The importance and adaptive value of life history evolution for metapopulation dynamics

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Data-archive: Metadata population dynamics in artificial metapopulations data are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.18r5f (De Roissart, Wang &

Bonte 2015). Modeling code is available on: https://github.ugent.be/pages/dbonte/eco_evo-metapop/ (ODD protocol in supplementary material)

Abstract:

1. The spatial configuration and size of patches influence metapopulation dynamics by altering colonisation-extinction dynamics and local density-dependency. This spatial forcing then additionally impose strong selection pressures on life history traits, which will in turn feedback on the ecological metapopulation dynamics. Given the relevance of metapopulation persistence for biological conservation, and the potential rescuing role of evolution, a firm understanding of the relevance of these eco-evolutionary processes is essential.

2. We here follow a system's modelling approach to disentangle the role of this spatial forcing (classical, mainland-island or patchy metapopulation types) relative to realistic life history evolution for metapopulation demography as quantified by (meta)population size and variability. We developed an individual based model based on earlier experimental evolution with spider mites to perform virtual translocation and invasion experiments that would have been otherwise impossible to conduct.

3. We show that (1) metapopulation demography is more affected by spatial forcing than by life history evolution, but that life history evolution contributes substantially to changes in local and especially metapopulation-level population sizes, (2) extinction

rates are minimised by evolution in classical metapopulations, and (3) evolution is optimising individual performance in metapopulations when considering the importance of more cryptic stress resistance evolution.

4. We thus provide evidence that metapopulation-level selection maximises individual performance and more importantly, that –at least in our system- evolutionary changes impact metapopulation dynamics, especially factors related to local and metapopulation sizes.

Introduction

Many, not to say all, species inhabit spatially heterogeneous and structured habitat. Spatial structure is an inherent property of natural systems because of spatial variation in the availability of diverse niche components, or because of human-induced fragmentation (Fahrig, 2003). When species move among patches of suitable habitat, local demography will be coupled with global metapopulation dynamics (Wang, Haegeman, & Loreau, 2015) and thereby impact colonization-extinction dynamics (Cheptou, Hargreaves, Bonte, & Jacquemyn, 2017). Because the nature of these dynamics affects individual components of fitness, they are in turn anticipated to impose a strong selection on life history traits (Bonte & Dahirel, 2017; Olivieri, Couvet, & Gouyon, 1990). This tight coupling between metapopulation functioning and evolution renders eco-evolutionary dynamics especially important in metapopulations of organisms that experience evolutionary change at contemporary timescales (Hanski, 2012; Hanski & Mononen, 2011). Given the relevance of metapopulation persistence for biological conservation, and the potential rescuing role of evolution, a firm understanding of the relevance of these eco-evolutionary processes is essential (Kinnison & Hairston, 2007).

To date, metapopulation viability is commonly studied from an ecological perspective as human pressures impose changes in habitat, matrix composition, population sizes and population connectivity. These factors immediately impact the demographic properties within metapopulations (Hanski & Gilpin, 1997). Increased patch isolation does for instance enforce increased dispersal mortality, local patch quality can affect local growth rates, and patch size will eventually determine local carrying capacities, thus population sizes and the subsequent resilience to demographic stochasticity. High local population and metapopulation sizes and

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asynchrony in local population fluctuations generally maximise metapopulation long-term survival and thus persistence (Hanski, 1998; Molofsky & Ferdy, 2005; Wang et al., 2015). The spatial setting is thus a well acknowledged ecological factor affecting different properties of the metapopulation functioning. We refer to these ecological drivers as *spatial forcing*.

The spatial structure of metapopulations does equally impact trait evolution at the local and metapopulation-level (Cheptou et al., 2017). These are predominantly studied from a theoretical perspective with a strong focus on the evolution of dispersal and dispersal syndromes. While dispersal is a central trait in life history (Bonte & Dahirel, 2017), other traits have been documented to evolve in parallel, and often in unpredictable ways. Few empirical studies tested theoretical predictions beyond dispersal evolution, but recent work provides evidence of multivariate life-history evolution in metapopulations (De Roissart et al., 2016; Duplouy, Ikonen, & Hanski, 2013). Different and contrasting selection pressures act at the individual and metapopulation-level (Aspi, Jäkäläniemi, Tuomi, & Siikamäki, 2003; Laiolo et al., 2012). Maximisation of individual fitness does therefore not necessarily lead to an optimised metapopulation persistence. It is for instance known that dispersal is not evolving to the best for the metapopulation, thus not evolving to such levels that performance in terms of metapopulation size or survival is maximised (Delgado, Ratikainen, & Kokko, 2011). In the extreme, evolution may induce evolutionary suicide and compromise conservation efforts (Olivieri, Tonnabel, Ronce, & Mignot, 2016). Such scenarios occur for instance when habitat fragmentation select against dispersal, thereby imposing a negative feedback between patch occupancy, inbreeding and extinction risk.

Metapopulation persistence is affected by individual life history variation (Bonte & Dahirel, 2017). Because life history evolution takes place at the same temporal scale as changes in habitat fragmentation and the resulting demography (Cheptou et al., 2017), a tight feedback between the ecological and evolutionary dynamics (eco-evolutionary dynamics; [Hendry; intro this issue]) is expected (see Fig. 1). For instance, local population sizes are determined by local carrying capacities in heterogeneous metapopulations when connectivity is low, but with increased connectivity metapopulation size will be larger than the sum of local carrying capacities (Zhang et al., 2017). Metapopulation size will therefore be determined by spatial forcing and the joint evolution of dispersal and local adaptation. The long-term research on the Glanville fritillary demonstrated the tight eco-evolutionary coupling between dispersal evolution and metapopulation dynamics (Fountain, Nieminen, Sirén, Wong, & Hanski, 2016; Hanski & Mononen, 2011; Hanski, Mononen, & Ovaskainen, 2011; Hanski & Saccheri, 2006). While we have some insights on the importance of spatial forcing for the evolution of (some specific) traits, we lack any understanding on its feedback on metapopulation functioning, except for some theoretical work focusing on the eco-evolutionary feedback with range expansions and patch occupancy [Govaert et al. this special issue].

