dispersal.

**Keywords:** dispersal kernel, dispersal evolution, local extinctions, spatial correlation, experimental evolution

## Introduction

Dispersal between more or less distinct and isolated habitat patches is essential for the long-term persistence of populations in a spatially structured environment. This idea represents the core of the metapopulation concept (Hanski and Gaggiotti 2004) and as our environment is continuously being degraded and fragmented due to anthropogenic land use change, the importance of dispersal cannot be overestimated. Beyond influencing local dynamics the joint processes of dispersal and local adaptation shape the distribution of species on earth (Kubisch et al. 2014) and are therefore of fundamental importance in ecological and evolutionary research.

Dispersal evolution has been well studied during the last decades (reviewed in Bowler and Benton 2005; Ronce 2007; Clobert et al. 2012) and — as the feedback between ecological changes and evolution can occur very rapidly — dispersal evolution can potentially lead to evolutionary rescue (Gonzalez et al. 2013) or to evolutionary suicide (Parvinen 2007; Poethke et al. 2011a). Dispersal evolves as a consequence of factors selecting for lower or higher dispersal rates and distances. While various costs of dispersal (reviewed in Bonte et al. 2012) select against dispersal, fitness benefits related to the avoidance of competition and especially kin competition (Hamilton and May 1977), inbreeding avoidance (Bengtsson 1978) and temporally variable habitats (McPeck and Holt 1992) increase dispersal. The effect of local extinctions on dispersal evolution has been subject to theoretical and empirical studies (e.g. Comins et al. 1980; Roff 1994; Friedenberg 2003) which demonstrated the evolution of elevated dispersal rates as a risk spreading strategy. Additionally, benefits of dispersal are attributed both to the recolonization of empty patches and to the escape from competition, although this may depend on whether local extinctions are due to environmental pressures or to feedbacks with demographic processes (Poethke et al. 2003).

Important shortcomings of a large number of these studies are the lack of an explicit representation of spatial structure, the very simplistic assumptions regarding the dispersal process, with emphasis on emigration rate rather than dispersal distances, and the sole consideration of uncorrelated random extinction events in the landscape. As a consequence, the evolution of dispersal distances is theoretically (but see e.g. Hovestadt et al. 2001; Bonte et al. 2010; North et al. 2011; Skelsey et al. 2013) and especially empirically understudied (but see Bitume et al. 2013). Despite the awareness of spatial autocorrelation in extinction events in nature due to habitat fragmentation (Kallimanis et al. 2005) or disease spread (Muller-Landau et al. 2003), theoretical predictions suggesting that autocorrelated extinction patterns lead to larger dispersal distances (Muller-Landau et al. 2003; Kallimanis et al. 2006; North et al. 2011) remain untested.

We decided to follow an experimental evolution approach (Kawecki et al. 2012) and to use the spider mite *Tetranychus urticae* as a model organism to study the effect of spatial correlation in population extinctions on the evolution of dispersal distances. We specifically tested the hypothesis that spatially correlated extinctions lead to larger dispersal distances, i.e. to more long-distance dispersal (LDD) than uncorrelated extinctions. Additionally, we supplemented our empirical findings with results from a simple individual-based model. By modelling the distribution of dispersal distances (dispersal kernel) as a function-valued trait (Dieckmann et al. 2006), our model allowed us to predict the evolutionarily stable shape of the dispersal kernel. Previous theoretical work on dispersal distances (e.g. North et al. 2011) did not usually take into account that selection may change the shape of this distribution as specific functional relationships are assumed a priori (but see e.g. Hovestadt et al. 2001; Starrfelt and Kokko 2010).

## Material, Methods and Model description

### Study organism

Our study organism, *Tetranychus urticae*, is a haplodiploid polyphagous spider mite well known to cause serious damage to crops and plants in general. These mites have high fecundities and relatively short generation times of approximately 10 days which makes them ideal study organisms for experimental evolution (e.g. Li and Margolies 1994; Belliure et al. 2010; Macke et al. 2011; Bitume et al. 2011). *T. urticae* may disperse aerially (Li and Margolies 1993, 1994) in response to deteriorating habitat conditions, but they usually disperse on foot on the same host or towards neighboring host plants.

