

LETTER

Spatial connectedness imposes local- and metapopulation-level selection on life history through feedbacks on demography

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Abstract

Dispersal evolution impacts the fluxes of individuals and hence, connectivity in metapopulations. Connectivity is therefore decoupled from the structural connectedness of the patches within the spatial network. Because of demographic feedbacks, local selection also drives the evolution of other life history traits. We investigated how different levels of connectedness affect trait evolution in experimental metapopulations of the two-spotted spider mite. We separated local- and metapopulation-level selection and linked trait divergence to population dynamics. With lower connectedness, an increased starvation resistance and delayed dispersal evolved. Reproductive performance evolved locally by transgenerational plasticity or epigenetic processes. Costs of dispersal, but also changes in local densities and temporal fluctuations herein are found to be putative drivers. In addition to dispersal, demographic traits are able to evolve in response to metapopulation connectedness at both the local and metapopulation level by genetic and/or non-genetic inheritance. These trait changes impact the persistence of spatially structured populations.

Keywords

Arthropoda, connectedness, connectivity, experimental evolution, habitat fragmentation.

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INTRODUCTION

Habitat fragmentation is, besides habitat loss, one of the most important human-induced drivers of biodiversity decline (Collinge, 1998; Forman, 2000; Heilman *et al.*, 2002). Most species live in spatially heterogeneous landscapes of suitable habitat patches that are interspersed by unsuitable matrix and connected by dispersal. Connectivity is a species or even population-specific metric that quantifies the fluxes of individuals among patches in the spatial network. It is determined by the individual movement capacities and the number of effective successful dispersers among patches (Tischendorf & Fahrig, 2001). This connectivity is to a large extent determined by the connectedness of the metapopulation. Connectedness defines to which extent a landscape facilitates or impedes the movements of organisms and their genes (Taylor *et al.*, 1993; Rudnick *et al.*, 2012), and refers to its structural properties like the number, shape, dimensions and proximity of the suitable patches (Tischendorf & Fahrig, 2000; Wang *et al.*, 2014).

Loss of connectivity decreases the chances of reestablishment of extinct populations, thereby putting the metapopulation at risk (Fuller *et al.*, 2015; Thompson *et al.*, 2017). Connectivity conservation is thus central to metapopulation persistence. While the ecological effects of connectedness loss are well studied from a theoretical (Melián & Bascompte, 2002; Kondoh, 2003; Liao *et al.*, 2017) and empirical perspective (Dobson *et al.*, 2006; Fenoglio *et al.*, 2010; Valladares *et al.*, 2012), evolutionary consequences are equally anticipated but rarely directly tested (Cheptou *et al.*, 2017). The evolution of inbreeding, mating systems or dispersal rates has been rarely studied so far (Stow *et al.*, 2001; Fahrig, 2003; Andersen *et al.*, 2004; Aguilar *et al.*, 2006; Keyghobadi, 2007; Bonte *et al.*, 2018).

Dispersal is anticipated to be a prime target of selection in metapopulations (Bonte & Dahirel, 2017). It integrates multiple processes during departure, transience and settlement and should therefore not be treated as a simple trait related to emigration alone (Bowler & Benton, 2005; Clobert *et al.*, 2009). It can be assumed that connectedness loss mostly influences the costs of transfer as movement becomes more expensive with increasing distance. These costs are known to lead to the evolution of decreased departure rates (Bonte *et al.*, 2003). Evolutionary adaptations to reduce costs of the other dispersal phases may, however, arise as well (Clobert *et al.*, 2012). Costs and trade-offs may manifest themselves during each of these three phases (Bonte *et al.*, 2012), and interactions with other life history traits like reproduction or stress resistance (Bonte *et al.*, 2012) give rise to the evolution of life history syndromes (i.e., consistent correlations of dispersal-related traits; Clobert *et al.*, 2009). These syndromes can be genetically determined at the individual level but they may equally emerge from joint evolution at the population and metapopulation level (Clobert *et al.*, 2012).

Changes in fluxes among patches are known to directly impact metapopulation and local population dynamics (Cheptou *et al.*, 2017; Bonte *et al.*, 2018). These demographic changes result from direct changes in the spatial structure of the network, for instance by changes in connectedness, patch size or the presence of external extinctions or from trait evolution (De Roissart *et al.*, 2015; Bonte & Bafort, 2019). Moreover, spatial networks are usually heterogeneous and modular with respect to their topology (Fahrig, 2003; Urban & Skelly, 2006; Ferrari *et al.*, 2007). A few patches are typically more connected to others and thereby serve as hubs in the network (Van Langevelde, 2000; Calabrese & Fagan, 2004). Such asymmetries in connectedness impact local

immigration/emigration balances and can lead to source–sink dynamics (Poethke *et al.*, 2011; Dey *et al.*, 2014; Wang *et al.*, 2015). When emigration rates are equal among patches, net immigration rate increase in the most connected patches, thereby elevating local resource competition (Baguette & Schtickzelle, 2003; Amarasekare, 2008; see also Box 1). Local competition can then impose selection on traits related to stress resistance, or select for a reduced population growth rate to counter resources overshooting in kin-structured populations (McClain, 1995). Finally, if emigration–immigration balances change across patches, different levels of relatedness may affect local reproductive (Macke *et al.*, 2011) and dispersal strategies (Van Petegem *et al.*, 2018). As a result, even in metapopulations consisting of a network of patches with identical habitat, local selective pressures can be different (Rossetti *et al.*, 2014) and local selection on traits related to density dependence, kin competition and stress resistance may act in concert with metapopulation-level selection on dispersal.