Several statistical and empirical approaches have been developed to quantify the relative contribution of ecology and evolution in demographic and phenotypic change. These approaches rely either on experimental manipulations of evolvability (Becks, Ellner, Jones, Hairston, & Hairston Nelson G., 2010; Turcotte, Reznick, & Daniel Hare, 2013; Turcotte, Reznick, & Hare, 2011) or statistical partitioning based on price and breeder equations or the use of Integral Projection Matrices (Coulson, 2012; Coulson et al., 2011; Smallegange & Coulson, 2013;

Vindenes & Langangen, 2015) in time series. An alternative, to date largely unexplored, is the use of a systems approach to forecast patterns at higher metapopulation order from lower-order individual variation in life history traits (Evans et al., 2013; Evans, Norris, & Benton, 2012). Because metapopulation dynamics are by definition determined by processes at lower individual hierarchy, individual-based models are highly appropriate to perform in silico experiments in systems where sound in vivo experiments are impossible to conduct at the required detail and replication. Especially when data are sparse, difficult, and expensive to collect, systems approaches enable the development of a predictive ecology, which embraces stochasticity (Travis et al., 2013).

We follow this philosophy with as specific aim to test how evolved variation in life-history traits affects metapopulation dynamics. We build on earlier experimental work demonstrating a profound impact of metapopulation structure on both local and metapopulation-level demography, life-history evolution and gene expression in a model species, the spider mite *Tetranychus urticae* (De Roissart et al., 2016; De Roissart, Wang, & Bonte, 2015). We developed and analysed an individual-based metapopulation models closely parameterised to the experiment outlined above. The metapopulation model does not incorporate adaptive dynamics, but instead generates metapopulation dynamics in response to the empirically derived evolved individual-level life history variation. In this way, we show that the evolved trait variation in our experiments had in general a weak impact on metapopulation functioning except for metrics related to local and metapopulation size, and that most variation in the metapopulation dynamics is related to spatial forcing. Virtual invasion experiments demonstrated subsequently the adaptive value of evolutionary change in individuals evolving in

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classical metapopulations, but initially not for individuals with an evolutionary background in the other metapopulation types. By including conditional stress tolerance by means of lowered mortality rates under starvation, evolved strategies showed adaptive value in all metapopulation types.

(Meta)population metrics	local density	Metapopulation size	patch extinction rate	alpha variability	Spatial synchrony	gamma variability
Classical		-	+	+	-	-
Mainland-island			-	-	-	-
Traits	Survival	Time till maturity	daily fecundity	Longevity	dispersal rate	sex ratio
Classical			+	-		
Mainland-island		+	+			+

Table 1: Schematic overview of the observed metapopulation dynamics and evolutionary change in life history traits in experimental classical and mainland-island metapopulations relative to patchy metapopulations (see (De Roissart et al., 2016)).
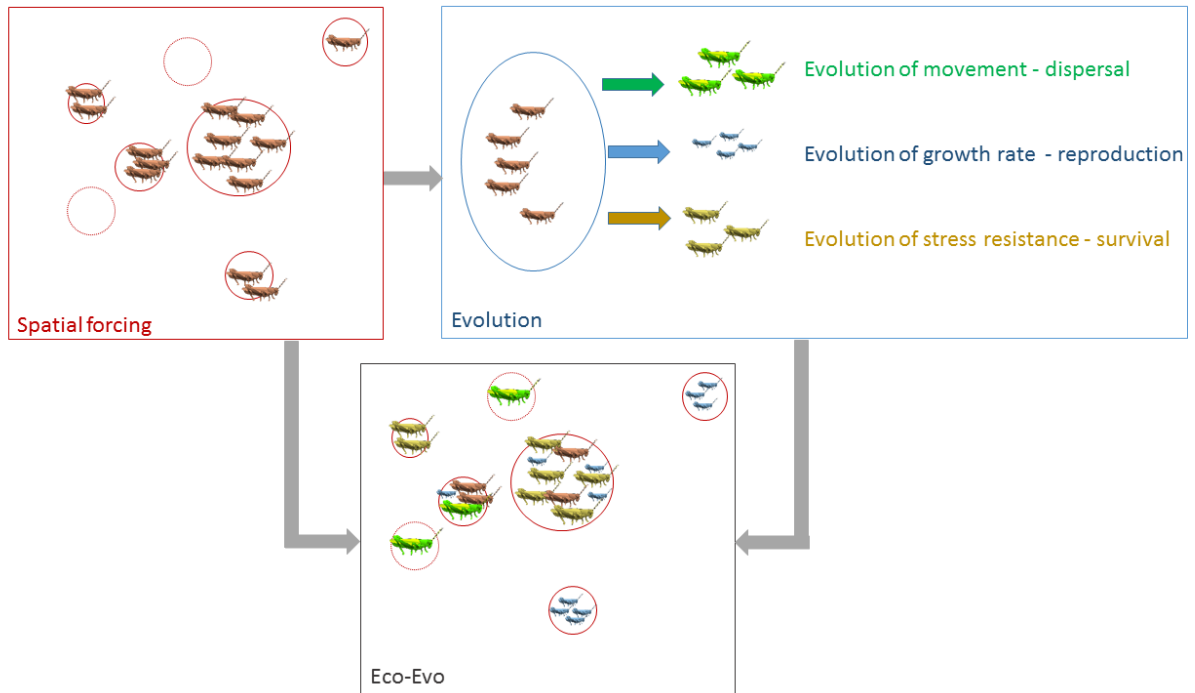
Fig. 1: Conceptual overview. Metapopulation dynamics as quantified by mean and variance of local and metapopulation size are affected by the specific spatial components of the metapopulation like patch size, connectedness and patch persistence (dashed lines versus full lines). These attributes thus induce spatial forcing (**red box**). Changes in this spatial configuration equally drive life history evolution, for instance by selection of dispersal, reproduction and survival (**blue box**). Spatial sorting (**Eco**) combined and evolution (**Evo**) then jointly determine metapopulation dynamics (**grey box**).

