Unexpected evolution following connectedness loss

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Abstract

Connectivity loss is a renowned ecological threat for biodiversity and metapopulation persistence and anticipated to impose strong evolutionary dynamics. While selection is typically expected to act on dispersal-related trait that are expressed at the metapopulation-level, demographic changes in complex spatial networks may impose local divergence in life histories as well.

We engaged in experimental evolution, using metapopulations of spider mites *T. urticae* as a model to understand how connectedness loss affects trait evolution. Mites were introduced in spatial networks with non-equally connected local patches. In order to separate processes of local and metapopulation-level selection, we implemented a reshuffling treatment.

A decreased connectedness selected for increased starvation resistance, delayed dispersal timing and a reduced intrinsic growth rate. Reshuffling did not destroy any of these evolutionary processes, indicating that metapopulation-level selection was prominent. Intrinsic growth rates were, however, systematically lower in individuals that originated from the most connected local patch. Because this pattern was maintained under reshuffling, fast epigenetic evolution must have been acting as well.

We thus demonstrate multivariate selection on traits following connectedness loss related to population growth rate and dispersal, but not dispersal rate per se. We attribute these evolutionary dynamics to feedbacks between costs of dispersal and spatial demographic variation. Since these results could not be predicted from simple theory, they demonstrate the

need to incorporate multivariate trait evolution at multiple level to understand eco-evolutionary dynamics in metapopulations.

Introduction

Connectivity loss influences metapopulations dynamics at every level of biological organization, from individuals to ecosystems (Gibbs and Stanton, 2001; Crooks, 2002; Cushman, 2006). Connectivity is a species-specific metric, always determined by the species' movement capacity and its population-level dispersal among patches (Tischendorf and Fahrig, 2001). In contrast, the connectedness of patches within spatial networks is only dependent on the extent to which a landscape facilitates or impedes the movements of organisms and their genes among resource patches (Taylor *et al.*, 1993; Rudnick *et al.*, 2012). It is therefore affected by the structural properties - the number, shape, dimensions and distance of the suitable patches - inside a landscape (Tischendorf and Fahrig, 2000; Wang, Blanchet and Koper, 2014). Connectedness thus impacts connectivity by mediating both the ecological and evolutionary determinants of biological fluxes among patches (Bonte, Masier and Mortier, 2018).

Besides habitat loss, habitat fragmentation of natural habitats is one of the most important human impacts on biodiversity (Collinge, 1998; Forman, 2000; Heilman *et al.*, 2002). Connectivity loss is therefore central to metapopulation conservation as it decreases the (re-) establishment of extinct population, thereby putting the metapopulation at risk (Fuller, Doyle and Strayer, 2015; Thompson, Rayfield and Gonzalez, 2017). While the ecological effects on single species, and those integrated into food and mutualistic networks are well studied from a theoretical (Melián and Bascompte, 2002; Kondoh, 2003; Liao *et al.*, 2017) and empirical perspective (Dobson *et al.*, 2006; Fenoglio *et al.*, 2010; Valladares, Cagnolo and Salvo, 2012), evolutionary impacts are anticipated as well, but rarely holistically approached (Cheptou *et al.*, 2017). Indeed, the evolutionary feedbacks are especially studied by empiricism and theory with a strong focus on either the evolution of inbreeding, mating systems and dispersal rate (Stow *et*

al., 2001; Fahrig, 2003; Andersen, Fog and Damgaard, 2004; Aguilar *et al.*, 2006; Keyghobadi, 2007; Bonte, Masier and Mortier, 2018).

Dispersal is anticipated to be a prime target of selection in metapopulations (Bonte and Dahirel, 2017), but should not be treated as a simple trait related to emigration rate, as it integrates multiple processes during the phases of departure, transience and settlement (Bowler and Benton, 2005; Clobert *et al.*, 2009). Costs and trade-offs may manifest themselves among these three phases, but also in interaction with other life history traits (Bonte *et al.*, 2012), thereby leading to syndromes at both the individual, population and metapopulation-level (Clobert *et al.*, 2012). It can be assumed that connectedness loss mostly influence the costs of the transfer phase, thereby imposing selection on departure rates (Bonte *et al.*, 2003). Evolutionary feedbacks to reduce dispersal costs may, however, be prominent on the other dispersal phases as well and result in dispersal syndromes (Clobert *et al.*, 2012). Feedbacks on (pre-) departure behaviours (Derr, Aldent and Dinglet, 1981; Bell *et al.*, 2005; Cañete *et al.*, 2007), dispersal timing (Lakovic, Poethke and Hovestadt, 2015), movement (Korb and Linsenmair, 2002; Baguette and Van Dyck, 2007) and post-settlement strategies (Vessby and Wiktelius, 2003; Hansson, Bensch and Hasselquist, 2004) are becoming well-documented. Because interactions and/or trade-offs between two or more of these traits are also possible (Hazell *et al.*, 2005; van der Linde and Sevenster, 2006), complex multivariate selection is expected to be the rule in metapopulations.

