Metapopulation connectedness and the evolution of multiple life-history traits

Abstract

Loss of habitat connectivity is a well-known threat to biodiversity and metapopulation persistence and anticipated to strongly affect evolutionary dynamics. While selection is typically expected to act on dispersal-related traits that are expressed at the metapopulation-level, demographic changes in complex spatial networks may cause life histories to diverge between local patches as well. However, the exact consequences of reduced connectedness on life-history traits have never been quantified in detail.

We used experimental metapopulations of two-spotted spider mites to investigate how connectedness loss affects trait evolution. Mites were introduced in spatial networks with different levels of connectedness among local patches. In order to separate processes of local and metapopulation-level selection, we implemented a randomization treatment by redistributing mites across all local patches of certain metapopulations.

A decreased metapopulation connectedness selected for increased starvation resistance and delayed dispersal timing. Reshuffling did not alter 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 selection on multiple 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. With longer dispersal, starvation resistance improved, possibly to face longer periods

in the matrix without resources; at the same time, lower dispersal costs translated into a quicker decision to disperse as the net loss/gain ratio was more favourable.

Our results demonstrate the need to incorporate multivariate trait evolution at multiple spatial scales to understand eco-evolutionary dynamics in metapopulations.

Introduction

Besides habitat loss, habitat fragmentation is one of the most important human-induced drivers of declines in biodiversity (Collinge, 1998; Forman, 2000; Heilman *et al.*, 2002). Most species live in spatially heterogeneous landscapes of suitable habitat patches interspersed with areas of less suitable matrix. In such landscapes, dispersal enables the exchange of individuals among populations of different habitat patches, resulting in an overarching metapopulation. Loss of habitat connectivity influences metapopulation 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, determined by the species' movement capacity and its dispersal between populations living in different patches (Tischendorf and Fahrig, 2001). In contrast, the connectedness of resource 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 these patches (Taylor *et al.*, 1993; Rudnick *et al.*, 2012). It is therefore affected by the structural properties –the number, shape, dimensions and interdistance– of the suitable patches within a landscape (Tischendorf and Fahrig, 2000; Wang, Blanchet and Koper, 2014). Connectedness thus impacts connectivity by mediating both the ecological and evolutionary determinants of the flows among patches of both individuals and genes (Bonte, Masier and Mortier, 2018). Loss of habitat connectivity decreases the chances of reestablishment of extinct populations, thereby putting the metapopulation at risk (Fuller, Doyle and Strayer, 2015; Thompson, Rayfield and Gonzalez, 2017). Habitat connectivity is thus central to metapopulation conservation.

While the ecological effects of reduced habitat connectivity 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 directly tested (Cheptou *et al.*, 2017). Studies on the evolutionary consequences of connectivity loss have mostly focused on the evolution of inbreeding, mating systems or dispersal rates (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 during each of these three phases, often in interaction with other life history traits (Bonte *et al.*, 2012), leading to life-history syndromes at both the individual, population and metapopulation-level (Clobert *et al.*, 2012). It can be assumed that connectedness loss mostly influences the costs of the transfer phase, thereby imposing selection by lowering departure rates (Bonte *et al.*, 2003). Evolutionary adaptations to reduce costs of the other dispersal phases may, however, be prominent as well and result in dispersal syndromes (Clobert *et al.*, 2012). Evolutionary changes in (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) in response to altered habitat connectedness 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.

Habitat 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). A few patches are typically more connected to others and thereby serve 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 resource competition (Baguette and Schtickzelle, 2003; Amarasekare, 2008). Such 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.