Methods

A short overview of the preceding experimental evolution

In the experimental evolution (De Roissart et al., 2016, 2015), mites from one genetically variable source population were either placed in a metapopulation consisting of nine equally sized patches (*patchy metapopulation*), nine patches with the same amount of resources randomly assigned to each patch every week until the metapopulation carrying capacity was reached (*classical metapopulation*), or six patches of which three were of double size (*mainland-island metapopulation*). Patches consist of leaves of 20 cm², or 40 cm² for the large patches in the mainland-island metapopulations. Patches were isolated from each other by a tanglefoot© matrix preventing mites from dispersing by walking, but a wind current (2 m/s) facilitated aerial dispersal of the mites two times a week during the entire period of the experiment. Because of the passive aerial dispersal, all patches are equally isolated from each other since probabilities of immigration were not distance-dependent, only area-dependent (De Roissart et al., 2015). Metapopulation resources were renewed weekly by adding fresh bean leaves according to the treatment. No leaves were removed before complete deterioration preventing the enforcement of extinction. Dispersal in the metapopulation was thus random regarding immigration and at high cost. The metapopulation-level food availability as defined by the total availability of leaf surface over subsequent generations was thus identical among treatments. An overview of the measured individual life history traits and metapopulation dynamics can be found in Table 1.

We found divergent multivariate trait evolution in metapopulations of equal metapopulation carrying capacity, but with either patches of variable size (*mainland-island metapopulations*) or

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of varying size in space and time (*classical metapopulation*) relative to metapopulations consisting of equal sized and stable patches (*patchy metapopulation*). Life-history evolution did not affect rates of intrinsic growth under optimal conditions, but gene-expression data and performance experiments in a challenging environment demonstrated enhanced stress resistance in mites that evolved in both mainland-island and classical metapopulations. The exact translation of this stress resistance towards life-history reaction norms is unknown. We quantified metapopulation functioning (De Roissart et al., 2015) in parallel: relative to patchy metapopulations, patch extinction rates, local variability in populations size over time (alpha variability) increased in classical metapopulations, while overall metapopulation size, spatial synchrony (an analogue measure as cross-correlations in the population time series) and variability in the total metapopulation size over time decreased. Patch extinction rates and the different variability metrics were found to be lowest for mainland-island metapopulations. An overview of the main results from the experimental metapopulations are given in Table 1.

The model algorithm

The model is individual-based and simulates mite development and population dynamics as in the experiments (De Roissart et al., 2016, 2015) on a daily basis for 1200 days. The evolved traits, as determined at the end of the experimental evolution (see (De Roissart et al., 2016) and Table 1) were used to parameterize the model. Individuals carry alleles that determine survival rate during development, age at maturity, longevity, probability of being female (sex ratio). A total of 900 mites with trait variation as quantified by (De Roissart et al., 2016) are initialized in each metapopulation (100 individuals per patch unit). Parameterisation of feeding rates and

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thresholds of starvation were based on simple experiments where different stages (larvae, nymphs, adult males and females) of mites were allowed to feed on fresh bean leaves or left to survive without food. Feeding rate was assessed by quantifying the surface of bean leaves with chlorophyll removed by the different stages during one day. These experiments were separately performed with mites not originating from the experimental metapopulations and thus reflect values under optimal conditions. Unknown parameters were estimated using approximate Bayesian methods for individual-based models (see Supplementary material 1) based on the observed local and metapopulation-level demography so that overall emerging metapopulation and population statistics from the model fitted the experimentally observed ones.

An overview of the parameter setting can be found in Table S1 in supplementary material. All females in the metapopulation are expected to mate, so to have female offspring. To avoid selection during the simulations and thus to maintain the experimentally quantified genetic variation no genetic algorithms were implemented. Instead, new-born mites received a random trait value from the appropriate distribution. Dispersal is modelled as a global dispersal in 1-2 day old females among all patches at the experimentally derived rate and dispersal cost. As in the experimental metapopulations, dispersal is only possible every three days. Besides these experimentally derived individual measures, additional density dependency in dispersal and survival (as measured at the population level in (De Roissart et al., 2015)) were implemented. Resources were refreshed as in the parallel experiments and feedbacks between population size and stage structure and resource use were thus emerging processes. As for the empirical experiments that served as base for the model, we calculated the following metrics related to demography and metapopulation dynamics (Table 1): mean local population size, mean

metapopulation size, patch extinction probability, local variability in population size (alpha variability), spatial synchrony in population sizes and metapopulation-level variability of the entire metapopulation size (gamma variability). The complete model description can be found in Supplementary material 1.

Virtual experiments

1. Reciprocal metapopulation translocation experiment: partitioning the effects of trait variation and spatial forcing for metapopulation dynamics

   Are evolved strategies to the benefit of the metapopulation? We initialized individuals characterized by trait distributions that evolved in each of the experimental metapopulation types in each of the three metapopulation types. So, 30000 simulations were run for each metapopulation scenario, 10000 with trait values that evolved in the matching metapopulation, and 2 x 10000 with trait distributions from mites evolved in the alternative metapopulation context. Because traits are randomly assigned each generation, no selection is allowed. The resulting metapopulation-level properties were quantified (see Table 1) and enabled us to:

   a. quantify the importance of evolutionary background (individual variation as derived from experimental evolution) versus spatial forcing (metapopulation structure) on local and metapopulation-level demographic metrics. We partitioned variance in all metapopulation metrics by means of constrained ordination (RDA; (Oksanen, Blanchet, Kindt, Legendre, & O'Hara, 2016)).

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b. assess to which degree metapopulations initialised with mites from the matching evolved experimental metapopulation performed better than those from the non-matching metapopulations. If evolution of individual mites is of benefit to the metapopulation, local- and metapopulation size is expected to be maximized, extinction probability, local and metapopulation-level variability and spatial synchrony to be minimised. We thus interpret metapopulation statistics as a proxy of metapopulation fitness.