Patches are usually not organized in regular, symmetrical spatial networks. In reality, spatial networks are heterogeneous and modular with respect to their topology (Fahrig, 2003; Urban and Skelly, 2006; Ferrari, Lookingbill and Neel, 2007). Few patches are typically more connected to others and serve thereby as hubs in the network (Van Langevelde, 2000; Calabrese

and Fagan, 2004). Such asymmetries in connectedness impact local immigration/emigration balances and lead to source-sink dynamics and the emerging metapopulation dynamics (Poethke, Dytham and Hovestadt, 2011; Dey, Goswami and Joshi, 2014; Wang, Haegeman and Loreau, 2015). When dispersal rates are equal among patches, highly connected patches experience a net immigration rate, thereby imposing an increased resources competition (Baguette and Schtickzelle, 2003; Amarasekare, 2008). Such local competition can then impose selection on traits related to stress-resistance, or selecting for reduced growth rate to counter overshooting in kin-structured populations (McClain, 1995). Finally, if emigration-immigration balances change across patches, different levels of relatedness may feedback on local reproductive (Macke, Bach and Olivieri, 2011) and dispersal strategies (Van Petegem *et al.*, 2017). As a result, even in metapopulations consisting of a network of identical habitat, local selective pressures can be different (Kawecki and Ebert, 2004; Valladares *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.

Given the importance of trait evolution for metapopulation dynamics, persistence and rescue, a deep understanding of the eco-evolutionary effects resulting from connectivity loss is essential to guide future conservation actions under global change (Travis *et al.*, 2013; Urban *et al.*, 2016). While a profound theory is a first needed step in this direction, but often fail to capture the complexity of multivariate trait selection, we here set-up an experimental evolution study using experimental metapopulation with the spider mite *Tetranychus urticae* as model organism (Fronhofer *et al.*, 2014; De Roissart, Wang and Bonte, 2015; Van Petegem *et al.*, 2018), differing in connectedness only. Such an approach ensures a high level of control on environmental variables and the statistical power coming from a high number of replicates and individuals involved with feasibility and flexibility. In order to separate local and

metapopulation-level selection, we disrupted local selection by applying a reshuffling procedure in part of the experiments. We quantified evolutionary divergence in a suite of traits related to dispersal, growth rate and stress resistance by breeding mites at the end of the experimental procedure for two generation under common garden.

Materials & Methods

Species description

The model species used for this experiment is the haplodiploid spider mite *Tetranychus urticae* Koch (Acarina: Tetranychidae), also known as "two-spotted spider mite", one of the most important herbivore pest worldwide and a commonly used model species (Grbic *et al.*, 2007). Its small dimensions allow large populations to be raised in relatively small spaces, while retaining the possibility of individual-based analysis. The generation time is around 15 days at 30 °C (Hance and Impe, 1999), and its fecundity is high (Tehri, 2014). The base population of spider mites used to initialize the experiment was collected from a stock of *T. urticae* belonging to the "LS-VL" strain. The original population was collected in October 2000 from a botanical garden in Ghent (Belgium) where pesticides had not been used for at least ten years (Van Leeuwen *et al.*, 2008; Cazaux *et al.*, 2014), and raised on bean plants (*P. vulgaris* L., variety 'Prelude') since then.

Experimental evolution

We developed experimental metapopulations, with each setup composed by nine patches disposed on a three-by-three grid. Each patch consisted of a square cut (5*5cm^2) from a bean leaf collected from ~2 weeks old plants. The patches were connected to each other using Parafilm bridges: each bridge was 0.5 cm wide, while the length varied accordingly to the connectedness treatment (see further). The leaves and bridges were mounted on a bed of wet cotton, to keep them hydrated and to prevent mites from escaping or to disperse outside the designed pathways. Every setup was separately stored into Vaseline-coated, open plastic boxes to further reduce the risk of contamination between treatments. Distilled water was added daily

to the cotton to maintain the moisture. The boxes were placed inside two walk-in climatically controlled rooms, with a constant temperature (25°C) and a 16-8 LD photoperiod for the whole duration of the experiment. To exclude any possible environmental effect due to the room itself, the boxes were randomly shuffled once per week.