Box 1 Asymmetric immigration rates

Theoretical demonstration of how differences in local connectedness impose asymmetric immigration rates, and thus mean carrying capacity. In a spatial network as implemented in our experimental evolution, we assume local resource availability determining local carrying capacity K , and dispersal rates d . If we assume the population to be regulated at K , then dK individuals are emigrating from each patch, and those emigrants will be equally divided across the number of connections to the other patches C . Given a certain dispersal mortality μ , each ‘target’ patch will then receive $(1 - \mu) \times (d \times K/C)$ immigrants. If dispersal is occurring after local density regulation (as expected in our experiments because of female dispersal), then the eventual population size will be largest on the most connective patches and reaching a new equilibrium.

$$\dot{K}_n = K_n - \left(\frac{d \times K_n}{C_n} \right) + \sum_{p=1}^{p=m(m \neq n)} \frac{d \times K_p}{C_p} \quad (1)$$

This yields for the different local patches to the following K_n :

-Central patch:

- emigrants: $(d \times K/8)$
- immigrants: $4(d/3) + 4(d/5) = (32/15)d \approx 2.13d$

-Corner patches:

- emigrants: $(d \times K/3)$
- immigrants: $2(d/5) + d/8 = (21/40)d \approx 0.52d$

-Side patches:

- emigrants: $(d \times K/5)$
- immigrants: $2(d/3) + 2(d/5) + d/8 = (143/120)d \approx 1.19d$

We engaged in experimental evolution with the spider mite *Tetranychus urticae* as a model (Fronhofer *et al.*, 2014; De Roissart *et al.*, 2015; Van Petegem *et al.*, 2018) to test whether and how different levels of habitat connectedness affect trait evolution. We particularly focused on traits related to dispersal and reproduction as theory predicts these to be under regional and/or local selection in metapopulations (Duputié & Massol, 2013; Berdahl *et al.*, 2015). We expected individuals in less connected metapopulations to evolve a lower propensity of dispersal, or to evolve lower dispersal costs by means of a higher resistance to the environmental conditions during transfer (e.g. food deprivation). We disrupted putative local selection resulting from systematic changes in densities, and *kin* (genetic relatedness) and *kind* (phenotypic similarity) structure (Van Petegem *et al.*, 2018) by reshuffling mites among local patches in some of the metapopulations.

We eventually obtained a deeper mechanistic understanding of the emerging trait divergence by relating it directly to the quantified local population dynamics.

MATERIALS AND METHODS

Experimental evolution

Individuals from our focal species, the two-spotted spider mite *Tetranychus urticae* Koch were collected from our stock population (see Supplementary Materials S11 for a more detailed description) and introduced in 24 artificial habitats composed by a 3×3 grid of food patches (bean leaves cuts) connected by Parafilm® bridges (see Fig. 1). Because of the patch network design, each patch had a different level of connectedness inside the metapopulation (further referred to as *local connectiveness*), with central patches having the highest number of links (8), corner patches the lowest (3) and side patches as intermediate (5) value. The bridges varied in length between metapopulations, the bridges varied in length between 4, 8 and 16 cm, thus determining the *metapopulation connectedness* of each setup. Dispersal was considered expensive in our experiment both because individuals are not able to forage on Parafilm® and because of the risk of ending up into the wet cotton during movement and drowning. These transfer costs increase with bridge length.

Each connectedness level was replicated 8-fold, three of which were subjected to a randomisation procedure of the adult females. We implemented this randomisation procedure to test whether performance would evolve in response to local connectedness as well. In the randomisation treatments, all females from a single metapopulation were collected once per week using a thin pen brush, pooled together on a fresh bean leaf to reduce stress as much as possible and then randomly redistributed among the patches of the same metapopulation while maintaining the same local densities as before the collection. This treatment thus destroys any genetic structure of the metapopulation, but maintains the metapopulation demography as reflected in the local densities and temporal changes herein. Since individuals are dispersing among patches in between the shuffling treatments, they experience identical transfer costs as the non-randomised experimental metapopulations. In order to ensure comparable levels of handling

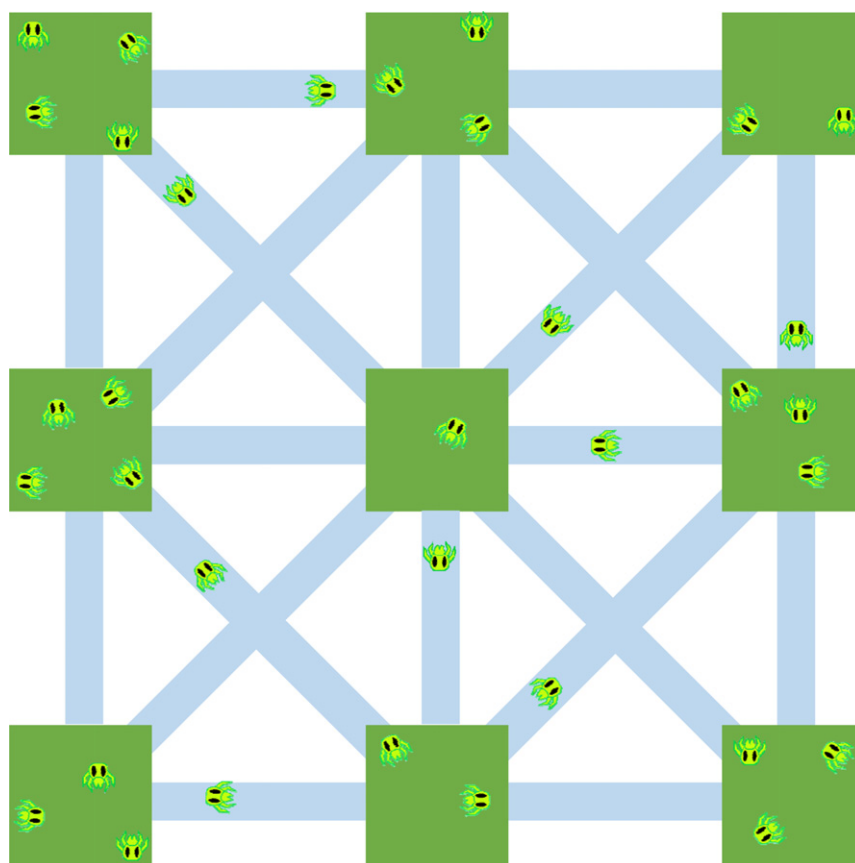


Figure 1 Schematic representation of the long-term (6 months) experimental setups. Nine identical patches were arranged in a 3×3 grid and connected using Parafilm bridges. The length of the bridge (X cm in the picture) was dependent on the treatment; the diagonal bridges varied depending on the value of X .