In the present study, we used the same mite strain as Bitume et al. (2013). Populations were maintained on bean plants (*Phaseolus vulgaris*, cultivar: Sanguigno 2, Bingenheimer Saatgut, Germany; reared

at 22°C, 16:8 h photoperiod) at 22°C, approx. 60% humidity and a 16:8 h photoperiod. All experiments were carried out under these conditions.

## Experimental mesocosms

We built experimental spatially structured populations of spider mites consisting of 4 x 4 patches (one bean leaf in wet floral foam per patch; approx. 5 x 5 cm; approx. two weeks old). These patches were linked to their four (respectively three for the outer patches and two for the patches in the four corners) nearest neighbours by PVC bridges (12 cm long, 2 mm diameter). The bean leaves were replaced once per week and mites were allowed to move from old to new leaves for three days.

We ran one control and two experimental treatments with four replicates each for approximately 10 generations (November 2012 to March 2013). The control treatment (C) did not include any extinctions. In the first experimental treatment (TR) extinctions were applied randomly, i.e. four leaves were removed per mesocosm once per week and replaced with fresh ones resulting in an extinction rate of 0.25. These leaves were selected randomly (function “sample”; R version 2.15). In the second extinction treatment (TC) we always replaced a block of 2 x 2 leaves which led to spatially correlated extinctions while keeping the extinction rate constant. Again, out of nine possible 2 x 2 blocks one was chosen randomly as above.

## Measurement of dispersal distances and life-history traits

After 10 generations of selection in the above described mesocosms we transferred the spider mites into a common garden (bean leaves on wet cotton in Petri dishes; 22 cm diameter) for a period of one generation in order to minimize the influence of maternal effects (Macke et al. 2011). Subsequently, dispersal distances were measured in analogy to Bitume et al. (2013) in a linear setup consisting of seven bean leaves connected by bridges as described above. Initially 50 randomly chosen mites were placed on the first patch and the distribution of individuals was recorded for seven days. During this time span mites started to lay eggs. Thus, we only used the position of adults for the analysis.

We additionally measured life-history traits (daily fecundity, longevity, developmental time, time to maturity, sex ratio, juvenile mortality, hatching rate) in order to quantify the effect of our selection treatment on these. The traits in question were recorded on two offspring of 50 randomly chosen females per treatment resulting in a total of 300 mites. Each egg was placed on a 1cm<sup>2</sup> piece of bean leaf and its development, sex and life span were recorded. Females were mated with randomly chosen males from the same treatment, and subsequently daily fecundity was measured.

## Statistical analysis

All statistical analyses were performed using the statistical software R version 2.15. We modeled the probability distribution of spider mites along the linear set-up (the dispersal kernel) at day seven using an ordered multinomial logistic regression (“polr” function of package “MASS”; for details see Bitume et al. 2013). “Treatment” (C, TR, TC) and “replicate” (1 to 4) were used as explanatory variables.

The life-history data were analysed using GLMMs (“glmmPQL” function of package “MASS”) with “mothers” nested in “replicate” as random effects. For population level measurements such as sex-ratio, hatching rate or juvenile mortality only “replicate” was used as a random effect. If homogeneity of variance was given, a Poisson (daily fecundity, longevity, time to maturity) or binomial (sex ratio, hatching rate, juvenile mortality) error distribution was used, if not, the data were transformed (developmental time) and a Gaussian error distribution was used.

## Individual-based model

The individual-based simulation was developed as a simple model of a spatially structured population of individuals with non-overlapping generations and natal dispersal. Such models have been commonly used previously (e.g. Hovestadt et al. 2001; Fronhofer et al. 2011) to analyze the eco-evolutionary dynamics of dispersal. These models can take into account demographic and environmental stochasticity and extinctions. Note that such simple models are not thought to be an accurate representation of the complexities of any specific natural system (all models are “wrong” but may be useful; see Kokko 2005) but try to capture their most important properties.