Given the importance of trait evolution for metapopulation dynamics, persistence and rescue, a deep understanding of the eco-evolutionary effects of connectivity loss is essential to guide future conservation actions (Travis *et al.*, 2013; Urban *et al.*, 2016). We studied experimental evolution in the spider mite *Tetranychus urticae* (Fronhofer *et al.*, 2014; De Roissart, Wang and Bonte, 2015; Van Petegem *et al.*, 2018), to test whether and how different levels of habitat connectedness affect trait evolution in a mite model system. We particularly focused on traits

related to dispersal and reproduction as theory predicts these to be under regional and/or local selection in metapopulations. We expected individuals evolving in more fragmented habitats to be characterised by a lower propensity of dispersal, as it is a more costly event in such habitats, or to evolve lower dispersal costs by means of a higher resistance to the environmental conditions during transfer (e.g., food deprivation). In order to separate local and metapopulation-level selection, we disrupted local selection by reshuffling mites among local patches in part of the metapopulations, to remove both *kin* (genetic relatedness) and *kind* (phenotypic similarity) structure (Van Petegem *et al.*, 2018) and leave the pure environmental effect of the habitat connectedness level.

Materials & Methods

Species description

Our study species is the haplodiploid spider mite *Tetranychus urticae* Koch (Acarina: Tetranychidae), one of the most important herbivore pests worldwide and a commonly used model species (Grbic *et al.*, 2007). The species has a generation time of approximately 15 days at 30 °C (Hance and Impe, 1999), and its fecundity is high (Tehri, 2014). The stock "LS-VL" population was initiated from wild-caught mites from the Ghent University botanical garden in Belgium in October 2000 (Van Leeuwen *et al.*, 2008; Cazaux *et al.*, 2014), and maintained on bean plants (*P. vulgaris* L., variety 'Prelude') since then.

Experimental evolution

We developed experimental metapopulations, with each setup composed of nine habitat patches organized in a three-by-three grid. Each patch consisted of a square (5 cm × 5 cm) cut from a bean leaf collected from ~2 weeks old plants. The patches were connected to each other by Parafilm bridges: each bridge was 0.5 cm wide, while the length varied according 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 dispersing outside the designed pathways. Each experimental metapopulation was separately kept in a Vaseline-coated, open plastic box to further reduce the risk of mites escaping. Distilled water was added daily to the cotton to keep moisture levels constant. The boxes were placed inside two climatically controlled walk-in rooms, with a constant temperature (25°C) and a 16-8 LD photoperiod for the whole duration of the experiment. To exclude any possible effect of location within the room, the position of all boxes was randomized once per week.

The “metapopulation connectedness” treatment consisted of 3-by-3 grids of patches connected by bridges of 4, 8, or 16 cm of length. Diagonal bridges, whose length was dependant on the grid bridges length, were added to connect the central and corner patches and the four lateral patches (see fig.1).

Although individual mites are able to walk distances up to several meters per day (Krainacker and Carey, 1990), these lengths were chosen because the lengths of 8 or 16 cm were demonstrated 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 total area of leaves and, hence, resource availability was identical across all the connectedness treatments. As a result of the patch network design, each patch had a different level of connectedness inside the metapopulation (further referred to as *local connectedness*), with central patches having the highest (connected to every other patch), corner patches the lowest (connected only to three other patches) and side patches as intermediate (connected to five patches) value.

Each connectedness treatment had eight replicates, 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 randomization 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, maintaining the same local densities but reshuffling the individuals so that any one of them could randomly end up on any patch of its metapopulation. In order to ensure comparable levels of handling stress between treatments, the females from the non-randomization systems were also collected, not randomized and placed back on their original patch briefly afterwards.

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 evolution, hence rendering this effect statistically significant).

All experimental metapopulations (24 in total) were initialized in September 2016 with five freshly inseminated females and 2 additional adult males on each patch (hence 1272 individuals overall) using a soft-haired brush and monitored for two 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).

All patches in each experimental metapopulation were replaced weekly on the same day with new freshly-cut bean leaf squares. The adult females, randomized or not, were directly moved onto the new leaves as described higher. 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