For the closely connected setup, a length of 4cm was used; this length was doubled (8cm) for the intermediate setup and squared (16cm) for the loosely connected one. In the same setup, every bridge had the same dimensions. Although individual mites are able to walk distances up to several meters per day (Krainacker and Carey, 1990), these lengths were chosen because they were demonstrate to constrain dispersal and impose selection due to reduced feeding time and distance-dependent mortality costs of ending up in the cotton (Bitume et al., 2013 and Masier et al., unpub data).

The amount of leaf area (and hence resource availability) was identical for all metapopulation connectedness treatments. As a result of the patch network design, each patch had a different level of connectedness inside the metapopulation, with central patches at the highest (connected to every other patch), corner patches at the lowest (connected only to three other patches) and side patches as intermediate (connected to five patches). Each connectedness treatment was five times replicated. Another three replicates were installed in which adult females were randomized every week across the patches for the whole duration of the experiment. This treatment allowed us to separate local selection arising from genetic adaptation and kin-competition from metapopulation-level evolution.

At the beginning of the experiment (Sept. 2016), all the replicates were initialized using the same number of individuals from the base population: 5 adult females and 2 adult males were put on each patch (1272 individuals overall) using a soft-haired brush and monitored for two weeks to insure the settlement of the population. In the randomization treatments, females from the same metapopulation were collected using a thin hairbrush, pooled together on a fresh bean leaf to reduce stress as much as possible and then randomly redistributed on the patches, maintaining the same numbers but reshuffling the individuals. In order to ensure comparable levels of handling stress between treatments, the females from the non-randomization systems were equally collected, not randomized and but back to their original patch briefly afterwards. The leaves were also refreshed parallel with this mite handling, using new freshly-cut bean leaf squares. Old leaves were then laid upon the new ones, supported by toothpicks to avoid mould spread, and left in position for 48h before being disposed of. This was done to allow larvae, juveniles and adult males to move from the old leaf to the new one, as well as to provide some time for the eggs left on the old leaf to hatch (Praslicka and Huszár, 1989). Every setup got all

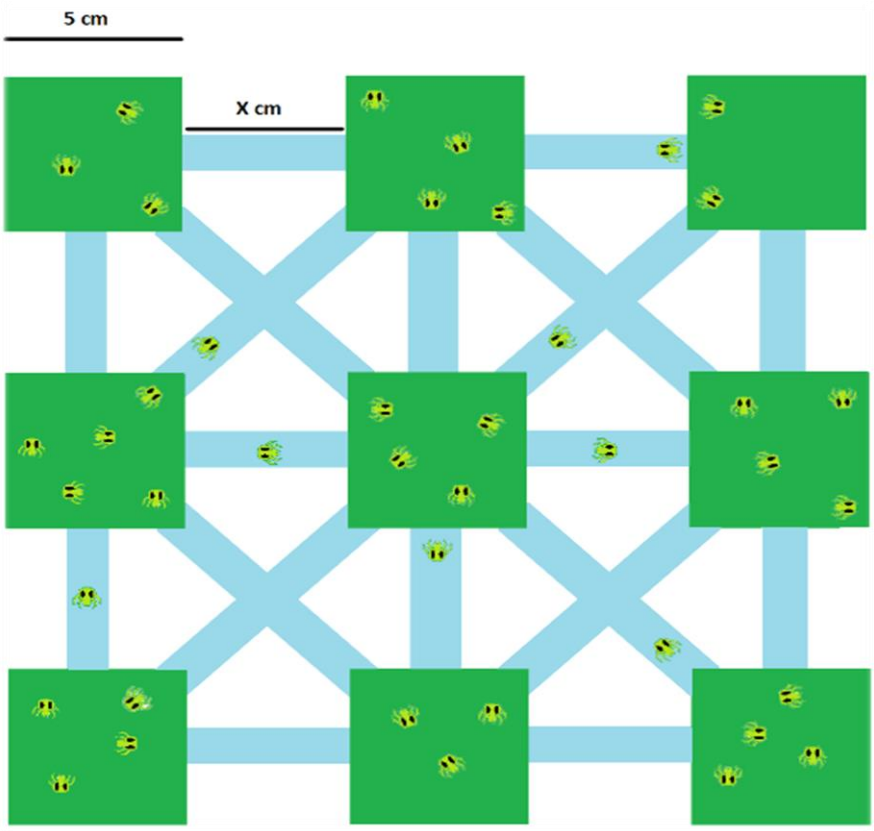

Fig. 1: schematic representation of the long-term experimental setups. Nine identical patches were arranged in a 3-by-3 grid and connected using Parafilm bridges. The length of the bridge (X cm in the picture) was dependent to the treatment; the diagonal bridges varied accordingly.

its patches refreshed the same day, and only once per week regardless of leaves quality and conditions to insure a constant inflow of resources.