The model was designed to roughly represent the experimental setting described above: the simulated world consists of  $4 \times 4$  patches, where each patch is connected to its four nearest neighbours (respectively three at the edges and two in the corners). Local patch dynamics are assumed to be density dependent and to follow the general model provided by Beverton and Holt (1957) where newborn individuals in patch  $i$  at time  $t$  survive to maturity with the probability

$$s_{i,t} = \frac{1}{1 + a \cdot N_{i,t}} \quad (1)$$

where  $a = (\lambda - 1)/K$  with  $K = 250$  as the local carrying capacity (roughly estimated from the mesocosms),  $N_{i,t}$  as the population size in patch  $i$  at time  $t$  and  $\lambda = 5$  which represents the net mean number of offspring per female and generation. As the model includes demographic stochasticity, the number of offspring a female gives birth to is drawn from a Poisson distribution with mean  $\lambda \cdot s_{i,t}$ . We tested alternative models of density dependence, e.g. the Ricker model, and found that our results were not qualitatively sensitive to these assumptions.

The dispersal submodel is in many aspects analogous to Poethke et al. (2011b): individuals choose a direction, here one of four possibilities, respectively three for edges and two for corners. As we do not model information use, this direction is kept until the individual reaches its dispersal distance. If an individual reaches an edge, its movement path is redirected into a randomly chosen direction depending on the connectivity of the edge patch while excluding the direction it came from. This results in two possible directions for edges and only one for corners. We tested different edge conditions (e.g. wrapped boundary conditions); these assumptions changed the shape of the evolutionarily stable dispersal kernel only slightly (especially the maximum distance travelled) but did not alter the qualitative differences between the tested extinction scenarios.

Every individual is characterized by a distribution of dispersal distances (dispersal kernel) implemented as a function-valued trait (Dieckmann et al. 2006). More specifically, the kernel is defined by seven values (adding up to one) representing the probabilities of reaching one of seven distance classes after dispersal. One distance class equals the distance of one patch and the first distance class represents the probability of staying in the natal patch, i.e. if an individual draws the third distance class from its distribution, it will disperse to the second patch in a given direction. This approach is commonly used if one does not want to assume any specific dispersal kernel function a priori (Hovestadt et al. 2001; Starrfelt and Kokko 2010).

For simplicity the model is phenotypic and individuals reproduce asexually. Offspring inherit their parent's dispersal kernel subject to small mutations (mutation probability  $m = 0.0001$ ) on the probability of dispersal to each distance class. Mutational increments are drawn from a Gaussian distribution with mean zero and standard deviation 0.2. To guarantee positive numbers, values below zero are set to zero. After mutation the distance distribution is renormalized to sum up to one.

The only parameter we could not estimate from the empirically collected data was the cost of dispersal, which summarizes all possible factors (risk, time, energy, etc.) that make dispersal costly (for a review see Bonte et al. 2012). We therefore simply assume a per step mortality cost  $\mu_d$  and can then calculate the mortality for reaching a certain dispersal distance as

$$\mu = 1 - e^{-\mu_d \cdot d} \quad (2)$$

where  $d$  is the distance travelled.

All analyses were run for a total of 5000 generations. For each of the three scenarios — 1) control (C) without extinctions, 2) random extinction (TR) with four patch extinctions per generation and 3) clumped extinctions (TC) with one extinction of a  $2 \times 2$  block as described above — we ran 50 replicate simulations. As we could not estimate per step dispersal mortality from our empirical results, we ran simulations for  $\mu_d = 0.05, 0.1, 0.15, \dots, 0.25$ . We additionally did a sensitivity analysis for fecundity and carrying capacity (see Supporting Information S2).

## Results

Our results clearly show the impact of the spatial correlation of local patch extinctions (Fig. 1). The statistical analysis indicates that the control and the two extinction treatments differ significantly from each other (ordered multinomial logistic regression; TC:  $t = 2.64$ ,  $p = 0.008$ ; TR:  $t = 4.00$ ,  $p < 0.001$ ;

replicates:  $t = 1.28$ ,  $p = 0.20$ ; Tukey post-hoc test: C-TC:  $z = 2.64$ ,  $p = 0.02$ ; C-TR:  $z = 4.00$ ,  $p < 0.001$ ; TC-TR:  $z = 2.44$ ,  $p = 0.035$ ).