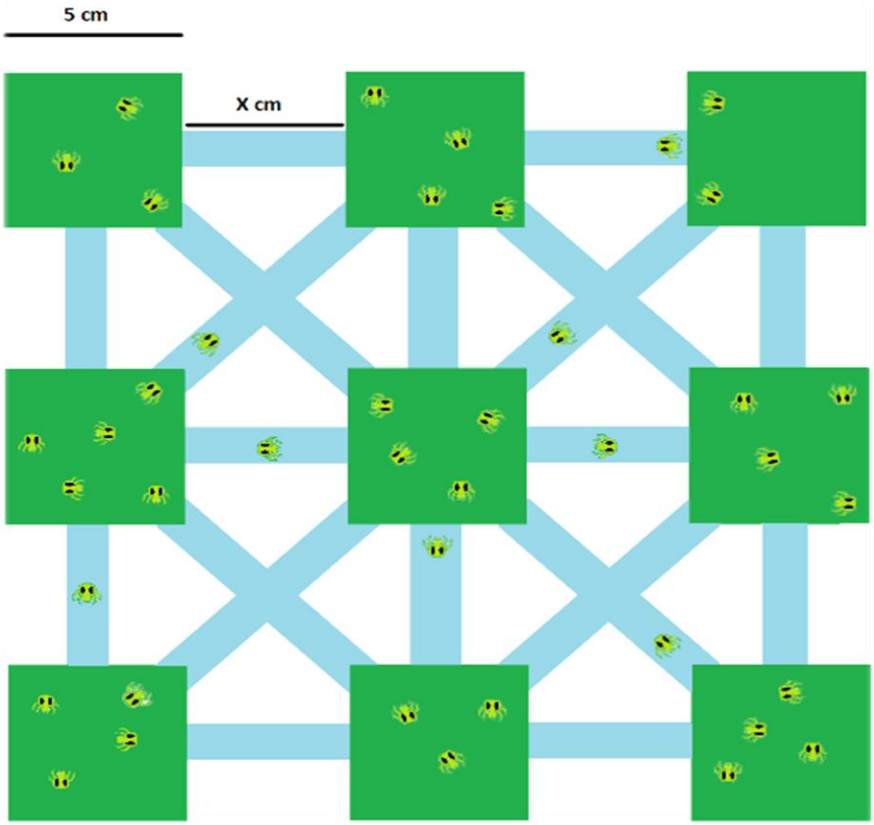


Fig. 1: schematic representation of the long-term (6 months) experimental setups. Nine identical patches were arranged in a 3-by-3 grid and connected using Parafilm bridges. The length of the bridge (X cm in the picture) was dependent on the treatment; the diagonal bridges varied depending on the value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

was done to allow larvae, juveniles and adult males left on the old leaves to move to the new ones, as well as to provide some time for the eggs laid on the old leaf to hatch (Praslicka and Huszár, 1989).

Trait evolution following common garden

25 weeks from the start of the experiment (approx.12 generations under the experimental conditions; (Hance and 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. Each F0 female was allowed to lay eggs for two days on a standardised bean leaf, and offspring were subsequently raised under comparable densities (~ 2 individuals × cm^{-2}), at 30°C, a 16-8 L/D photoperiod and food *ad libitum*. This procedure enabled us to study traits independent of plastic responses to the experienced conditions in the metapopulation. We interpret, as others, any trait variation as genetic variation although intergenerational effects cannot be ruled-out. 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. For reasons of feasibility, we chose to maximise trait quantification across rather than within experimental metapopulations to ensure maximal independent replication: in some cases, we then chose to pool together offspring originating from different patches of the same metapopulation to insure a sufficiently high number of individuals was used.

Dispersal Propensity

This test was performed at metapopulation level.

The propensity and the timing of dispersal were tested using a standardized setup of two-patch systems, each composed of two 2.5 cm × 1.5 cm patches connected by an 8 cm long, 1 cm wide Parafilm bridge. On the starting patch, we placed females from F1 at densities varying between 5 and 40 individuals, thereby generating a density gradient between 1.3 and 10.4 individuals/cm^2. The two patches were then connected and monitored for four days. 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. Freshly moulted F1 females (the dispersing sex) reared for one generation under common garden conditions from the same experimental metapopulation replicate were put together on the source patch for the dispersal trial, in order to simulate a composition similar to the original metapopulation. Therefore, data could only be analyzed in function of the metapopulation typology as this is the anticipated unit of selection.