Trait evolution: preliminary procedure

25 weeks from the start of the experiment (approx.12 generation at the experimental conditions (Hance and Impe, 1999)), we collected individuals from all the different patches to quantify ecological traits.

To purge maternal effect, a one-generation-long common garden round was conducted. From each patch, five adult females were collected and put separately on single bean leaves (area: 3.75 cm-2), for a total of 45 individuals from each experimental metapopulation (1080 individuals overall). Females from the starting stock population were collected as well to control for life history changes due to the current experimental conditions (i.e., plant quality). Individuals were reared at 30°C, under a 16-8 L/D photoperiod until the F1 generation reached the adult stage (~7 days later) and used for trait assessment.

Trait evolution: trait quantification and statistical analysis

a) Dispersal propensity

The propensity and the timing of dispersal was tested using series of two-patch systems, each composed by two 2.5x1.5 cm² patches connected by a 8cm long, 1cm wide Parafilm bridge to provide a standardized setup. On the starting patch, we placed females from F1 at four different densities: 1.3 (5 individuals), 2.6 (10 individuals), 5.3 (20 individuals) or 10.6 (40 individuals) females cm-2. The two patches were then connected and monitored for four days. Each day, the number of individuals on the starting and ending leaf were recorded, along with the number

of individuals on the bridge at the moment of the census. Each day, the target leaf was refreshed to prevent successfully dispersed females to move back to the starting patch. To ensure balanced designs with respect to densities, individuals coming from different patches of the same metapopulation were pooled together as to represent the composition of the original metapopulation. Data could hence not be analysed relative to the position of the local patch in the network.

The experiment consisted of 78 different systems, for a grand total of 1330 monitored individuals. We analysed both the fraction of emigrants (individuals leaving the source patch) and the fraction of immigrants (individuals successfully settling on the target patch). The proportions were analysed using generalized linear mixed model with a binomial error structure and logit-link, using the metapopulation ID as random effect. Temporal changes in emigration rate were analysed by survival analysis (Cox model, R package *coxme*) using cumulative proportions of emigrating individuals as censors and considering the replica number as a random effect. In order to facilitate interpretation and because of convergence failure of the three-way interaction in the Cox model with random effects, all survival analyses were completed per density treatment.

b) Starvation Resistance

We tested starvation resistance by monitoring individual survival without food. One experimental arena for each metapopulation was prepared (total: 25 arenas), each consisting of a 25cm^2 square cut from a black plastic sheet mounted on a wet cotton bed and fixed in position by paper strips to prevent mites from escaping. For each metapopulation, ~ 5 F1 adult females from the common gardens were placed into each of these arenas (109 individuals overall). Individuals coming from different patches of the same metapopulation were pooled together as to represent the composition of the original metapopulation. The plates were then stored at room temperature (~25°C). Based on exploratory trials, we compared the survival percentage after

48h, as this time appeared to be most discriminatory regarding the death/survival balance. Data were analysed by generalized linear mixed modelling using a binomial distribution, using the metapopulation ID as random effect.

c) Intrinsic Growth rate

Single fertilized females from the F1 generation were collected and placed individually on 2.5x1.5 cm^2 bean leaf cuts, mounted on a bed of wet cotton and kept in place with paper strips. From each metapopulation, one or two females per patch were collected, for a grand total of 370 females across the 24 metapopulations. The leaves were placed into heated cabinet, kept at 30°C for ten days with a 16-8 L/D photoperiod and moisturized daily 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. We compared the number and the age classes of all individuals recorded at day 6 to avoid effects of overlapping generations. We run a GLM assuming a quasi-Poisson distribution for the count data, to correct for the spotted overdispersion of the data with a simple Poisson distribution (Cameron and Trivedi, 1990). We use the treatment as independent variable (fragmentation level and randomization, as well as their interaction), plus the relative connectedness of the patch the F0 individual came from (centre, corner or edge), and again, the metapopulation as random effect.

Results

1) Dispersal propensity

Evolved emigration and immigration rate (success rate) was not dependent on the connectedness, initial density and reshuffling treatment (Table 1).