stress between treatments, the females from the non-randomisation systems were also collected, not randomised and placed back on their original patch briefly afterwards. We focused on adult females as they are the main dispersal stage for our focal species (Bitume *et al.*, 2011). Contrasting trait values between the randomised and non-randomised experimental metapopulations indicate whether performance evolved at the metapopulation level (no randomisation effects expected), and/or the local level (randomisation would then remove any signature of local selection).

All experimental metapopulations (24 in total) were initialised in September 2016 with five freshly inseminated females and two additional adult males on each patch (hence 1512 individuals overall) using a soft-haired brush and monitored for 2 weeks to ensure the settlement of the population. This standardised initialisation ensures equal starting conditions and sufficient genetic variation (as for instance demonstrated in Van Petegem *et al.*, 2018). Given the high intrinsic growth rate of the species, populations reached carrying capacity after approximately two generations. We analysed mean population sizes with GLM having metapopulation and local connectedness as categorical factor and time as a continuous covariate. Experimental metapopulation replicate was modelled as a random factor. Local fluctuations were

quantified as their alpha variability, as determined by the coefficient of variance of the local population sizes in time (Wang & Loreau, 2014). These were equally analysed using GLM with experimental metapopulation as a random factor. A more detailed outline of the focal species and the long-term experimental setup can be found in Supplementary Materials S11.

Trait evolution following common garden

Twenty-five weeks from the start of the experiment (*c.* 12 generations under the experimental conditions; Hance & Van Impe, 1999), we collected individuals from all the different patches to quantify whether relevant ecological traits had evolved in response to metapopulation connectedness. We quantified performance and dispersal in adult females that were raised for one generation under common garden conditions (see further). We used five adults from each patch in each experimental metapopulation, hence 45 F0 individuals per experimental metapopulation (45×24 individuals in total), as the starting material for a generation of F1 females reared under identical conditions. We placed the five females coming from a same patch together into the same common garden and we kept them separated from all the others. F0 females were allowed to lay eggs for 2 days on a

standardised bean leaf, and offspring were subsequently raised under comparable densities (~ 2 individuals/cm²), at 30 °C, a 16-8 L/D photoperiod and food *ad libitum*, insured by the low density in relation with the leaf area (~ 25 cm²). This procedure enabled us to study traits independent of plastic responses to the experienced conditions in the metapopulation. After one generation spent in common environment, eventual maternal effects would be mitigated and any difference between lines can be considered because of the evolutionary divergence (Macke *et al.*, 2011).

Given the extent of the trait quantification experiments, F1 offspring were distributed across experiments to quantify (1) dispersal, (2) starvation resistance and (3) reproductive performance.

Below, the structure and statistical analysis for each life history trait are presented. We present the full models, so including interactions, even when non-significant. We conclude the trait and population analyses with a cross-experimental metapopulation correlation analyses (Pearson's correlation).

DISPERSAL PROPENSITY

This test was performed at metapopulation level. Freshly moulted (1–4 day old) and inseminated females are the dispersing stages in this species (Li & Margolies, 1993, 1994). Such individuals were used for the experiments after rearing one generation under common garden conditions from the same experimental metapopulation replicate. Therefore, data could only be analysed in function of the metapopulation typology, as this is the anticipated unit of selection. The propensity and the timing of dispersal were tested using a standardised setup of two-patch systems, each composed of two 2.5×1.5 cm² patches connected by an 8 cm long, 1 cm wide Parafilm[®] bridge. On the starting patch, we placed females from F1 at different densities, generating a density gradient between 1.3 and 10.4 individuals/cm². We spanned this range by ensuring equal sample sizes as much as possible around low (5 individuals), intermediate (10) and high (40) densities, the lowest density being similar to what found in nature under a mild infestation scenario (Helle & Sabelis, 1985). A complete set of trials was performed for each metapopulation, with one replica for each density. The two patches were then connected and monitored for 4 days, as the chance of adult individuals older than 5 days to disperse is low (Li & Margolies, 1993, 1994). Each day, the number of individuals on the starting and the other leaf was recorded, along with the number of individuals on the bridge at the time of the census. The target leaf to which dispersal took place was refreshed after each count to prevent successfully dispersed females from moving back to the starting patch.

We ran in total 78 two-patch dispersal trials, for a grand total of 1330 monitored individuals. We analysed both the fraction of emigrants over the duration of the experiment (dispersal rate; individuals leaving the source patch over 4 days) and immigrants (immigration rate; individuals successfully settling on the target patch over 4 days), and their daily changes during the experiment. These fractions were analysed using generalised linear mixed model with a binomial error structure and logit-link; metapopulation connectedness, presence/absence of randomisation (categorical) and density on the

starting patch (continuous), as well as their two- and three-way interactions were considered as explanatory variables. Day of the test was added for evaluating the temporal dynamics. The metapopulation replicate was added as random effect to control for dependency in responses from individuals originating from the same experimental metapopulation.