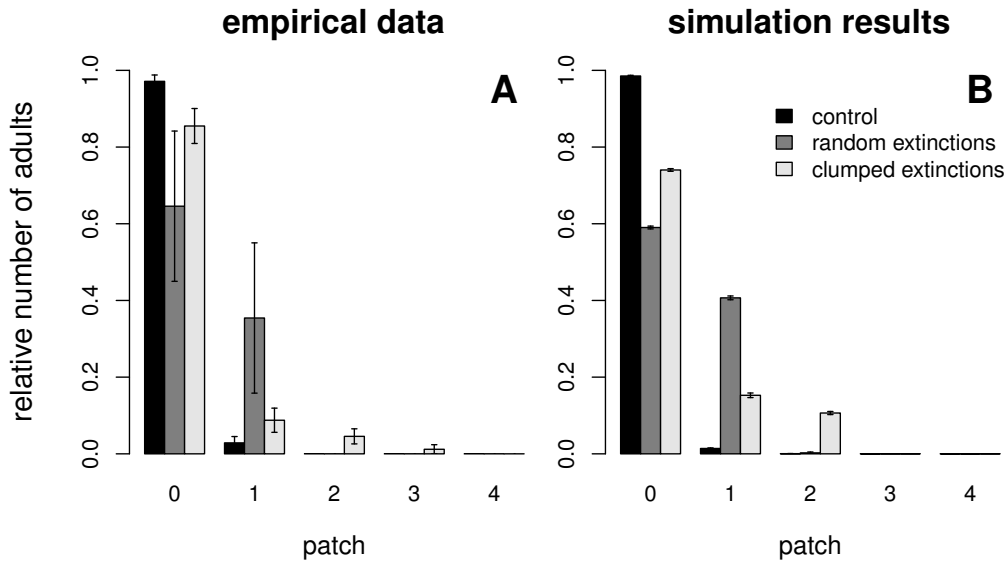


Figure 1: Empirically recorded and simulated evolutionarily stable distribution of dispersal distances depending on the extinction treatment (control: C; random extinctions: TR; clumped extinctions: TC). Panel A depicts the empirical data recorded from the linear bioassay at day seven after approx. 10 generations of selection and one generation of common garden (mean  $\pm$  s.e.). The untransformed count data (median and quartiles) can be found in the Supporting Information S1. The results from the individual-based model shown in panel B represent the evolutionarily stable distribution of dispersal distances (distance probability density function). This pattern is robust to variation in important model parameters (see Supporting Information S2 for a sensitivity analysis). The results are averaged over 50 replicate simulation runs (mean  $\pm$  s.e.). Note that the abrupt end of the simulated kernels is due to edge effects intrinsic to the connectivity pattern of the mesocosms. We suggest that the good fit of our empirical results to the simulated data is due to the relatively strong selective pressures of the extinction scenarios. By contrast, the edge effects are weaker and can therefore not be observed in the empirical data. Simulation parameters:  $K = 250$ ,  $\lambda = 5$ ,  $\mu_d = 0.2$ .

Generally, extinctions favored the evolution of more dispersal (Fig. 1; median number of dispersers: C: 0.5; TR: 4; TC: 3; see Supporting Information S1 for the data). While spatially correlated extinctions (TC) selected for less dispersal than random extinctions (TR) — the relative number of individuals in the starting patch is larger for TC (Fig. 1 A) — this treatment led to more LDD (kurtosis TR: -1.5, TC: 8.2; 95th percentile TR: 1, TC: 1.7; data of the replicates were pooled). This combination of overall less emigration but more long-distance dispersal explains why spatially correlated extinctions did not lead to higher mean dispersal distances (K: 0.0; TR: 0.3; TC: 0.2; data of the repeats were pooled). Note that the dispersers did move further on average (K: 1.0; TR: 1.0; TC: 1.4; only dispersers, i.e. individuals that were not in patch 0; data of the repeats were pooled).

In general, the life-history traits showed no consistent evolutionary reaction to patch extinctions (table 1). We found a non-significant trend to more r-selected traits in the treatments TR and TC. The control had both the highest juvenile mortality (GLMM; TC:  $t = 0.97$ ,  $p = 0.37$ ; TR:  $t = 1.53$ ,  $p = 0.18$ ) and time to maturity (GLMM; TC:  $t = -3.02$ ,  $p = 0.02$ ; TR:  $t = -1.05$ ,  $p = 0.32$ ) and the lowest hatching rate (GLMM; TC:  $t = 0.833$ ,  $p = 0.44$ ; TR:  $t = 1.72$ ,  $p = 0.14$ ). The random extinction treatment had the lowest juvenile mortality and the highest hatching rate. We also examined longevity (GLMM; TC:  $t = 0.465$ ,  $p = 0.658$ ; TR:  $t = -0.706$ ,  $p = 0.507$ ), developmental time (GLMM; TC:  $t = -1.58$ ,  $p = 0.16$ ; TR:  $t = -0.16$ ,  $p = 0.88$ ), sex ratio (GLMM; TC:  $t = -1.681$ ,  $p = 0.143$ ; TR:  $t = -1.336$ ,  $p = 0.23$ ) and mean daily fecundity (GLMM; TC:  $t = 0.247$ ,  $p = 0.811$ ; TR:  $t = -0.02374$ ,  $p = 0.982$ ), but these other life-history traits were not sensitive to the extinction treatments.