2. Invasion experiment

Are evolved strategies to the good of the individual? We expect evolution in the experimental metapopulations to increases individual fitness, so to be adaptive at the individual level. We therefore introduced a rare mutant with traits from the matching metapopulation into fully functional metapopulations (pseudo-equilibrium reached at 600 time steps) initialised with mites from a different, so non-matching evolutionary context. Increases in population size of the mutant at short and longer time frames then demonstrate the adaptive value of the evolved individual strategy. A total of 90 (10/patch) mutant individuals were introduced in contrasting metapopulations of ~20000 individuals. 1000 independent runs per invasion scenario were completed.

Because transcriptomic and physiological analyses indicated evolved stress resistance in mites from classical and mainland-island metapopulations (De Roissart et al., 2016), we additionally performed invasion experiments by allowing 10, 25 and 50% lower mortality rates under food shortage. This enabled us to test the prediction that such evolved stress resistance as translated in higher starvation tolerance would increase individual

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performance and invasibility. We calculated for each metapopulation type populated by individuals that evolved under the non-matching contexts its *invasibility* by individuals that evolved in the matching metapopulation context as the proportion of metapopulations where the matching genotypes survived (attaining increasingly higher population sizes). High invasibility rates of the matching genotypes then indicates that the evolved life history traits are adaptive at the individual level.

Results

Reciprocal metapopulation translocation experiment

Evolutionary changes in life history traits explained 11.2% of the total variation in the suite of metapopulation and population demographic metrics, while 57% was explained by spatial forcing (Table 2). Especially mean population sizes at the local and metapopulation-level were strongly affected by the evolved trait variation (Table 2). More specifically, mites that evolved in patchy metapopulations systematically reached high local and metapopulation densities (see Fig 2).
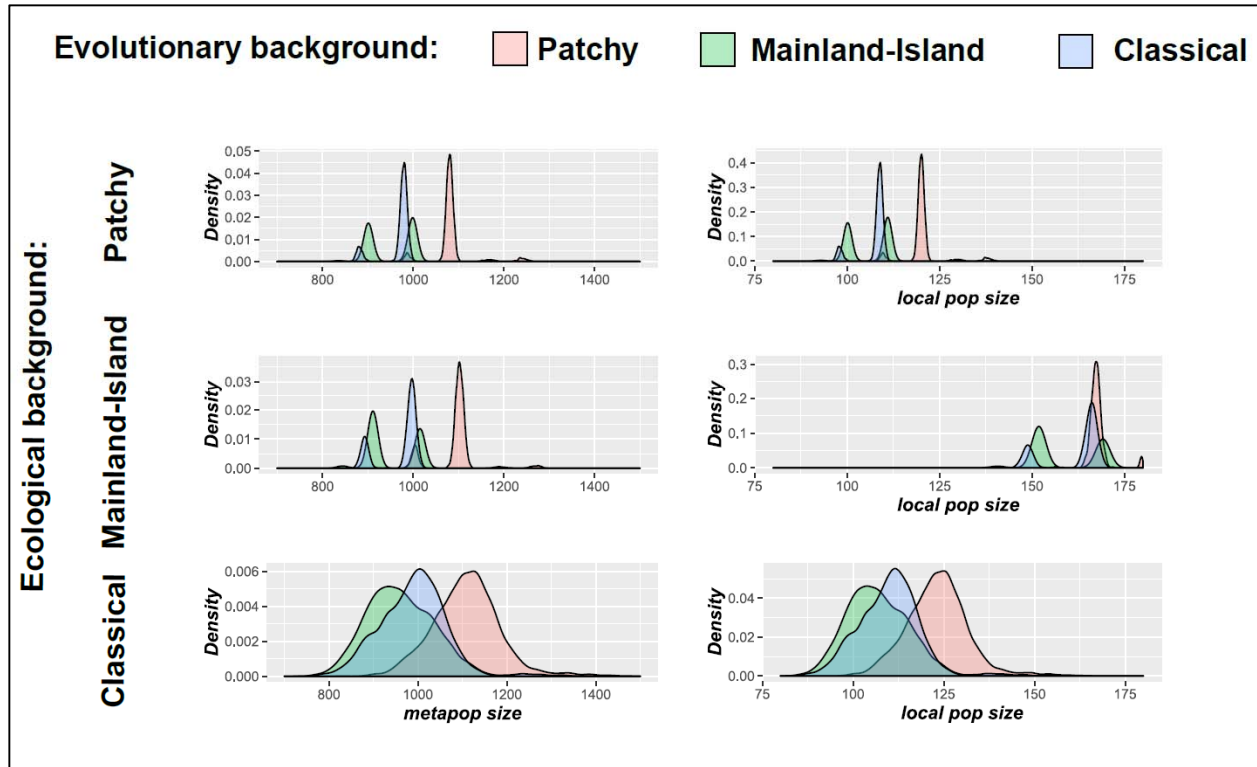
Fig 2. Distribution of different population sizes obtained by the virtual translocation experiments. Left panels represent the distribution of metapopulation sizes; those at the right local population sizes. Upper panels show results from virtual translocations in patchy metapopulation, Middle those from Mainland-Island metapopulations and lower ones those from classical metapopulations. Colours indicate the different evolutionary background of the introductions. The metapopulation typology (spatial forcing) is the main determinant of alpha, gamma variability and spatial synchrony. Results from virtual translocation experiments show across the metapopulation contexts highest average population and metapopulation sizes for mites with an evolutionary background from patchy populations. Population sizes are thus not maximized when genotypes match their metapopulation background

Metrics related to spatial and spatiotemporal variance in metapopulation size and local population size were predominantly impacted by spatial forcing (Table 2), with highest contributions of the spatial forcing reached for the metrics at the local level (alpha variability and local population size). Alpha and gamma variation were highest, spatial synchrony lowest in classical metapopulations (Fig 3). Spatial synchrony is highest in mainland–island