Finally, we modelled the day at which each individual dispersed as the relevant individual trait (dispersal timing) as a dependent variable in a linear model, using again metapopulation connectedness, presence/absence of randomisation (categorical) and density on the starting patch (continuous covariate) as explanatory variables, along with their two-way and three-way interactions. We used a Poisson distribution for count data with low mean. The metapopulation replicate and dispersal trial replicate were here as higher added as random factors. Only individuals that performed a dispersal event were included in this analysis so to render this analysis complementary to the dispersal rate analyses.

STARVATION RESISTANCE

This test was performed at metapopulation level. One experimental arena was prepared for each metapopulation (25 arenas in total: 24 metapopulations + 1 from the stock as external control). Each arena consisted of a 25 cm² square cut from a black plastic sheet mounted on a wet cotton bed into a plastic Petri plate and fixed in position by wet paper strips: the strips partially overlapped with the plastic (~ 3 mm) to form a wet barrier and deter mites from falling into the cotton. For each experimental metapopulation replicate, five 1- to 2-days old F1 adult females from the common gardens were placed into an arena. Individuals coming from different patches of the same metapopulation were pooled together as to represent the composition of the original metapopulation. The five out of nine most abundant local populations at the moment of the F0 individual's collection were selected to collect the F1 females. The Petri plates were then stored at room temperature ($\sim 25^\circ\text{C}$). Based on exploratory trials, we compared the survival percentage after 48 h, as this time appeared to be most discriminatory regarding the death/survival balance. Data were analysed by generalised linear mixed modelling using a binomial distribution, with the connectedness level and presence/absence of randomisation as explanatory categorical variables. As we were only able to have one experimental trial per experimental metapopulation replicate, no random effects were added.

REPRODUCTIVE PERFORMANCES

This test was performed at local population and metapopulation level. Single fertilised females from the F1 generation reared under standardised conditions were collected and placed individually on 2.5×1.5 cm² bean leaf cuttings, mounted on a bed of wet cotton and kept in place with paper strips. From each experimental metapopulation, one or two females were collected from each patch, depending on the availability of individuals, for a grand total of 370 females across the 24 metapopulation replicates. The leaves were placed in a temperature regulated cabinet at 30°C for 10 days

with a 16-8 L/D photoperiod. They were daily moisturised to prevent desiccation of the leaves and the escape of the mites through the cotton layer. Each female was monitored daily, recording her status (dead or alive), as well as the number of eggs, larvae and juveniles present on the patch. The number of individuals from these three age classes was subsequently summed as a measure of reproductive performance. We ran a GLM assuming a quasi-Poisson distribution for the count data, to correct for overdispersion (Cameron & Trivedi, 1990). Reproductive performance at day 6 was used as the dependent variable to avoid effects of overlapping generations, as the following generation F2 individuals did not yet reach adulthood at the time. As reproductive performance was hypothesised to evolve in relation to local conditions as well, we added patch location of the F0 females (centre, corner or edge) as an independent categorical variable in addition to the earlier used metapopulation-level connectedness and randomisation treatments. The experimental metapopulation replicate was added as random effect to control for shared evolutionary history. As the reproductive rate was calculated at patch or treatment level but not at the individual level, females that died before the end of the test were retained in the analysis as their performances still impacted the reproductive success of their (meta-)population of origin. A complementary analysis was performed to check if the day of death was significantly different between treatments, using the same model structure as previously described.

LINKING TRAITS TO LOCAL POPULATION DYNAMICS

In search for a more mechanistic explanation of the underlying drivers of the observed trait divergence, we added mean

local population sizes and their coefficient of variance as quantified over the entire experiment or only the last 4 weeks (~ last two generations) to the above described models as (1) an additive covariate to test whether within-treatment variation in evolved traits could be explained by the local population dynamics, or (2) replacing the treatments, hence inferring trait-population dynamics across all experimental metapopulation (reduced model). Results from the additive models are provided in Supplementary Material SI2, while those from the reduced models (Analysis of Deviance, Type III test) are reported in the result section.

RESULTS

Trait evolution

Dispersal

Evolved emigration and immigration rates (success rate) during the organism's dispersal window of four days were not dependent on the connectedness or randomisation treatment; only the starting density had a significant and positive (see Fig. SI3.1 in Supplementary Materials SI3) impact on the emigration rates (Table 1). Individuals that evolved in the metapopulations with the lowest level of connectedness showed overall delayed timing of dispersal (day of departure) (Fig. 2a), but this effect was especially pronounced when no randomisation was applied (significant interaction randomisation treatment x metapopulation level of connectedness; Table 1). This delayed timing is reflected in a significant interaction of the cumulative emigration rate in relation to the time of testing (day 1–4), the metapopulation connectedness and the randomisation treatment (Analysis of Deviance, Type

Table 1 Full model analysis of deviance table (Type III Wald χ^2 -tests) for emigration and immigration rate and dispersal timing in relation to the connectedness, randomisation of the metapopulation in which individuals evolved and density in the dispersal trial