Independent variable	Dependent variable	Chisq.	df	p-level
Emigration rate	(Intercept)	160.345	1	<0.001
	Connectedness	0.4190	2	0.8110
	Randomization	0.7281	1	0.3935
	Starting Density	0.0247	1	0.8751
	Connectedness * Randomization	0.0599	2	0.9705
	Connectedness * Starting Density	25.286	2	0.2824
	Randomization * Starting Density	0.0061	1	0.9378
	Connectedness * Randomization * Starting Density	0.8299	2	0.6604
Immigration rate	(Intercept)	27.953	1	0.0945
	Connectedness	0.4834	2	0.7853
	Randomization	0.3086	1	0.5785
	Starting Density	0.0209	1	0.8852
	Connectedness * Randomization	0.3000	2	0.8607
	Connectedness * Starting Density	10.412	2	0.5942
	Randomization * Starting Density	0.0623	1	0.8029
	Connectedness * Randomization * Starting Density	0.4938	2	0.7812

Table 1: Full Model Analysis of Deviance table (Type III Wald chisquare tests) for both emigration and immigration rate in relation to the connectedness, randomization of the metapopulation in which individuals evolved and density in the dispersal trial.

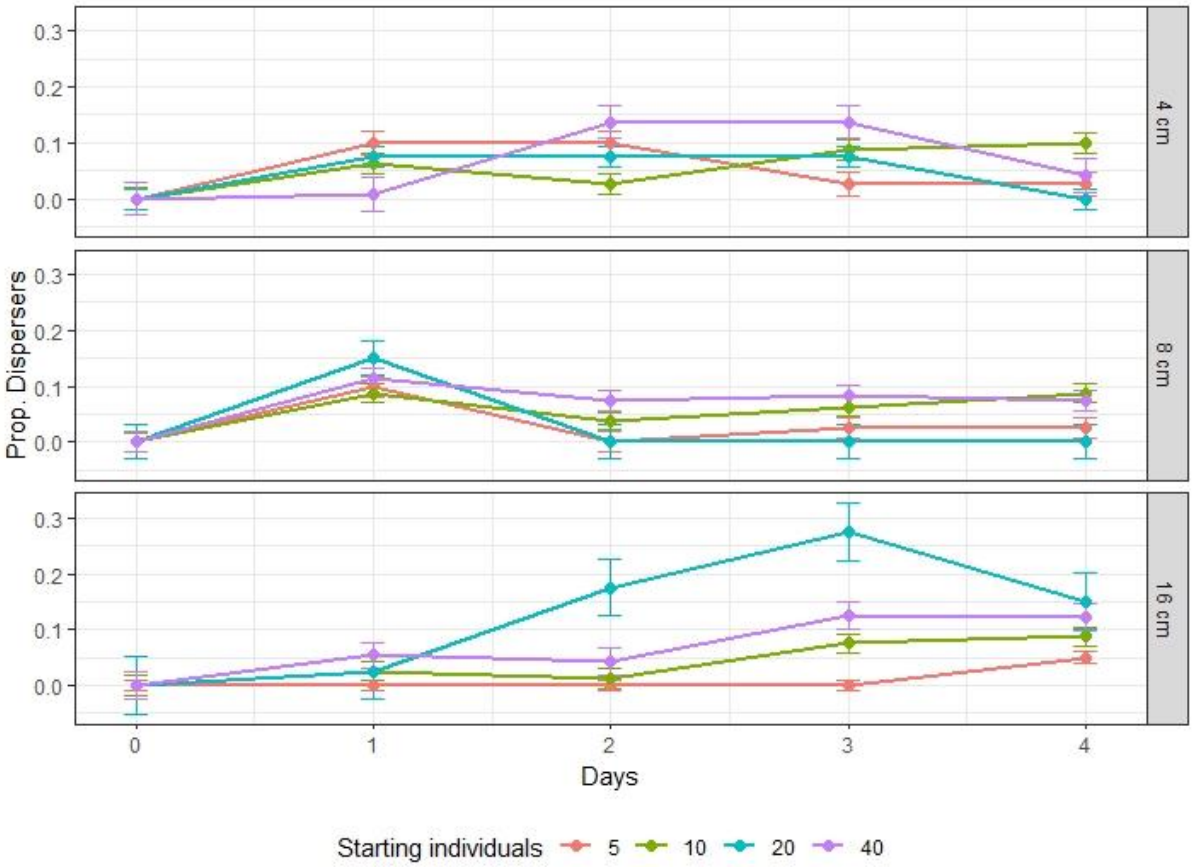

Fig. 2: temporal variation in emigration rates in relation to the metapopulation connectedness and the starting densities in the dispersal trial (the non-significant randomization treatments are not visualized)

Since dispersal was either overall low or high at respectively low and high densities, survival analysis only revealed significant effects of connectedness (Analysis of Deviance, Type III test: χ^2=11.79, P=0.003) at intermediate densities (See supplementary material). At this density (blue lines in Fig. 2), dispersal was delayed in mites that have evolved in the least connected metapopulation.

2) Starvation resistance

The proportion of individuals surviving 48 hours 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: χ^2=11.88, P=0.003; Fig. 3). Survival rates did not differ between the randomisation procedures (Analysis of Deviance, Type III test: χ^2=0.12, P=0.720) nor on the interaction between both (Analysis of Deviance, Type III test: χ^2=0.85, P=0.651).