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metapopulations. Despite the overall low contribution of evolution to metapopulation variability statistics, gamma and alpha variability is systematically lowest for genotypes that evolved in mainland-island metapopulations, and highest for individuals with an evolutionary history from classical metapopulations.
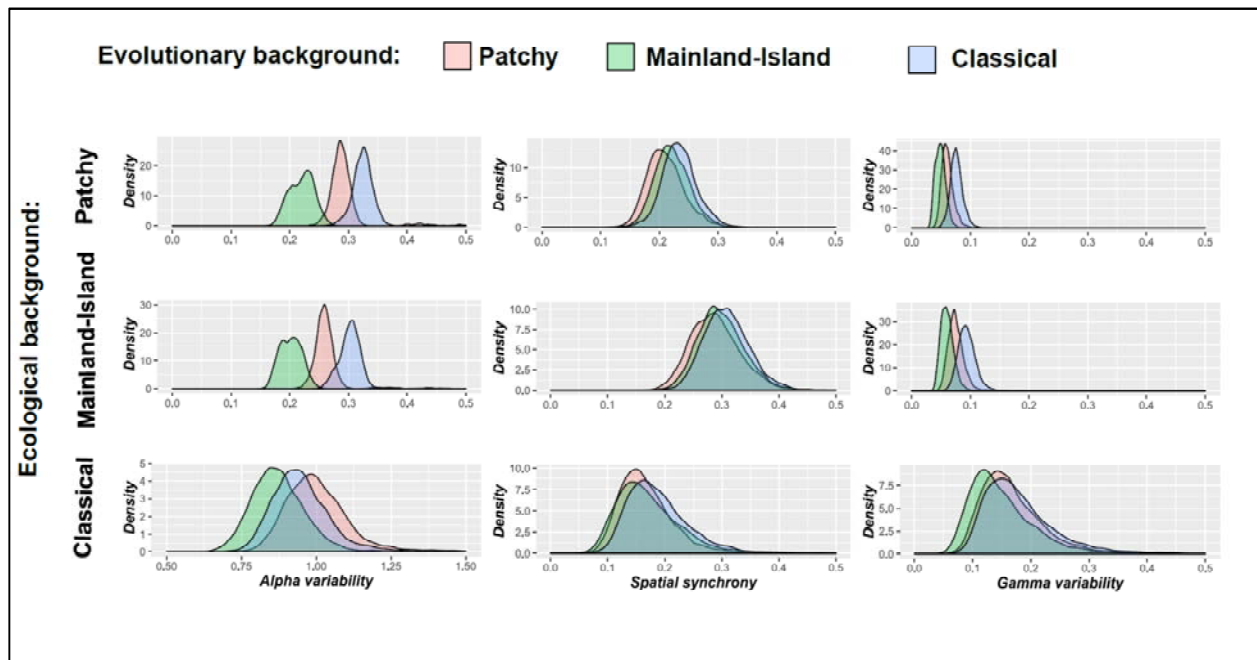

Fig. 3. Distribution of different metapopulation variability measures obtained by the virtual translocation experiments. Panels are horizontally ordered according to the three metrics (left: alpha variability, Middle: spatial synchrony; Right: Gamma variability). Upper panels show results from virtual translocations in patchy metapopulation, Middle those from Mainland-Island metapopulations and lower ones those from classical metapopulations. Colours indicate the different evolutionary background of the introductions. The metapopulation typology (spatial forcing) is the main determinant of alpha, gamma variability and spatial synchrony. Note that ranges along X-axis is different for alpha variability in classical metapopulations relative to patch and mainland-island metapopulations.

Metapopulation typology accounted for 44% of the variation patch extinction (Table 2), while overall the contribution of evolution was marginal. This low impact of evolution is because extinctions were absent in the mainland-island and virtually absent in the patchy

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metapopulation (mean of 0.00012±0.00005 [0-0.0002 CI]). In the classical metapopulations, daily patch extinction risks varied between 0 and 0.028, and are overall lowest under the matching evolutionary context (mean of 0.0069±0.0055 [0-0.0244 CI]), so when populated by genotypes that evolved in classical metapopulations. Daily extinction risks were highest for individuals with an evolutionary background in the patchy (mean of 0.0084±0.0066 [0-0.0278 CI]) and the mainland-island metapopulations (mean of 0.0078±0.0066 [0-0.0256 CI]).

In conclusion, metapopulation dynamics are predominantly shaped by spatial forcing, but evolved trait variation may induce shifts in metapopulation functioning. We found no indications that evolution maximised population sizes or minimised local and metapopulation-level variability and spatial synchrony. Reduced rates of extinction risk and alpha variability in the matching context for classical metapopulations indicate, however, a shift towards adaptations to the good of this metapopulation type.

Metric	Spatial forcing	Evolved trait	Residual variation
All metapopulation metrics	0.570	0.112	0.311
Gamma variability	0.612	0.045	0.343
Alpha variability	0.945	0.018	0.140
Spatial synchrony	0.593	0.018	0.389
Local population	0.849	0.078	0.074
Extinction	0.441	0.001	0.558

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Metapopulation size	0.008	0.512	0.480

Table 2. Variance partitioning of the six metapopulation metrics according to spatial forcing (metapopulation type), evolved trait variation and its covariation. The proportion of residual variation is given in the last column.

Invasion experiments

Mites that evolved in mainland-island metapopulations were least able to invade their matching metapopulation context. Genotypes that evolved in patchy or classical metapopulations had highest probability to invade their matching context, especially when the metapopulation was populated by genotypes with an evolutionary background from mainland-island metapopulations (Table 3).

Metapopulation context	Evolutionary background of the metapopulation		
	Patchy	Mainland-island	Classical
Patchy		0.633	0.292
Mainland-island	0.028		0.004
Classical	0.233	0.686	

Table 3: invasiveness of genotypes into their matching metapopulation occupied by individuals with a non-matching evolutionary history. The rates thus indicate the proportion of successful invasions of matching genotypes into their own metapopulation context populated by individuals that evolved in a different metapopulation type.