Dependent variable	Explanatory variable	d.f.	χ^2	Pr(> χ^2)
Emigration rate	Metapopulation Connectedness	2	1.5251	0.6765
	Randomisation	1	0.0172	0.8957
	Starting Density	1	7.96	0.0048**
	Metapopulation Connectedness × Randomisation	2	0.1978	0.9058
	Metapopulation Connectedness × Starting Density	2	2.0713	0.3549
	Randomisation × Starting Density	1	0.3847	0.5351
	Metapopulation Connectedness × Randomisation × Starting Density	2	3.5738	0.1675
Immigration rate	Metapopulation Connectedness	2	0.6346	0.8885
	Randomisation	1	0.5902	0.4423
	Starting Density	1	0.3421	0.5586
	Metapopulation Connectedness × Randomisation	2	0.6865	0.7095
	Metapopulation Connectedness × Starting Density	2	1.3771	0.5023
	Metapopulation Randomisation × Starting Density	1	0.0099	0.9208
	Metapopulation Connectedness × Randomisation × Starting Density	2	1.1632	0.5590
Individual dispersal day	Metapopulation Connectedness	2	17.1631	0.0001875***
	Randomisation	1	1.7121	0.1907190
	Starting Density	1	0.0001	0.9916746
	Metapopulation Connectedness × Randomisation	2	7.0688	0.0291764*
	Metapopulation Connectedness × Starting Density	2	0.7331	0.6931065
	Randomisation × Starting Density	1	0.5802	0.4462486
	Metapopulation Connectedness × Randomisation × Starting Density	2	4.4365	0.1087995

* ≤ 0.05

** ≤ 0.01

*** ≤ 0.001

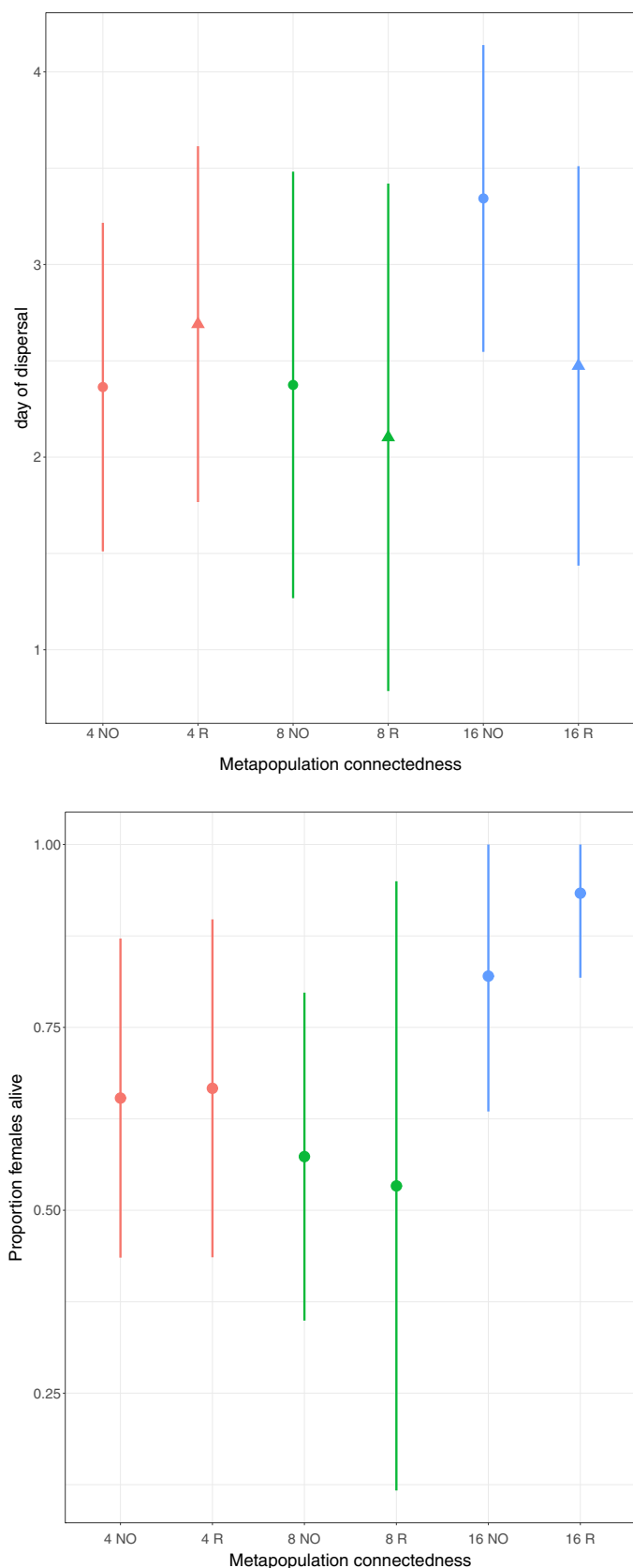


Figure 2 (a: top panel): the effect of connectedness on the individual day of dispersal in the different treatments ($M \pm SD$). (b: bottom panel): proportion of alive individuals ($M \pm SD$) after 48 h depending on the treatment of the source metapopulation.

III test: $\chi^2 = 14.57$, $P = 0.024$), with accordingly significantly lower dispersal rates at day 2 only for individuals that evolved in the least connected metapopulations (see Fig. SI3.2 and Table SI3.1 in Supplementary Information SI3).

Starvation resistance

The proportion of individuals surviving 48 h of starvation only depended on the connectedness experienced during experimental evolution, with highest survival rates for individuals that evolved in the least connected metapopulation relative to the two other treatments (Analysis of Deviance, Type III test: $\chi^2 = 11.89$, $P = 0.003$; Fig. 2b). Survival rates did not differ between the randomisation procedures (Analysis of Deviance, Type III test: $\chi^2 = 0.12$, $P = 0.720$) nor on the interaction between both (Analysis of Deviance, Type III test: $\chi^2 = 0.85$, $P = 0.651$).

Reproductive performance

The number of the females that died during the test did not differ among treatments (see Supplementary Materials SI4). The local connectedness of the patch the individuals originated from affected reproduction significantly (Analysis of Deviance, Type III test: $\chi^2 = 9.6736$, $P = 0.008$, Fig. 3). In general, reproductive performance was overall the lowest in offspring from individuals that were collected in the central patch (Post hoc Tukey test: corner-centre contrast: t -ratio = -2.895 , $P = 0.0112$; edge-centre contrast: t -ratio = -3.073 ; $P = 0.0065$). Reproductive performance was not affected by the metapopulation connectedness or the randomisation procedure (see Table SI4.2 in Supplementary Materials SI4 for the complete analysis).