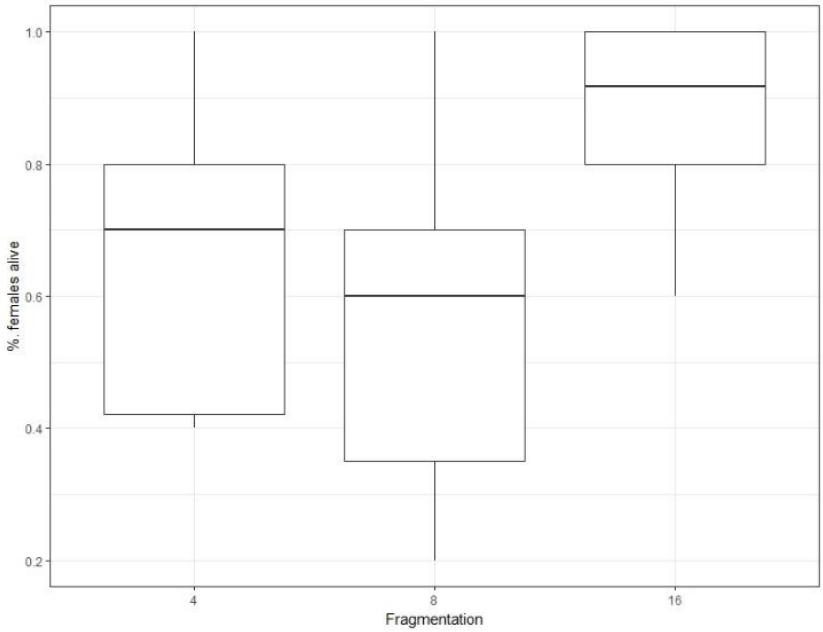

Fig. 3: proportion of alive individuals after 48h divided by the fragmentation level experienced during the experiment. Non-significant randomization treatments are not visualized.

3) Intrinsic growth rate

The position of the patch within the network and metapopulation connectedness were highly significant after accounting for interactions, pointing at their overall impact (Table 2, Fig. 4). Despite these main effects, they depended on the interaction as well, with growth rates not being different among metapopulation contexts for the central patches. Intrinsic growth rates were significantly higher in individuals that evolved in the most connected metapopulation relative to the others (Posthoc Tukey test with Holm adjustment: 4-8cm contrast: z=-3.03, P=0.003; 4-16cm contrast: z=-3.16; P=0.003). Similarly, growth rates were overall lowest in offspring from

individuals that were collected in the central patch (Posthoc Tukey test with Holm adjustment: corner-centre contrast: z=2.79, P=0.012; edge-centre contrast: z=2.86; P=0.012).

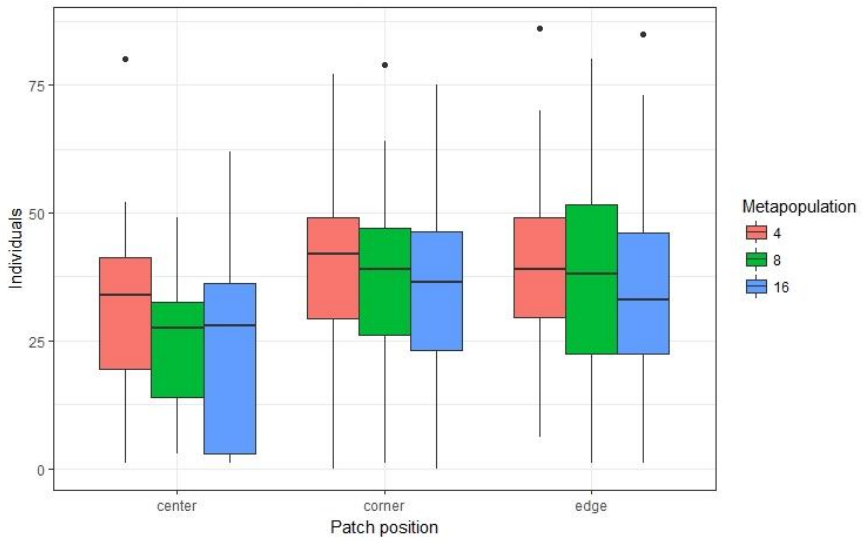

Fig. 4: Number of alive offspring after 6 days, divided by fragmentation treatment (colors) and relative position of the origin patch of the individuals (before common garden period).