The additional invasion experiments where we implemented a 10, 25 and 50% lower mortality rate under starvation in genotypes from mainland-island metapopulations, increased the invasibility their matching metapopulation contexts towards 37, 82 and 100% and 32, 52 and 87.5% when they were respectively populated by mites with an evolutionary history from patchy and classical metapopulations. Implementation of a starvation resistance of 10% in mites from

classical metapopulations, increased their invasibility in the matching context already towards 84.2% when occupied with mites from mainland-island metapopulations and 57.3% when occupied by mites from patchy metapopulations, and was more than 95% under a starvation resistance of 25 and 50%. Implementing starvation resistance thus also increased the adaptive nature of the life history evolution, especially in mites that evolved in mainland-island metapopulations.

Discussion

Changes in the spatial structure of populations have a strong impact on demography and genetics. Theory predicts that a coupling between ecological and evolutionary dynamics may affect functioning and performance of the metapopulation (Ezard, Côté, & Pelletier, 2009; Hanski & Mononen, 2011; Kinnison & Hairston, 2007). Understanding to which degree metapopulation dynamics are affected by evolutionary dynamics is essential for conservation, as conflicts between individual and metapopulation goods may both increase or decrease metapopulation performance in terms of persistence and size, and eventually lead to evolutionary rescue or suicide (Delgado et al., 2011). Because different populations are connected by dispersal in metapopulations, dispersal is expected to be a central life history trait for these eco-evolutionary dynamics (Bonte & Dahirel, 2017). Many theoretical, but also experimental studies using bacterial and protist populations confirm this view (Bell & Gonzalez, 2011; Fronhofer & Altermatt, 2015). In reality, evolutionary dynamics are not restricted to dispersal evolution, but comprise multivariate selection on a wide array of traits, as earlier reported for our experimental system (De Roissart et al., 2016). By building further on this experimental work using an arthropod model, we here show that about 40% of the metapopulation dynamics, as measured

by metrics related to population size means and variances, are determined by the spatial setting *per se*. From these performance metrics, average local population sizes are up to 20% determined by evolutionary changes in life history traits, total metapopulation sizes up to 50%. Overall, our estimates of the contribution of evolution to population sizes are in line with those estimated for phenotypic change in freshwater crustaceans and rotifers and for community and ecosystem response following guppy evolutionary change after predator introduction in Trinidadian streams (Ellner, Geber, & Hairston, 2011).

Evolutionary changes in life history explained between 20% and 50% of all variation in population sizes among the three experimental metapopulation types. Although the magnitude of this impact is the result from our chosen spatial settings, it nevertheless demonstrates the potentially strong impact of evolution on the eventual reached population sizes in metapopulations. As metapopulation size was largely constrained by the experimental setup and deliberately fixed for all treatments, it is not surprising that the contribution of spatial forcing is low. It remains nevertheless surprising that the effectively reached populations sizes depend on the evolutionary history. Metapopulations occupied by virtual mites that evolved in patchy metapopulations reached highest local and metapopulation sizes overall. The observed life history evolution in mainland-island and classical metapopulations did consequently not optimise population sizes because they were not largest in their matching context. Because demographic variability was predominantly determined by spatial forcing, variability and spatial synchrony were neither found to be lowest under matching scenarios. Local and metapopulation-level variability was overall lowest for genotypes that evolved within mainland-island metapopulations. While local extinction rates were predominantly determined by spatial

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forcing and only relevant in classical metapopulations, a reduced rate was found for matching genotypes. Life-history evolution thus improved metapopulation dynamics that improve persistence to some degree only in our classical experimental metapopulations.

The predicted local population and metapopulation sizes under genotype-metapopulation matching accord with those obtained from empirical work. Although earlier experiments were only replicated three times, it is interesting to note that similar bimodal patterns in local population and metapopulation sizes were found in the experiments. These measures are time snapshots at the end of the experiment. The bimodal patterns result from temporal fluctuation with crowded patches dominated by long-lived adult females alternating with freshly colonised patches dominated by juveniles. Our model systematically predicted highest metapopulation sizes for genotypes from patchy metapopulations, independent of the metapopulation structure. Differences in population and metapopulation sizes across treatments are in line with those empirically derived (De Roissart et al., 2015) but differences between patchy metapopulations on the one hand, and mainland-island and classical metapopulations on the other hand are larger than observed. We only modelled variation in the experimentally derived life-history traits (De Roissart et al., 2016). These were all quantified under optimal conditions. Our invasion models suggest that the incorporation of conditional mortality, expressed as starvation resistance for genotypes originating from classical and mainland-island metapopulations rendered evolutionary life-history changes adaptive. Decreasing starvation mortality in the invasion experiments, gradually lowered differences in predicted average population sizes relative to those from patchy metapopulations and decreased variances for metapopulations populated by these genotypes, but not to such a degree that overall patterns changed towards optimised

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metapopulation functioning under matching contexts. Time and other practical constraints make it difficult for empiricists to measure life-history traits under different density conditions. An increased tolerance to starvation is, however, only one of the possible evolved conditional strategies related to a general stress resistance. Such a general stress resistance strategy was revealed by detailed transcriptomic and physiological analyses. Unfortunately, we obtained results from these molecular analyses not at the same time as the experiments were running, so we were unable to perform additional starvation or other stress resistance tests, except for the performance tests on a subordinate host plant (tomato), which in line with the molecular analyses showed a better performance for mites that evolved in the classical and mainland-island metapopulations. Other density- and condition-dependent strategies may equally generate feedback on population sizes. Changes in feeding efficiency as implemented into functional responses in a resource-consumer model for instance predicted elevated densities of protists in a range-expansion experiment (Fronhofer & Altermatt, 2015).