Trait correlations at the metapopulation level

Across experimental metapopulations, dispersal latency is positively correlated with reproductive performance ($r_{23} = 0.52$; $P = 0.012$). Populations that evolved a high intrinsic growth rate thus evolved a delayed dispersal. No correlation was found between starvation resistance and reproductive performances ($r_{23} = -0.119$; $P = 0.588$) or dispersal timing ($r_{23} = -0.162$; $P = 0.461$).

Linking traits to local population dynamics

Local mean densities and fluctuations herein did not differ statistically among treatments over the entire period of the experiment, and neither over the last 4 weeks (Supplementary Material SI2). Despite any clear trend in the local population dynamics across the connectedness and randomisation treatment, trait evolution could be related to the (average) local population dynamics (Fig. 4).

Local population dynamics did not explain additive variation in dispersal timing within the treatments, and neither were they directly related to the mean local population size ($\chi^2 = 0.02$; $P = 0.902$) and fluctuations (CV_{pop}) herein ($\chi^2 = 2.23$; $P = 0.134$) during the last 4 weeks of the experiment. Delayed dispersal evolved, however, in metapopulations characterised by more stable local populations ($\beta = -0.786$; $\chi^2 = 6.12$; $P = 0.013$) over the entire experimental evolution,

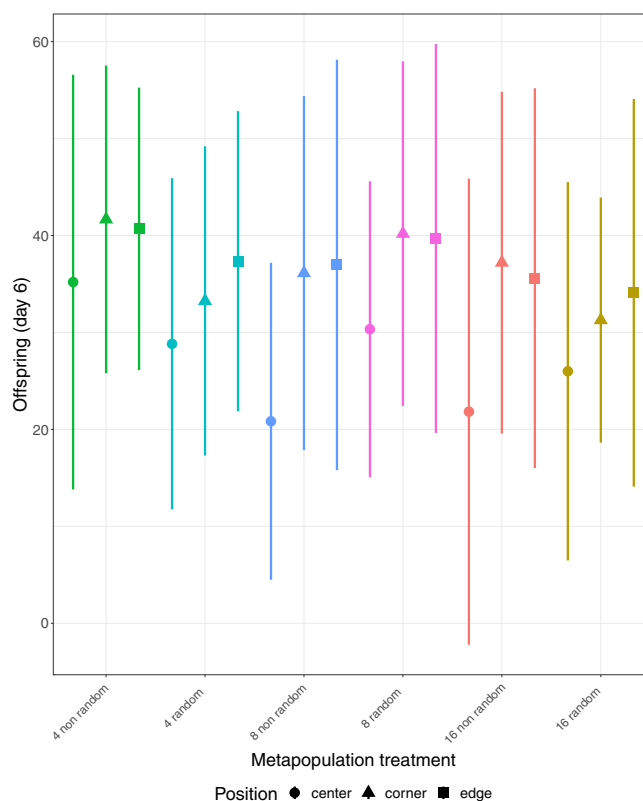


Figure 3 Reproductive performance measured as the number of offspring after 6 days ($M \pm SD$), for each combination of fragmentation treatment and relative position of the patch of origin of the individuals (before common garden period).

while population size did not affect it significantly ($\beta = 0.002$; $\chi^2 = 0.093$; $P = 0.76$).

Additive models for starvation resistance showed a tendency for evolved higher resistance in metapopulations with more stable and larger local population sizes within each of the treatments (see Supplementary Material SI2). This finding is pronounced across treatments, and both when linked to the local population dynamics as recorded over the entire experiment (mean population size $\beta = 0.063$; $\chi^2 = 3.42$; $P = 0.064$; CV_{pop} : $\beta = -2.58$; $\chi^2 = 3.26$; $P = 0.071$) and the last 4 weeks (mean population size: $\beta = 0.033$; $\chi^2 = 0.3.12$; $P = 0.077$; CV_{pop} : $\beta = -1.68$; $\chi^2 = 8.80$; $P = 0.016$).

Reproductive performance was negatively correlated with the mean population size during the last 4 weeks in both the additive (see Supplementary Material SI2) and the reduced model ($\beta = -0.035$; $\chi^2 = 4.42$; $P = 0.036$). No relationships were found with population dynamics over the entire experimental period (mean population size: $\chi^2 = 2.26$; $P = 0.132$; CV_{pop} : $\chi^2 = 0.02$; $P = 0.894$), and neither with local fluctuations during the last 4 weeks ($\chi^2 = 1.72$; $P = 0.192$).

DISCUSSION

Dispersal is a complex life history trait encompassing multiple, often tightly coupled stages. To date, most evidence for dispersal evolution in metapopulations stems from studies on emigration rate (Olivieri *et al.*, 1995; Mathias *et al.*, 2001; Gyllenberg *et al.*, 2002; Ronce, 2007). However, simultaneous

evolution of traits related to the multiple dispersal stages, including transience and settlement, has been theoretically demonstrated to lead to often complex feedbacks which may or may not impact the emigration rate (Travis *et al.*, 2013; Delgado *et al.*, 2014). Our experimental work demonstrates that changes in metapopulation connectedness altered the joint evolution of dispersal timing, dispersal costs and reproduction. Connectedness loss did not lead to the evolution of decreased emigration rates over the period in which individuals are able to disperse, so the individual dispersal capacity.