Table 1: Life-history traits (mean  $\pm$  s.e.) of *Tetranychus urticae* depending on the selection treatment. Longevity is the time span from egg deposition to death. Sex ratio is the relative number of females. While the developmental time describes the number of days spent as egg, time to maturity captures the time spent as larvae and nymphs.

	<b>control</b>	<b>random extinctions</b>	<b>clumped extinctions</b>
daily fecundity	7.5 $\pm$ 2.0	7.0 $\pm$ 2.2	7.4 $\pm$ 2.05
longevity [days]	20.7 $\pm$ 4.25	19.7 $\pm$ 4.3	22.2 $\pm$ 5.1
sex-ratio	0.49 $\pm$ 0.2	0.44 $\pm$ 0.03	0.41 $\pm$ 0.08
hatching rate	0.76 $\pm$ 0.09	0.91 $\pm$ 0.03	0.83 $\pm$ 0.05
juvenile mortality	0.36 $\pm$ 0.14	0.10 $\pm$ 0.05	0.18 $\pm$ 0.08
developmental time [days]	5.0 $\pm$ 0.15	4.84 $\pm$ 0.22	4.63 $\pm$ 0.3
time to maturity [days]	10.82 $\pm$ 0.34	10.67 $\pm$ 0.36	10.37 $\pm$ 0.5

## Discussion

The empirical data (Fig. 1 A) and the results from the individual-based model (Fig. 1 B) validate the hypothesis that spatially correlated extinctions select for LDD. In addition, we confirm previous empirical (Friedenberg 2003) and theoretical findings (e.g. Poethke et al. 2003) that local extinctions lead to increased dispersal rates. Most importantly, our study is the first to show empirically that the spatial correlation of such extinction events influences the entire distribution of dispersal distances (the dispersal kernel), as spatially correlated extinctions led to overall less emigration but more long-distance dispersal.

In line with previous empirical research on dispersal in *T. urticae* (Li and Margolies 1993), dispersal distance evolution did not seem to trade-off with fecundity or survival in our experiment. This causes unconstrained evolutionary trajectories of dispersal distances in relation to (correlated) patch extinctions, at least within the limitation of our experimental setup. Note that such rapid evolution as described here could be observed for areal dispersal in the same mite species (Li and Margolies 1994). Generally, mites appear to be good model organisms for the study of rapid evolutionary responses (Belliure et al. 2010).

Based on previous studies on spatially correlated disturbance, such as pest outbreaks (Muller-Landau et al. 2003), we had hypothesized that correlated extinction should lead to more LDD. What we had not predicted was the evolution of less dispersal under these conditions. However, both empirical and simulated data indicate this pattern which can be explained by the decreased benefit of dispersal to the next patch in the case of correlated extinctions. As, in case of a spatially correlated extinction, the probability is high that neighbouring cells become extinct as well, dispersal as a bet-hedging strategy (Ronce 2007) to these cells yields less benefit than in the case of uncorrelated extinctions. As a consequence, at least a fraction of the dispersers should disperse further. Yet, these dispersers will have to pay higher costs of dispersal to escape extinction, as costs are distance-dependent (Rousset and Gandon 2002). To our knowledge this aspect of correlated extinctions has not been predicted or observed previously because most studies on dispersal distances keep dispersal rates fixed or use predefined (mixed) Gaussian distance functions (e.g. Muller-Landau et al. 2003). By contrast, we analyze the evolution of the entire distribution of dispersal distances (see also Hovestadt et al. 2001; Rousset and Gandon 2002; Starrfelt and Kokko 2010, for theoretical approaches).