We ran in total 78 two-patches dispersal trials, for a grand total of 1330 monitored individuals. We analyzed both the fraction of emigrants (individuals leaving the source patch) and the fraction of immigrants (individuals successfully settling on the target patch). These fractions were analyzed using generalized linear mixed model with a binomial error structure and logit-link; metapopulation connectedness, presence/absence of randomization (categorical) and density on the starting patch (continuous), as well as their two- and three-ways interactions were considered as explanatory variables. The metapopulation replicate was added as random effect to control for dependency in responses from individuals originating from the same experimental metapopulation.

Finally we used the day at which each individual dispersed as a dependent variable in a linear model, using again metapopulation connectedness, presence/absence of randomization (categorical) and density on the starting patch (continuous covariate) as explanatory variables, along with their two- and three-ways interactions. We assumed a Poisson distribution for count data with low mean. The metapopulation replicate and dispersal trial replicate were here added as random factors to control for interdependence of data because of shared evolutionary history and experimental setup. Only individuals that performed a dispersal event were included in this analysis so to render this analysis complementary to the emigration analysis outlined higher. We complemented this analysis with a population-level test of the day at which each replicate reached or passed the 50% of its final number of dispersers ("Time50" from now on) and used this as a proxy for the dispersal timing of the population. As this analysis yields complementary and similar insights as the individual-based test, we provide these results in supplement (SI 1).

Starvation Resistance

This test was performed at metapopulation level.

One experimental arena was prepared for each metapopulation as well as one for the stock population as control (total: 25 arenas). Each arena consisted of a 25 cm^2 square cut from a black plastic sheet mounted on a wet cotton bed mounted into a plastic Petri plate and fixed in position by wet paper strips: the strips partially overlapped with the plastic (~3mm) to form a wet barrier and deter mites from falling into the cotton. For each experimental metapopulation replicate, 5 1-2 day 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 individuals collection were selected to collect the F1 females. The Petri 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 analyzed by generalized linear mixed modelling using a binomial distribution, with the connectedness-level and presence/absence of randomization 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 level.

Single fertilized females from the F1 generation reared under standardised conditions were collected and placed individually on 2.5 cm × 1.5 cm bean leaf cuttings, mounted on a bed of wet cotton and kept in place with paper strips. From each experimental metapopulation, 1-2 females were collected from each patch, for a grand total of 370 females across the 24 metapopulation replicates. The leaves were placed in a 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. The number of individuals from these three age classes were 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 and Trivedi, 1990). Reproductive performance at day 6 was used as the dependent variable to avoid effects of overlapping generations. 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 dependency by shared evolutionary history.

RESULTS

Dispersal Propensity

Evolved emigration and immigration rate (success rate) were not dependent on the connectedness or randomization treatment; only the starting density had a significant and positive (see figure in Supplementary Materials SI2) impact on the emigration rates (Table 1). Individuals that evolved in the most disconnected metapopulation showed a delayed timing of dispersal (day of departure) (Analysis of Deviance, Type III test: χ^2 =17.16, P= 0.00018). The same pattern was observed in the values of "Time50" at the population level (see supplementary material SI 1).

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

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, randomization of the metapopulation in which individuals evolved and density in the dispersal trial.