The evolution of dispersal timing has been theoretically addressed in response to either dispersal at adulthood (breeding dispersal) or at birth (natal dispersal) (Johst & Brandl, 1999; Hirota, 2004; Lakovic *et al.*, 2015, 2017), and only recent studies have started addressing the issue at a more detailed time scale (Li & Kokko, 2019). Here, we found evolved breeding dispersal to be delayed in the least connected metapopulations. The delay was especially pronounced in the non-randomised treatment, indicating that evolution in response to local kin or kind interactions, or other local selection pressures is a more prominent driver than metapopulation-level selection from changes in connectedness. Delayed dispersal can be mechanistically interpreted as a delayed density dependence as individuals delaying dispersal are more likely to be longer engaged in local competitive interactions. In this sense, it reflects density-dependent emigration strategies (Saether *et al.*, 1999; Hovestadt & Poethke, 2006) with density thresholds evolving to higher levels in disconnected metapopulations.

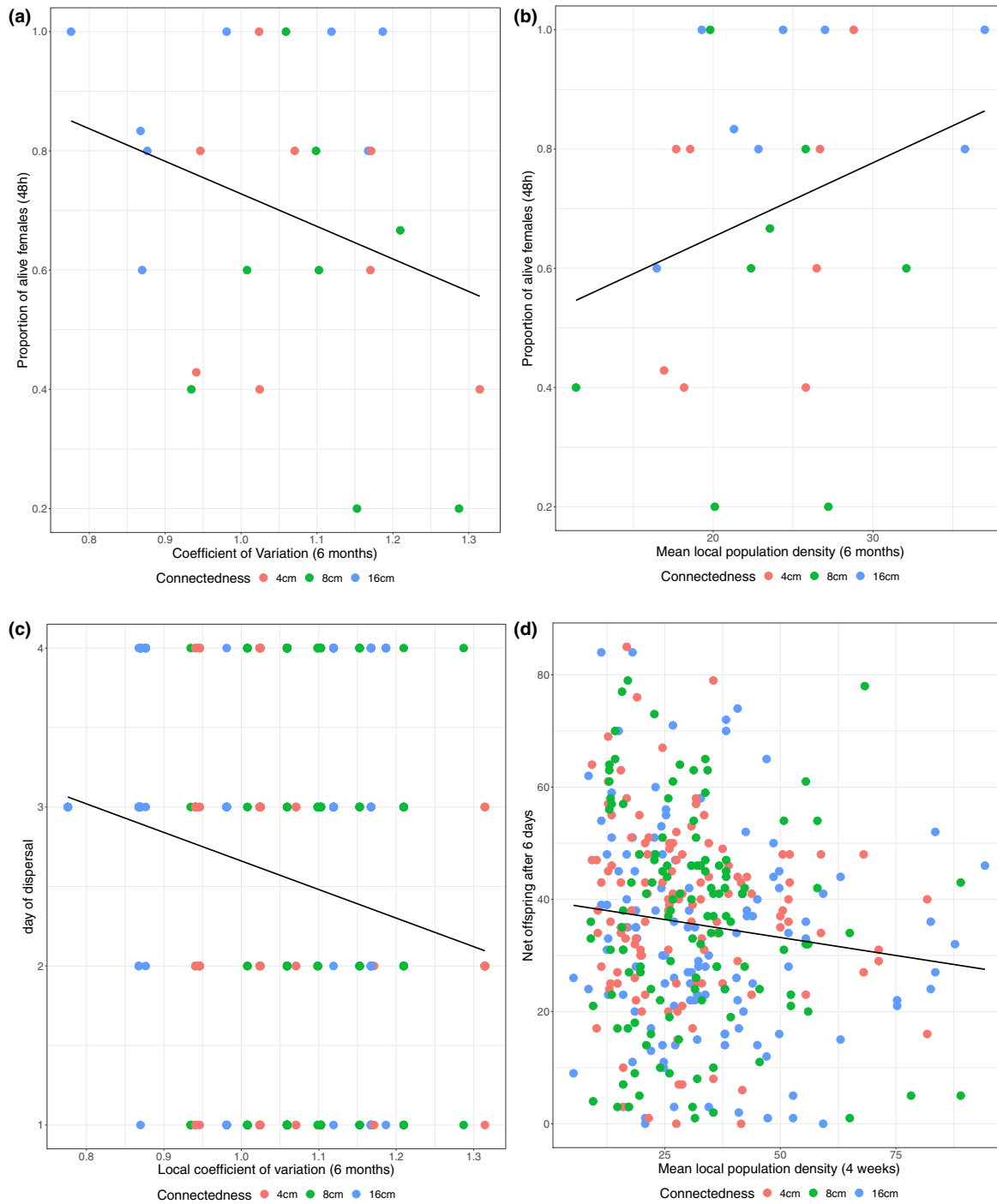


Figure 4 Effect of local fluctuations in densities (local coefficients of variation; left) and mean local population density (right) on the different evolved traits. (a) coefficient of variation over 6 months and survival rate after 48 h; (b) local population density over 6 months and survival rate after 48 h; (c) coefficient of variation over 6 months and dispersal timing; (d) local population density over the last 4 weeks and reproductive performance.

Theory demonstrates that dispersal evolves to higher rates in metapopulations that are subjected to stronger demographic fluctuations (Poethke *et al.*, 2003). Our findings suggest that a delayed dispersal will be associated with overall lower realised dispersal rates.