While the link between life-history evolution and metapopulation functioning is not straightforward, selection should maximise fitness and thus enable genotypes to invade their matching environment occupied by genotypes that have not evolved locally. Our invasion experiments confirmed this principle for individuals with an evolutionary background in patchy metapopulations. Virtual mites with traits from mainland-island and classical metapopulations were, however, not able to invade their matching metapopulation context, especially when these were occupied by genotypes from the patchy metapopulation. This apparent maladaptive evolution could be countered by translating the observed signals of stress resistance into reduced mortality rates under starvation. 10-25% lower mortality rates under starvation led to

successful invasions. Our study thus indicates that even small conditional changes in particular life history traits in spider mites, which were in line with insights from –omic approaches (De Roissart et al., 2016), were key to optimality under matching demographic conditions. This also implies that our estimate of the contribution of evolutionary change to metapopulation dynamics is likely a lower and conservative boundary. The overall level of explained variance by the spatial setting and evolution was, however, little affected when stress resistance was implemented (see Supplementary material 2).

We show that in our spider mite experimental metapopulations, both temporal variation in local and metapopulation size, as well as spatial synchrony are predominantly determined by the spatial configuration of the metapopulation, by spatial forcing. Local and metapopulation-level average population sizes are in contrast more determined by evolutionary dynamics. This finding implies that changes in spatial networks have the ability to affect spatiotemporal fluctuations in population sizes, thereby potentially compromising metapopulation viability, for instance by increasing population synchrony (Walter et al., 2017; Wang et al., 2015). Evolutionary dynamics may in contrast increase average population sizes thereby rescuing them from demographic and environmental stochasticity. These theoretical insights should in first instance be regarded as a proof of concept demonstrating that changes in spatial configuration in metapopulations may affect different properties of the metapopulation dynamics relative than evolution resulting from these changes in spatial structure, and that the contribution of evolution to metapopulation dynamics can be substantial.

Obviously, such insights could not be obtained from adaptive dynamic modelling. Such approaches typically focus on the optimisation of single, or few traits at maximum [Govaert et

al.; this special issue] while neglecting the complex architecture of the multiple life history traits that eventually determine the species' life history. As the genotypic variance/covariance matrix is unknown in many, not to say all species, system approaches like applied here are likely the only way to infer the importance of realistic genotypic changes on higher-level ecological dynamics. By embracing the complexity and the multivariate nature of life history evolution, approaches like applied here should speed-up the transition of the field of eco-evolutionary dynamics from a theoretical towards a predictive science relevant to understand the importance of individual processes for entire ecosystems.

At the scale of the experimental setup, our results point to the fact that changes in the arrangement of host plants, for instance in horticulture, may strongly affect densities and damage thresholds for pest species, both directly through spatial forcing and the resulting genetic changes in life history traits and physiology. In a more broader perspective, we show that local population sizes of species inhabiting metapopulations may benefit from metapopulation-level evolutionary changes in traits that are not traditionally linked to metapopulation persistence.

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References

Arnold, S. J., Bürger, R., Hohenlohe, P. A., Ajie, B. C., & Jones, A. G. (2008). Understanding the evolution and stability of the G-matrix. *Evolution; International Journal of Organic Evolution*, *62*(10), 2451–61. doi:10.1111/j.1558-5646.2008.00472.x

Aspi, J., Jäkäläniemi, A., Tuomi, J., & Siikamäki, P. (2003). Multilevel phenotypic selection on morphological characters in a metapopulation of Silene tatarica. *Evolution; International Journal of Organic Evolution*, *57*(3), 509–17. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12703940

Barrett, R. D. H., & Schluter, D. (2008). Adaptation from standing genetic variation. *TRENDS in Ecology & Evolution*, *23*(1), 38–44. doi:10.1016/j.tree.2007.09.008

Becks, L., Ellner, S. P., Jones, L. E., Hairston, N. G., & Hairston Nelson G., J. G. (2010). Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics. *Ecology Letters*, *13*(8), 989–997. doi:10.1111/j.1461-0248.2010.01490.x

Bell, G., & Gonzalez, A. (2011). Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science (New York, N.Y.)*, *332*, 1327–1330. doi:10.1126/science.1203105

Bonte, D., & Dahirel, M. (2017). Dispersal: A central and independent trait in life history. *Oikos*, *126*, 472–479. doi:10.1111/oik.03801

Cheptou, P. O., Hargreaves, A. L., Bonte, D., & Jacquemyn, H. (2017). Adaptation to fragmentation: Evolutionarydynamics driven by human influences. *Philosophical Transactions of the Royal Society B: Biological Sciences, 372*(1712). doi:10.1098/rstb.2016.0037

Coulson, T. (2012). Integral projections models, their construction and use in posing hypotheses in ecology. *Oikos, 121*(9), 1337–1350. doi:10.1111/j.1600-0706.2012.00035.x

Coulson, T., MacNulty, D. R., Stahler, D. R., vonHoldt, B., Wayne, R. K., & Smith, D. W. (2011). Modeling Effects of Environmental Change on Wolf Population Dynamics, Trait Evolution, and Life History. *Science, 334*(6060), 1275–1278. doi:10.1126/science.1209441

De Roissart, A., Wang, S., & Bonte, D. (2015). Spatial and spatiotemporal variation in metapopulation structure affects population dynamics in a passively dispersing arthropod. *Journal of Animal Ecology, 84*(6), 1565–1574. doi:10.1111/1365-2656.12400

De Roissart, A., Wybouw, N., Renault, D., Van Leeuwen, T., Bonte, D., & Pfrender, M. (2016). Life history evolution in response to changes in metapopulation structure in an arthropod herbivore. *Functional Ecology, 30*(8), 1408–1417. doi:10.1111/1365-2435.12612

Delgado, M. del M., Ratikainen, I. I., & Kokko, H. (2011). Inertia: the discrepancy between individual and common good in dispersal and prospecting behaviour. *Biological Reviews of the Cambridge Philosophical Society, 86*(3), 717–32. doi:10.1111/j.1469-185X.2010.00167.x

Duplouy, A., Ikonen, S., & Hanski, I. (2013). Life history of the Glanville fritillary butterfly in fragmented versus continuous landscapes. *Ecology and Evolution, 3*(16), 5141–5156. doi:10.1002/ece3.885

Ellner, S. P., Geber, M. A., & Hairston, N. G. (2011). Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecology Letters*. doi:10.1111/j.1461-0248.2011.01616.x