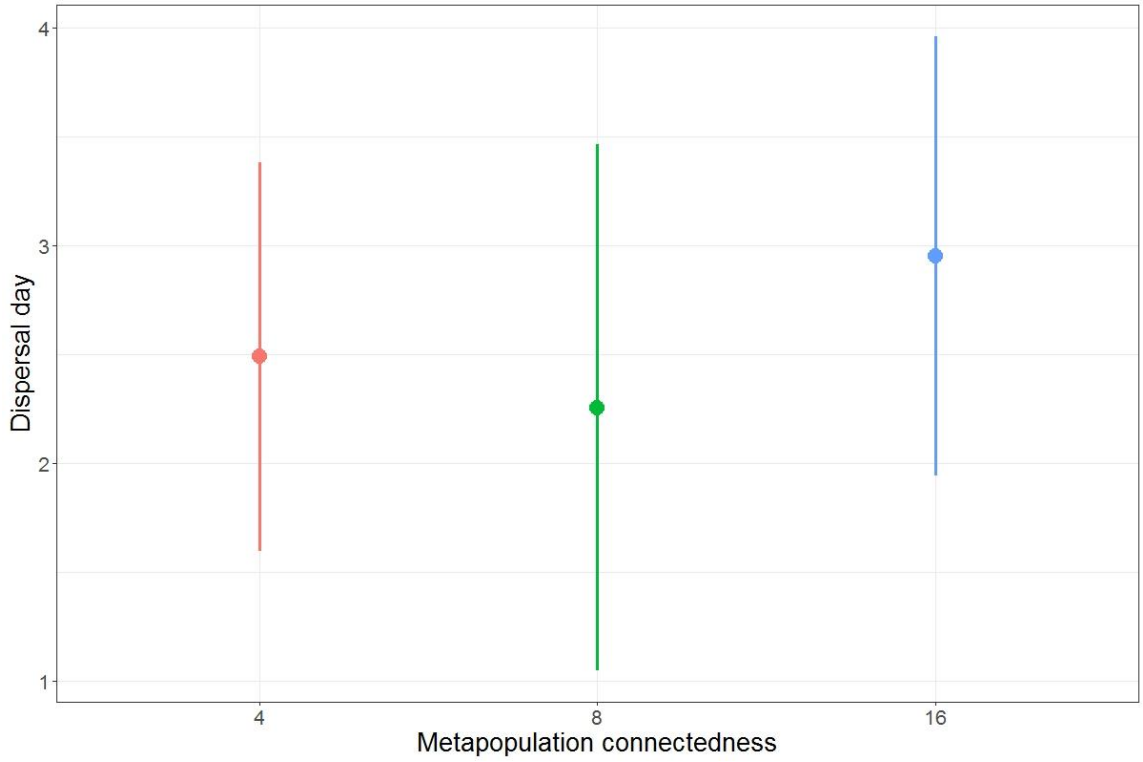


Figure 2: the effect of connectedness on the individual day of dispersal in the different treatments (means ± sd).

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=11.89, P=0.003; Fig. 3). Survival rates did not differ between the randomization 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).