Evolved intrinsic growth rates tended to depend on the interaction between the patch of collection, metapopulation connectedness and randomisation treatment, and on the 2-way interaction between randomisation and connectedness as well (Table 2). This two-way interactions shows that differences among metapopulations are steered by local selection, thus intrinsically demonstrating that the emergent metapopulation-level divergence results at least partially from indirect effects through feedbacks on local demography.

Dependent variable	Chisq.	Df	p-level
(Intercept)	1804.0217	1	< 0.0001
Position	8.8830	2	0.0117
Connectedness	15.3174	2	0.0005
Randomization	1.9118	1	0.1668
Position * Connectedness	13.1328	4	0.0106
Position * Randomization	4.2133	2	0.1217
Connectedness * Randomization	6.0659	2	0.0481
Position * Connectedness * Randomization	8.0225	4	0.0907

Table 2: Full Model Analysis of Deviance table (Type III Wald chisquare tests) for intrinsic growth rate as determined by the number of offspring produced by a single female after 6 days.

Discussion

Connectedness loss imposed fast life history evolution beyond the theoretical expectation of evolving dispersal rates. We demonstrate that, with increasing patch isolation, individuals evolve delayed dispersal and an increased starvation resistance. Intrinsic growth rate was systematically higher in individuals that evolved in the most connected metapopulation, and lowest when they originated from the highly connected central patch. The implemented randomisation procedure suggests the prevalence of epigenetic trait changes on intrinsic growth in relation to the local patch position.

Dispersal is a complex life history trait encompassing multiple, often tightly coupled stages. To date, most evidence from dispersal evolution in metapopulations stems from insights on emigration rate (Olivieri, Michalakis and Gouyon, 1995; Mathias, Kisdi and Olivieri, 2001; Gyllenberg, Parvinen and Dieckmann, 2002; Ronce, 2007), but incorporating evolution of traits across the multiple dispersal stages, including transience and settlement, has been theoretically demonstrated to lead to often complex dynamics which may or may not eventually impact the eventually reached emigration rate (Travis *et al.*, 2013; Delgado *et al.*, 2014). Our experimental evolution showed dispersal timing and the putative dispersal costs evolving and not emigration rates *per se.* The evolution of dispersal timing has been theoretically addressed in function of dispersal at adulthood (breeding dispersal) or at the early life stages (natal dispersal), and found to be merely a function of the pace of life (Johst and Brandl, 1999; Hirota, 2004; Lakovic, Poethke and Hovestadt, 2015; Lakovic, Mitesser and Hovestadt, 2017). Here, we found breeding dispersal strategies delayed in the least connected metapopulations. This can be mechanistically interpreted as a delayed density-dependence as individuals delaying dispersal are more likely to be engaged in local competitive interactions. In this sense, delayed dispersal reflects density-dependent emigration strategies (Saether, Engen and Lande, 1999; Hovestadt

and Poethke, 2006) with density-thresholds evolving to higher levels in disconnected metapopulations.

Starvation resistance evolved in parallel with dispersal timing, with individuals from the least connected metapopulation showing largest starvation resistance. Such an increased resistance on one hand reduced costs of local competition following delayed dispersal. As the dispersal event in our experimental metapopulations was costly, individuals may have adapted an "endurance-oriented" strategy, opposed to the "early leave" strategy of the averagely connected metapopulations. Alternatively, it may have evolved from enlarged transfer costs through the hostile matrix: increased starvation resistance should lead to enhanced survival when dispersing, and therefore compensates for the increased exposure to nutritional stress (Matsumura and Miyatake, 2018).

When integrated, evolution of delayed dispersal and the costs of dispersal then release selection on the emigration rate, equalising connectivity at the metapopulation-level among the different metapopulation despite variation in connectedness (Bélisle, 2005; Baguette and Van Dyck, 2007). We here thus illustrate the prevalence of expected but not yet documented eco-evolutionary feedbacks in metapopulations (Bonte, Masier and Mortier, 2018).

While increased dispersal costs are tempting explanation of the increased starvation resistance in the most disconnected metapopulations, it may have additionally evolved in response to the metapopulation demography if local densities are on average larger in disconnected metapopulations, or if high densities and thus resource competition are more frequently experienced. However, both at local and metapopulation level, no difference in the average number of individuals per week was found between treatments over the 6 months of the

experiment, and neither were local fluctuation in densities significantly different among the connectedness treatments (see supplementary material).