Individuals from the least connected metapopulation also evolved the largest starvation resistance, but independent of the randomisation treatment. As we found no correlation

between evolved starvation resistance and dispersal timing across metapopulations, both traits evolved jointly but independently in the non-randomised metapopulations. This accords with the perspective brought forward by Bonte & Doherty (2017) that dispersal needs to be treated as a central and independent trait in life history evolution. The evolution of starvation resistance can be intuitively explained as a response to metapopulation-level costs of dispersal, that is,

the energetic and risk costs during transfer on the bridges (Bonte *et al.*, 2012). However, as an increased starvation resistance was correlated to local population sizes across the treatments, more resistant individual may additionally evolve from feedbacks between connectedness and local population dynamics. An increased competition in metapopulations with more stable and higher local densities may hence be sufficient to induce the evolution of traits related to dispersal costs. The evolution of such an 'endurance-oriented' strategy evolved as a consequence in the least connected metapopulations. We here thus demonstrate the prevalence of a predicted but not yet documented eco-evolutionary feedbacks in metapopulations (Bonte *et al.*, 2018).

Building up energy reserves to survive long periods of food shortage is an expensive process that allocates resources from other vital processes. Starvation resistance is commonly associated with larger body mass, and usually has consequences on fertility, reproduction timing and longevity (Tessier *et al.*, 1983; Hoffmann & Harshman, 1999; Rion & Kawecki, 2007). However, we did not detect such trade-offs as reproductive performance only diverged in response to the local patch type and not in relation to the connectedness of the metapopulation in which they evolved. The systematic lower reproductive performances in individuals from central patches in the network are intriguing as patches were identical in terms of quality and size throughout the network in both the unmanipulated metapopulations (natural dispersal) and the ones that are shuffled. Reduced reproductive performance is expected to evolve in response to intense competition (Krüger *et al.*, 2002; Agrawal *et al.*, 2004) and patches with higher local connectedness should theoretically receive more individuals than those with fewer connections, independent of the metapopulation-level connectivity. While the mean and variance of local population sizes did not differ significantly in response to local and metapopulation-level connectedness, our analyses that linked traits and local populations at the metapopulation level demonstrated consistent lower reproductive performance in individuals that inhabited patches experiencing higher densities the last 4 weeks prior to the trait assessment.

Paradoxically, but in line with these findings, this signature was not destroyed by randomisation. This implies that the observed lower reproductive performance, as measured after one generation of common garden, must originate from epigenetics or persisting intergenerational plasticity rather than from fast genetic evolution. Such transgenerational plasticity is common in *T. urticae* (Bitume *et al.*, 2011; Magalhães *et al.*, 2014; Marinosci *et al.*, 2015; Van Petegem *et al.*, 2015), and even grandmaternal effects have been recorded in dispersal-related traits (Bitume *et al.*, 2014). As reproductive performance was positively correlated across metapopulations with dispersal latency, local condition thus affects body condition, dispersal timing and reproduction across generations in a tangled way.

Overall, this insight pleads for a careful interpretation of experimental common garden procedures that aim to separate plastic from genetic effects in trait expression. As even conditions experienced by grandmothers have the potential to impact life history traits in complex manners, common

garden experiments as performed by us and many others (see De Meester *et al.*, 2019) need to be interpreted with the needed precaution in terms of the exact underlying mechanism. Ideally they are accompanied by genomic analyses if the loci underlying trait expression are known (for dispersal some candidate genes have been detected; Saastamoinen *et al.*, 2018). From an ecological perspective, these insights remain nevertheless important as transgenerational effects may much faster than genetic selection feedback on the ecological dynamics (Galloway, 2005; Drummond & Ancona, 2015) and leave signals that are currently interpreted as feedbacks from genetic evolution (De Meester *et al.*, 2019).

We demonstrate that evolutionary dynamics in metapopulations do not follow simple theoretical predictions based on dispersal and genetic selection alone. Local and metapopulation-level dynamics interact with each other and influence the adaptation of the individuals at both levels, with ecological population dynamics influencing evolutionary dynamics and the other way around (Hanski, 2012). Stress resistance, for instance, which we found to evolve in response to habitat fragmentation, can potentially turn into pre-adaptation to other kind of stressors, that is, suboptimal host plants or novel habitats and enhance persistence under environmental change (Jenkins *et al.*, 1990; De Roissart *et al.*, 2016; Bisschop *et al.*, 2019).

Habitat fragmentation is a central tenet in conservation biology as it is expected to reduce connectivity and eventually lead to species loss and disintegration of local food webs (Thompson *et al.*, 2017). However, connectivity between patches can be evolutionary rescued through adaptation to higher dispersal costs or development of novel dispersal mechanisms (Kendrick *et al.*, 2017). Given that evolution of dispersal-related traits shifts cost-benefit balances towards a more beneficial ratio in metapopulations (Bonte *et al.*, 2012), these evolutionary dynamics adaptations will feedback on other traits (e.g. different allocation of energy reserves to reproduction) as well and thereby impact the ecological processes (Bonte *et al.*, 2018). Such an integrated view on dispersal, life history evolution and costs shifts in response to habitat fragmentation is currently lacking (Cheptou *et al.*, 2017) but highly needed to advance the predictive ecology of species and ecosystems, especially in the fast-changing world of today (Urban *et al.*, 2016). While theory focuses, for reasons of tractability, on simple dynamics (Govaert *et al.*, 2019), we are able to demonstrate more realistic multivariate life history divergence in response to changes in habitat connectedness as caused by extended evolutionary processes (Laland *et al.*, 2015; Futuyma, 2017).

The decoupling of habitat connectedness and population connectivity could impact predictions from theory that assumes a direct and positive link between dispersal and habitat connectedness (Legrand *et al.*, 2017). The evolution of often-overlooked traits like dispersal timing, stress resistance or individual growth rates rather than dispersal rates *per se* could then act as a rescue mechanism for fragmented populations through their impact on metapopulation variability, local stabilising and spatial synchronising effects (Wang *et al.*, 2015).

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AUTHORSHIP

D.B. and S.M. developed the experimental design; S.M. performed the experiments and the statistical analysis; both authors contributed to manuscript writing and D.B. contributed substantially to the revision.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dz08kprt0>.

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