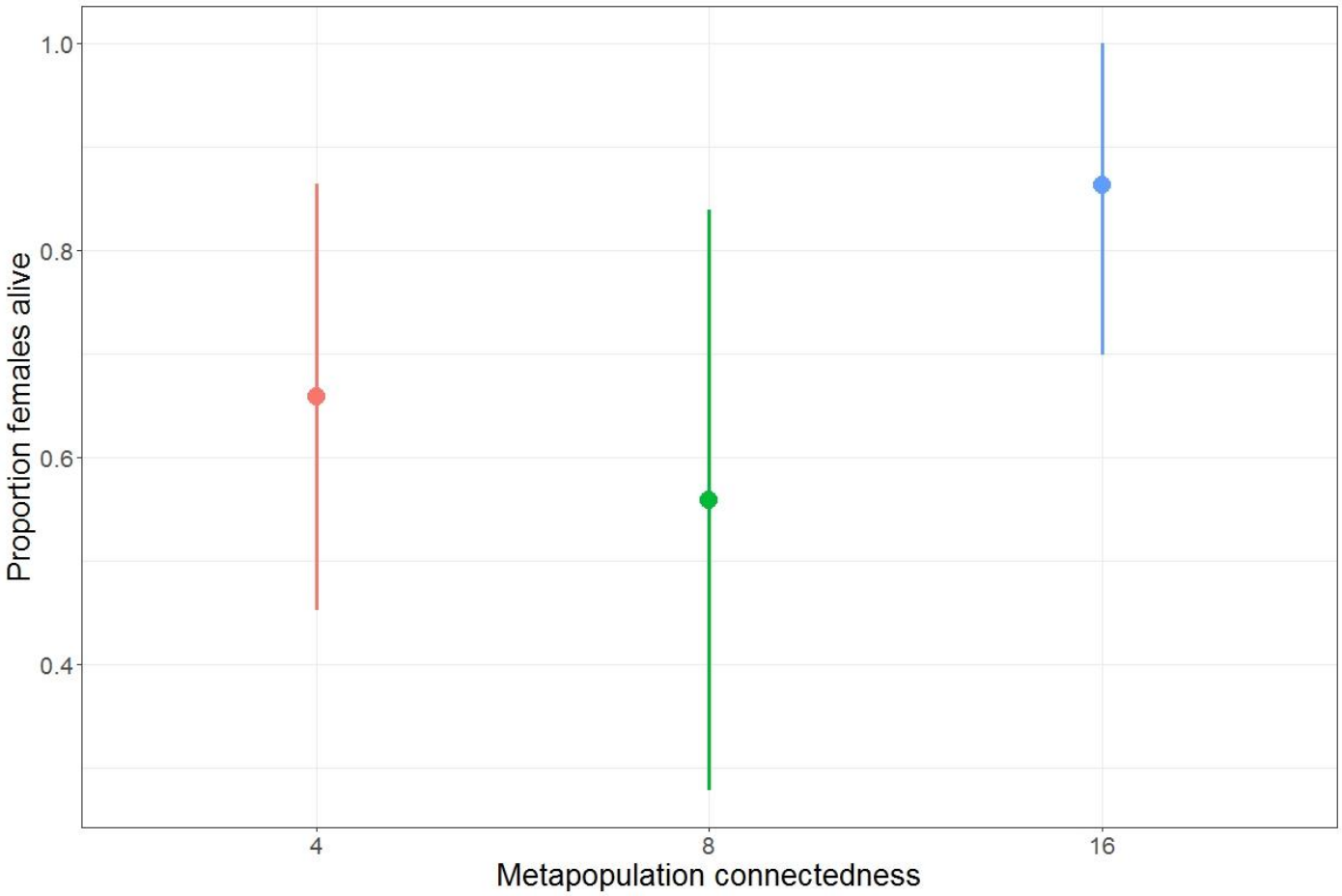


Fig. 3: proportion of alive individuals (means ± sd) after 48h depending on the connectedness of the source metapopulation.