Building up energy reserves to survive long periods of food shortage is a costly process that allocates resources, subtracting them from other processes. Starvation resistance is commonly associated with bigger body mass, and usually has consequences on fertility, reproduction timing and longevity (Tessier *et al.*, 1983; Hoffmann and Harshman, 1999; Rion and Kawecki, 2007). In line with this, growth rates evolved to higher values in the most connected metapopulation. We did, however, not find trade-offs at the individual or metapopulation-level between starvation resistance and intrinsic growth rates (see supplementary material), so metapopulation divergence in these traits resulted from joint, independent evolution rather than from the commonly assumed syndromal evolution. The higher growth rates in the most connected metapopulation suggest a relaxation of competition, that could be attributed to more frequent and faster emigration events (Krüger, Liversidge and Lindström, 2002; Agrawal, Underwood and Stinchcombe, 2004).

While metapopulation-level divergence in growth rates is suggesting complex evolutionary dynamics within spatial networks, the systematic lower intrinsic growth rates in individuals from central patches in the network are convincingly pointing at local selection. Our metapopulations were, however, not designed with central patches being intrinsically different in habitat quality. Therefore, local selection can only be attributed to emerging feedbacks from the metapopulation dynamics. Reduced intrinsic growth rates are expected to evolve in response to intense competition (Krüger, Liversidge and Lindström, 2002; Agrawal, Underwood and Stinchcombe, 2004). Given the equal emigration rates across the different levels of metapopulation connectivity, but differences in timing and starvation resistance at the

metapopulation level, we anticipate patches to lose individuals at a similar rate. Highly connected patches however, will always receive more individuals than those with less connections, independent of the metapopulation-level connectivity (see Box in supplementary material). Although we could not statistically detect systematic higher densities in the central patches, the expected asymmetrical dispersal rates may nevertheless impose higher levels of competition following local overshooting.

Paradoxically, the signature of local adaptation in the central patches was not destroyed by reshuffling. This implies that the observed lower growth rates, as measured after one generation of common garden, must originate from epigenetic rather than true genetic adaptation. Such fast adaptive trait changes are thus resulting from intergenerational plasticity and do allow populations to respond fast (< 1 generation time) to environmental change (Galloway, 2005; Drummond and Ancona, 2015). We have to date no insights on the exact mechanisms behind these epigenetic changes, but this study is adding evidence on their relevance for metapopulation dynamics. In this sense, it adds-up to the available evidence of non-genetic inheritance of traits related diapause (Oku, Yano and Takafuji, 2003) and both aerial (Van Petegem *et al.*, 2015) and ambulatory dispersal (Bitume *et al.*, 2011, 2014).

Connectedness loss is central to conservation and spatial planning (Cheptou *et al.*, 2017) as it is expected to reduce connectivity and eventually leading to species loss and disintegration of local food webs (Thompson, Rayfield and Gonzalez, 2017). However, connectivity between patches can be evolutionary rescued (Kendrick *et al.*, 2017). Given that evolution of dispersal related traits change cost-benefit balances in metapopulations (Bonte *et al.*, 2012), these evolutionary dynamics adaptations will feedback on other traits as well and thereby impact the ecological processes (Bonte, Masier and Mortier, 2018). Such a complex integrated view on

dispersal and life history evolution, and evolving costs in response to fragmentation is lacking (Cheptou et al. 2017) buy highly needed in order to advance the predictive ecology of species and ecosystems, especially in a fast-changing world like the one we are experiencing now (Urban *et al.*, 2016). While theory focuses, for reasons of tractability, on simple dynamics (Govaert *et al.*, 2018), we are able to demonstrate more realistic complex multivariate life history changes. We demonstrate that these evolutionary dynamics do not follow simple theoretical predictions focusing on dispersal alone, but instead that other traits are jointly evolving as well in response to both local- and metapopulation-level selection pressures, thereby imposing putative unpredictable ecological consequences in terms of population dynamics.

Local and metapopulation-level dynamics interact within 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, can potentially turn into pre-adaptation for different kind of stressors, i.e. suboptimal host plants or novel habitats and enhance persistence under environmental change (Jenkins, Chaisson and Matin, 1990; De Roissart *et al.*, 2016). Moreover, we show that evolutionary dynamics resulting from fragmentation also include epigenetic inheritance or intergenerational plasticity. The reduced intrinsic population growth of the most locally connected population was pertinent within the treatments where any local adaptation and genetic structure has been removed. As these responses are usually very fast to institute (Herman *et al.*, 2014), their role should never be underestimated and deserves more in-depth studies. Lastly, despite the different level of connectedness between patches, we located no differences in effective dispersal rates after four days, meaning that the connectivity and the gene flow between local populations were likely maintained. This decoupling of connectedness and connectivity could impact predictions

traditionally derived from theoretical ecological models and act as a rescue mechanism for fragmented populations, acting on metapopulation variability, local stabilizing and spatial synchronizing effects, especially in heterogeneous metapopulations (Wang, Haegeman and Loreau, 2015).

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