While previous work showed a tight coupling between the evolution of dispersal rate and dispersal distance (e.g. Bonte et al. 2010), our experiments demonstrate that the emigration and transfer phase of the dispersal process are subject to different cost-benefit balances, as described above. This leads to a decoupling of the evolutionary dynamics of dispersal rate (emigration) and distance (transfer) in the sense that more emigration does not necessarily lead to more LDD or vice versa. Yet, evidently the increased costs of more LDD do feed back on the dispersal rate and decrease it. As such, our work demonstrates the need to explicitly incorporate the different dispersal phases (emigration, transfer and immigration; Clobert et al. 2012) when modelling the eco-evolutionary dynamics of dispersal (Travis et al. 2012).

In the context of evolutionary rescue (Gonzalez et al. 2013) or suicide (Parvinen 2007; Poethke et al. 2011a) and metapopulation stability (Heino et al. 1997) our results provide fertile ground for further investigations. Spatially correlated extinctions will synchronize large parts of a spatially structured population eventually increasing global extinction risk. Selection for larger dispersal distances may even reinforce

this negative effect in two ways, firstly by increased dispersal mortality and secondly by synchronizing population dynamics further. Yet, the lower ES dispersal rates could attenuate global extinction risk and LDD could increase recolonization rates and thus occupancy.

Our findings also have immediate implications for non-equilibrium systems such as populations at expanding ranges and invasive species. Spatial selection (the spatial assortment of highly dispersive individuals at a range margin; see Phillips et al. 2008) and kin selection (Kubisch et al. 2013) are known to select for increased dispersal rates at range margins and Starrfelt and Kokko (2010) have shown theoretically that range expansions additionally lead to an increase in LDD. If expanding range fronts are exposed to spatially correlated extinctions, e.g. due to changes in resource availability or increasing habitat fragmentation, our results suggest that LDD would be selected for which would lead to a further increase in invasion speed.

These implications are not limited to actively moving taxa. LDD is well known to occur in plants (Nathan 2006) and passive dispersers mediated by wind (Nathan et al. 2002) or different dispersal vectors (Flörchinger et al. 2010; Fronhofer et al. 2013).

In summary, spatially correlated extinctions or, more generally, spatially correlated density-independent external factors (Moran effect; Hudson and Cattadori 1999; Liebhold et al. 2004) may not only drive ecological (population fluctuations and synchrony) but also evolutionary dynamics.

## Acknowledgements

We are grateful to an anonymous reviewer as well as to Ruth Shaw and Nicolas Perrin who helped us improve our manuscript through their very constructive comments. We would like to thank Annelies de Roissart, Thomas Igerst and Matthias Jäger who helped to set up the experiments and Claudia Gräfe, Thomas Wengenmayr, Bianca Becker, Anna Kreis and Sebastian Bott for collecting preliminary data. The Department of Botany II, University of Würzburg provided facilities and Jutta Winkler-Steinbeck helped a lot for growing plants. The Departments of Animal Ecology, University of Würzburg kindly provided the climate chambers. EAF was supported by a grant of the German Excellence Initiative to the Graduate School of Life Sciences, University of Würzburg.

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## Supporting Information S1

Fronhofer, E.A., Stelz, J.M., Lutz, E., Poethke, H.J. and Bonte, D.: Spatially correlated extinctions select for less emigration but larger dispersal distances in the spider mite *Tetranychus urticae*

Table S1.1: *Tetranychus urticae* dispersal distances from the linear bioassay. The table shows the median number of adults per patch after seven days over all four replicates for the control (C) and the two extinction treatments (TR, random extinctions; TC clumped extinctions). The 25th and 75th percentiles are reported in brackets.

	patch 0	patch 1	patch 2	patch 3	patch 4
<b>C</b>	22 (16.75; 27.50)	0.5 (0; 1.0)	0 (0; 0)	0 (0; 0)	0 (0; 0)
<b>TR</b>	12.5 (7.25; 17.25)	4.0 (1.0; 8.75)	0 (0; 0)	0 (0; 0)	0 (0; 0)
<b>TC</b>	16.5 (16.0; 19.25)	2.0 (1.5; 2.25)	1.0 (0.75; 1.25)	0 (0; 0.25)	0 (0; 0)