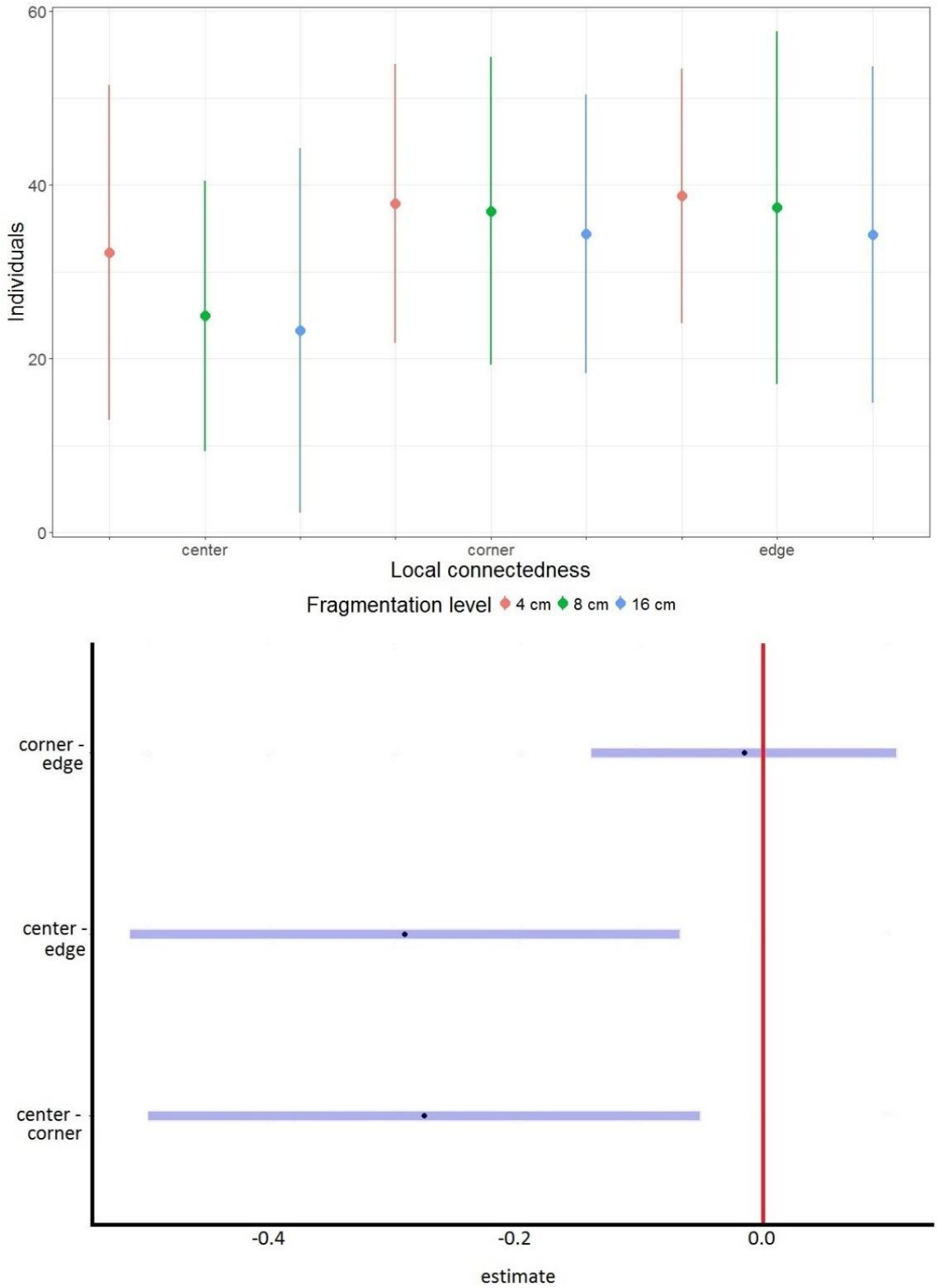
Reproductive performance

The local connectedness of the patch the individuals originated from affected reproduction significantly (Table 2, Fig. 4). In general, reproductive performance was overall the lowest in offspring from individuals that were collected in the central patch (Posthoc Tukey test: corner-center contrast: t-ratio = -2.895, P=0.0112; edge-center contrast: t-ratio = -3.073; P=0.0065). Reproductive performance was not affected by the metapopulation connectedness or the randomization procedure (see table 2).

Explanatory variable	**df**	χ^2	**Pr(>χ^2)**
Position	9.6736	2	0.007933(**)
Connectedness	3.2587	2	0.196056
Randomization	0.4209	1	0.516487
Position * Connectedness	1.6079	4	0.806379
Position * Randomization	0.8291	2	0.660647
Connectedness * Randomization	3.7884	2	0.150437
Position * Connectedness * Randomization	1.1641	4	0.883968

Table 2: Full Model Analysis of Deviance table (Wald χ^2 test) for intrinsic reproductive performances as determined by the number of offspring produced by a single female after 6 days.

Fig. 4a (upper panel): Number of alive offspring after 6 days (mean ± sd), for each combination of fragmentation treatment (colors) and relative position of the patch of origin of the individuals (before common garden period). Fig. 4b (lower panel): pairwise comparisons between offspring originating from patches with a different position within the metapopulation (with confidence intervals at 95%).



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, Michalakis and Gouyon, 1995; Mathias, Kisdi and Olivieri, 2001; Gyllenberg, Parvinen and Dieckmann, 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 dynamics which may or may not impact the emigration rate (Travis *et al.*, 2013; Delgado *et al.*, 2014). Our work on experimental evolution showed that changes in metapopulation connectedness altered the evolution of dispersal timing and resistance against starvation, a possible dispersal cost, and not of emigration rates *per se.* The evolution of dispersal timing has been theoretically addressed in response to either dispersal at adulthood (breeding dispersal) or at birth (natal dispersal) (Johst and Brandl, 1999; Hirota, 2004; Lakovic, Poethke and Hovestadt, 2015; Lakovic, Mitesser and Hovestadt, 2017).