Evans, M. R., Bithell, M., Cornell, S. J., Dall, S. R. X., Díaz, S., Emmott, S., … Benton, T. G. (2013). Predictive systems ecology. *Proceedings. Biological Sciences / The Royal Society*, *280*(1771), 20131452. doi:10.1098/rspb.2013.1452

Evans, M. R., Norris, K. J., & Benton, T. G. (2012). Predictive ecology: systems approaches. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1586), 163–169. doi:10.1098/rstb.2011.0191

Ezard, T. H. G., Côté, S. D., & Pelletier, F. (2009). Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *364*(1523), 1491–8. doi:10.1098/rstb.2009.0006

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics*, *34*, 487–515. doi:DOI 10.1146/annurev.ecolsys.34.011802.132419

Fountain, T., Nieminen, M., Sirén, J., Wong, S. C., & Hanski, I. (2016). Predictable allele frequency changes due to habitat fragmentation in the Glanville fritillary butterfly. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(10), 1600951113-. doi:10.1073/pnas.1600951113

Fronhofer, E. A., & Altermatt, F. (2015). Eco-evolutionary feedbacks during experimental range expansions. *Nature Communications*, *6*, 6844. doi:10.1038/ncomms7844

Hanski, I. (1998). Metapopulation dynamics. *Nature*, *396*, 41–49.

Hanski, I. (2012). Eco-evolutionary dynamics in a changing world. *Annals of the New York Academy of Sciences*, *1249*(1), 1–17. doi:10.1111/j.1749-6632.2011.06419.x

Hanski, I., & Gilpin, M. E. (1997). *Metapopulation biology: ecology, genetics, and evolution.* Academic Press.

Hanski, I., & Mononen, T. (2011). Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. *Ecology Letters*, *14*(10), 1025–34. doi:10.1111/j.1461-0248.2011.01671.x

Hanski, I., Mononen, T., & Ovaskainen, O. (2011). Eco-evolutionary metapopulation dynamics and the spatial scale of adaptation. *The American Naturalist*, *177*, 29–43. doi:10.1086/657625

Hanski, I., & Saccheri, I. (2006). Molecular-level variation affects population growth in a butterfly metapopulation. *PLoS Biology*, *4*(5), 719–726. doi:10.1371/journal.pbio.0040129

Kinnison, M. T., & Hairston, N. G. (2007). Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. *Functional Ecology*, *21*(3), 444–454. doi:10.1111/j.1365-2435.2007.01278.x

Laiolo, P., Obeso, J. R., Goodnight, C., Stevens, L., C, J. G., Schwartz, J., … Sheldon, B. (2012). Multilevel Selection and Neighbourhood Effects from Individual to Metapopulation in a Wild Passerine. *PLoS ONE*, *7*(6), e38526. doi:10.1371/journal.pone.0038526

Molofsky, J., & Ferdy, J.-B. (2005). Extinction dynamics in experimental metapopulations.

Proceedings of the National Academy of Sciences, *102*(10), 3726–3731.

doi:10.1073/pnas.0404576102

Oksanen, J., Blanchet, F., Kindt, R., Legendre, P., & O'Hara, R. (2016). Vegan: community ecology

package. *R Package 2.3-3*, Available at: https://cran.r-project.org/web/packa.

doi:10.4135/9781412971874.n145

Olivieri, I., Couvet, D., & Gouyon, P. H. (1990). The genetics of transient populations: Research at

the metapopulation level. *Trends in Ecology and Evolution*, *5*(7), 207–210. doi:10.1016/0169-

5347(90)90132-W

Olivieri, I., Tonnabel, J., Ronce, O., & Mignot, A. (2016). Why evolution matters for species

conservation: perspectives from three case studies of plant metapopulations. *Evolutionary*

Applications, *9*(1), 196–211. doi:10.1111/eva.12336

Smallegange, I. M., & Coulson, T. (2013). Towards a general, population-level understanding of

eco-evolutionary change. *Trends in Ecology and Evolution*. doi:10.1016/j.tree.2012.07.021

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., … Bullock, J. M. (2013).

Dispersal and species' responses to climate change. *Oikos*, *122*(11), 1532–1540.

doi:10.1111/j.1600-0706.2013.00399.x

Turcotte, M. M., Reznick, D. N., & Daniel Hare, J. (2013). Experimental test of an eco-evolutionary

dynamic feedback loop between evolution and population density in the green peach

aphid. *The American Naturalist*, *181 Suppl*, S46-57. doi:10.1086/668078

Turcotte, M. M., Reznick, D. N., & Hare, J. D. (2011). The impact of rapid evolution on population

dynamics in the wild: Experimental test of eco-evolutionary dynamics. *Ecology Letters*, *14*(11), 1084–1092. doi:10.1111/j.1461-0248.2011.01676.x

Vindenes, Y., & Langangen, Ø. (2015). Individual heterogeneity in life histories and eco-evolutionary dynamics. *Ecology Letters*, *18*(5), 417–432. doi:10.1111/ele.12421

Walsh, B., & Blows, M. W. (2009). Abundant Genetic Variation + Strong Selection = Multivariate Genetic Constraints: A Geometric View of Adaptation. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 41–59. doi:10.1146/annurev.ecolsys.110308.120232

Walter, J. A., Sheppard, L. W., Anderson, T. L., Kastens, J. H., Bjørnstad, O. N., Liebhold, A. M., & Reuman, D. C. (2017). The geography of spatial synchrony. *Ecology Letters*. doi:10.1111/ele.12782

Wang, S., Haegeman, B., & Loreau, M. (2015). Dispersal and metapopulation stability. *PeerJ*, *3*(January), e1295. doi:10.7717/peerj.1295

Zhang, B., Kula, A., Mack, K. M. L., Zhai, L., Ryce, A. L., Ni, W.-M., … Van Dyken, J. D. (2017). Carrying capacity in a heterogeneous environment with habitat connectivity. *Ecology Letters*, *20*(9), 1118–1128. doi:10.1111/ele.12807