## Supporting Information S2

Fronhofer, E.A., Stelz, J.M., Lutz, E., Poethke, H.J. and Bonte, D.: Spatially correlated extinctions select for less emigration but larger dispersal distances in the spider mite *Tetranychus urticae*

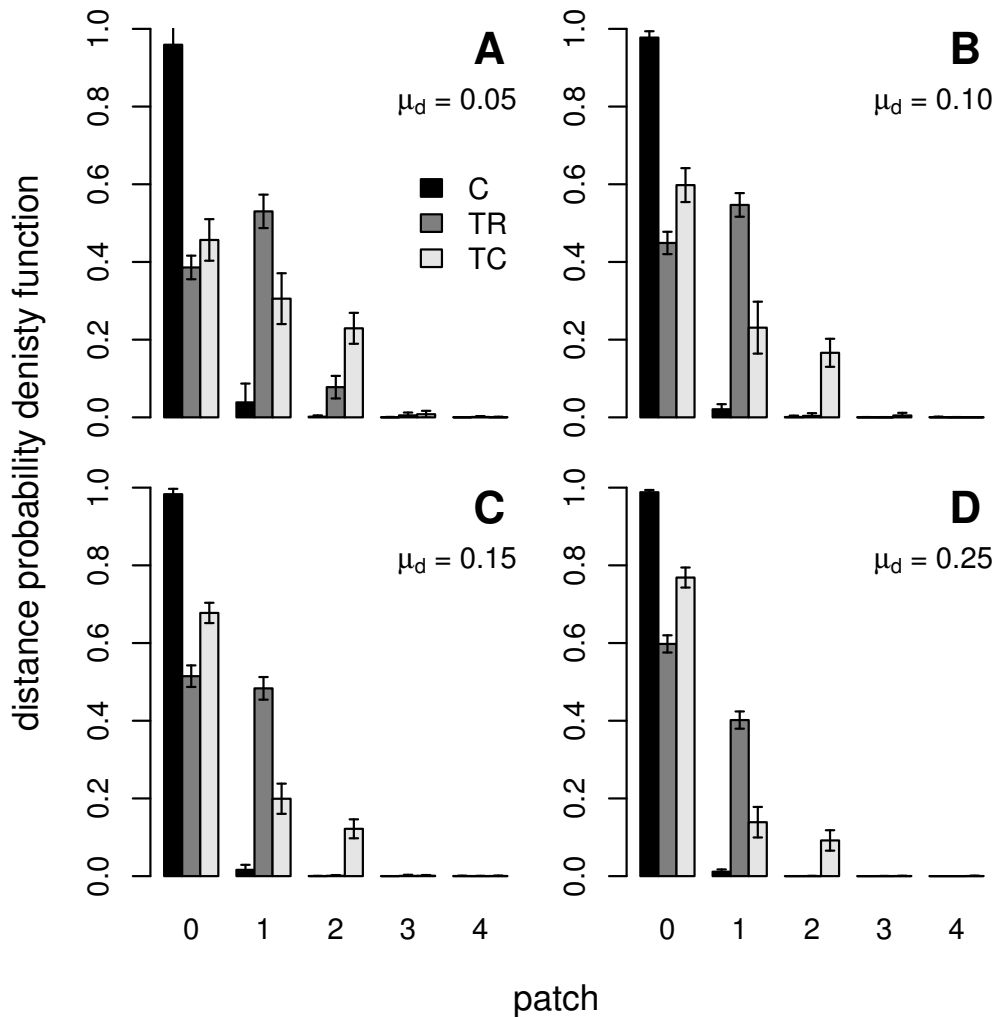


Figure S2.1: Sensitivity analysis for  $\mu_d$  — dispersal mortality. The results depict the evolutionarily stable distribution of dispersal distances (distance probability density function). The results are averaged over 50 replicate simulation runs (mean  $\pm$  s.d.). Our standard scenario assumes  $\mu_d = 0.2$ . Parameters:  $K = 250$ ,  $\lambda = 5$ .