Here, we found breeding dispersal was 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 the 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 in the least connected metapopulations, as

opposed to the "early leave" strategy of the more tightly connected metapopulations. Alternatively, it may have evolved from higher transfer costs through the hostile matrix: increased starvation resistance should lead to enhanced survival when dispersing through a matrix void of food resources, and therefore compensates for the prolonged 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, equalizing 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).

The higher starvation resistance found in the least connected metapopulations can not be explained by higher (local) population densities during the 6 months of the experiment, as no significant difference was found in local dynamics or population size (S3, S4 and Masier, *in prep*.).

While increased dispersal costs are tempting explanation of the increased starvation resistance in the most disconnected metapopulations, it may also have evolved in response to the metapopulation demography if local densities are on average higher in less connected 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 fluctuations (alpha variability *sensu latu*) in densities significantly different among the connectedness treatments (see supplementary material S3 and S4).

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). 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 is intriguing as (1) patches were identical in terms of quality and type throughout the network, and (2) dispersal is maintained as an individual trait in all metapopulation types, hence swamping putative local selection (Alzate *et al.*, 2017; Alzate, Etienne and Bonte, 2019).

The signature of local selection in the central patch is intriguing given the putative gene flow within networks. Local selection can thus only be attributed to emerging feedbacks from the metapopulation dynamics. Reduced reproductive performances 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 connectedness, but differences in timing and starvation resistance at the metapopulation level, we anticipate a similar rate of population decrease between patches due to emigration and resources deprivation. Patches with higher local connectedness however, will always receive more individuals than those with less connections, independent of the metapopulation-level connectivity (see Box 1 in supplementary material). Although we could not statistically detect systematically higher densities in the central patches, the expected asymmetrical dispersal rates may nevertheless impose higher levels of competition following local overshooting. At the same time, reduced individual growth rates could compensate locally

for an increased input of immigrants, thus explaining why the local densities were found not significantly different.

Even more paradoxical, this signature was not destroyed by randomization. This implies that the observed lower reproductive performance, as measured after one generation of common garden, must originate from persisting intergenerational plasticity rather than genetic evolution. Such an intergenerational plasticity enables populations to respond fast to environmental change (Galloway, 2005; Drummond and Ancona, 2015), and has been recorded in relation to dispersal-related traits before (Bitume *et al.*, 2011, 2014; Van Petegem *et al.*, 2015) as well as for diapause (Oku, Yano and Takafuji, 2003). The exact mechanisms behind these epigenetic responses remain, however, unclear.

Habitat fragmentation is a central problem in conservation biology as it is expected to reduce connectivity and eventually lead 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 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, Masier and Mortier, 2018).

Such an integrated view on dispersal, life history evolution and costs shifts in response to habitat fragmentation is lacking (Cheptou *et al.*, 2017) but 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.*, 2018), we are able to demonstrate more realistic multivariate life history evolution caused by altered

habitat connectedness. We demonstrate that these evolutionary dynamics do not follow simple theoretical predictions based on dispersal alone. One would expect lower dispersal rates between local populations with reduced connectedness, possibly coupled with a higher success rate as dispersing individuals are highly specialized in finding and reaching new suitable patches in the matrix (Bonte, Hovestadt and Poethke, 2010; Brisson, 2010).

Traits other than dispersal are jointly evolving as well in response to both local- and metapopulation-level selection pressures, thereby causing potentially unpredictable changes in population dynamics.

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, 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 had been removed. As these responses are usually very fast (Herman *et al.*, 2014), their role should not be underestimated and deserves more in-depth study. Lastly, despite the different levels of connectedness between patches, we found no differences in net dispersal rates after four days, meaning that the connectivity and the gene flow between local populations were basically maintained.

This decoupling of habitat connectedness and population connectivity could impact predictions traditionally derived from theoretical ecological models, that assume a direct and positive link

between global dispersal and habitat connectedness (Legrand *et al.*, 2017). The evolution of often-overlooked traits like dispersal timing or individual growth rates rather than dispersal rates themselves could then act as a rescue mechanism for fragmented populations through their impact on metapopulation variability, local stabilizing and spatial synchronizing effects (Wang, Haegeman and Loreau, 2015).

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