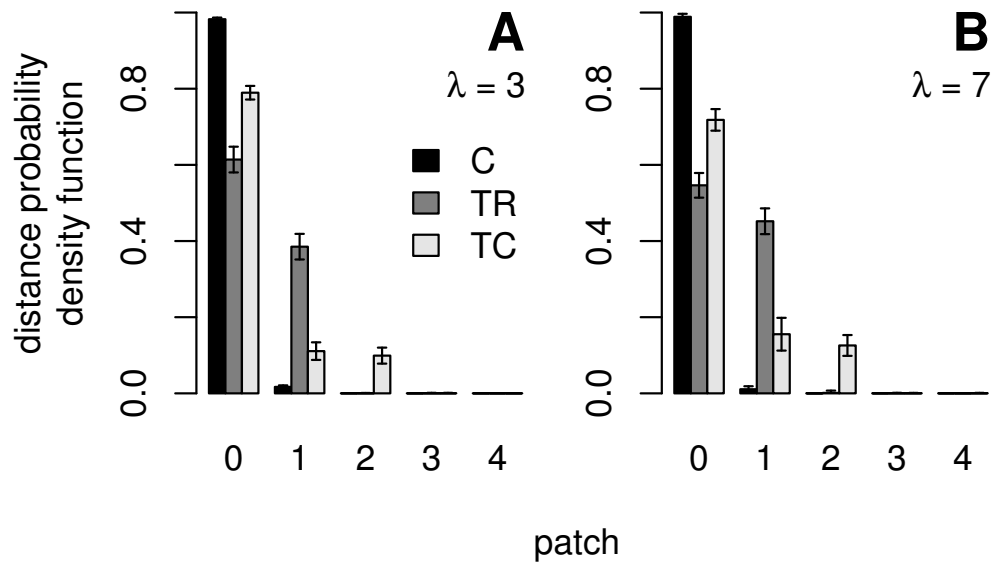


Figure S2.2: Sensitivity analysis for  $\lambda$  — fecundity. The results depict the evolutionarily stable distribution of dispersal distances (distance probability density function). The results are averaged over 50 replicate simulation runs (mean  $\pm$  s.d.). Our standard scenario assumes  $\lambda = 5$ . Parameters:  $K = 250$ ,  $\mu_d = 0.2$ .

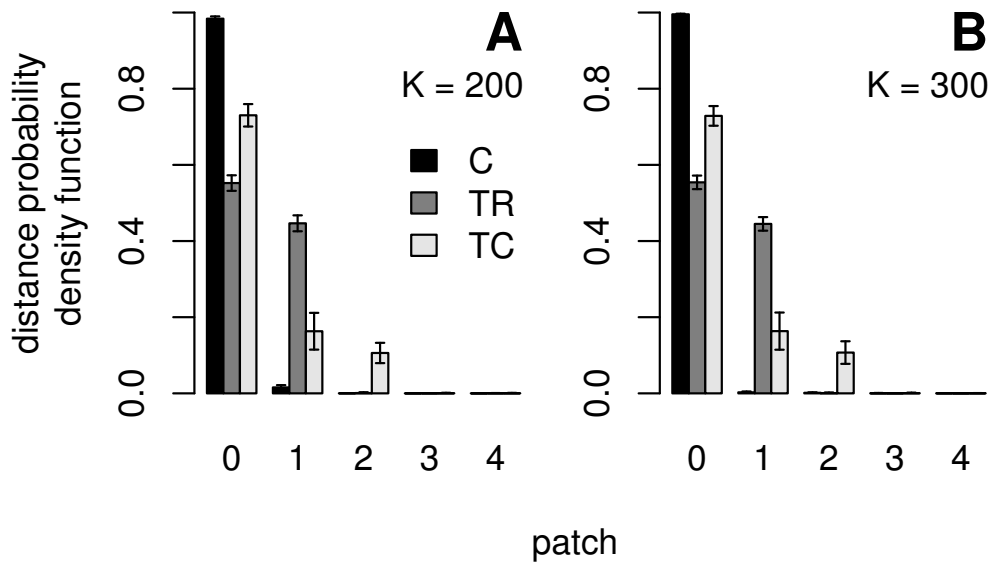


Figure S2.3: Sensitivity analysis for  $K$  — carrying capacity. The results depict the evolutionarily stable distribution of dispersal distances (distance probability density function). The results are averaged over 50 replicate simulation runs (mean  $\pm$  s.d.). Our standard scenario assumes  $K = 250$ . Parameters:  $\lambda = 5$ ,  $\mu_d = 0.2$ .