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

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Abstract:

The performance of populations is affected by environmental change and the resulting evolutionary dynamics. The spatial configuration and size of patches is known to directly influence metapopulation dynamics (spatial forcing). These metapopulation dynamics are also affecting and affected by life history evolution. 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.

We here follow a system's modelling approach to disentangle the role of metapopulation structure relative to evolution for metapopulation performance. We developed an individual based systems model that is strongly based and parameterized by results from experimental metapopulations with spider mites. This model enables us to perform virtual translocation and invasion experiments that would have been impossible to conduct in our experimental systems.

We show that (1) metapopulation demography is more affected by spatial forcing than by observed life history evolution, but that life history evolution contributes up to 20% of the variation in demographic measures related to spatiotemporal variance in population sizes, (2) metapopulation performance is not enhanced by evolution, and (3) evolution is optimising individual performance in metapopulations when considering the importance of so far overlooked stress resistance evolution.

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.

Key-words: systems ecology, *Tetranychus urticae*, fitness, invasion, translocation, demography, extinction

Introduction

Many, not to say all, species inhabit spatially heterogeneous and structured habitat. Spatial structure is an inherent property of natural systems because of geographical variation in the availability of diverse niche components, or because of human-induced fragmentation [1]. When species move among patches of suitable habitat, local demography will be coupled with global metapopulation dynamics [2] and thereby impact colonization-extinction dynamics [3]. 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 [4,5]. 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 [6,7]. 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 [8].

Maximisation of individual fitness should, however, not necessarily lead to a maximised performance at higher levels of biological organisation. 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 [9]. In the extreme, conflict between individual and metapopulation good may induce evolutionary suicide and compromise conservation efforts [10]. As for individual measures of fitness, metapopulation performance can be measured by several metrics. High local population and metapopulation sizes and asynchrony in local population fluctuations generally maximise metapopulation long-term survival and thus persistence [2,11,12]. Metapopulation persistence will thus be affected by individual life history variation [5], but also by its configuration through spatial forcing. Increased patch isolation for instance induces higher dispersal mortality, local patch quality may affect local growth rates, and patch size will eventually determine local carrying capacities and resilience to demographic stochasticity. Evolutionary factors and spatial forcing will determine the ecological demographics at both the local and metapopulation scale (see Fig. 1). Evolution is thus expected to act at different levels of biological organisation, and earlier work demonstrated often different and contrasting selection pressures at the individual and group level [13,14].

The impact of spatial structure on these eco-evolutionary dynamics is 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 [5], other traits have been documented to evolve in parallel, and often in unpredictable ways [15,16]. Few empirical studies tested theoretical predictions beyond dispersal evolution, but recent work provides evidence of multivariate life-history evolution in metapopulations [17,18]. These studies suggest that fitness can be maximized through the optimization of different trait combinations. Because multiple pathways of evolution may lead to optimized performance, thereby maintaining quantitative genetic variation, any inference on the adaptive value of these evolutionary changes and its relevance for higher-order dynamics remains extremely difficult [19–21].

Measuring fitness and optimality is not trivial in spatially structured systems because of disequilibrium conditions and the complex interplay between relatedness, spatial structure, and various sources of stochasticity [22]. The available approaches all have their strengths and weaknesses. They do however share the common rationale that adaptive mutant strategies should be able to invade if stochastic demographic extinction due to low invader population sizes can be overcome. The discussion on the

relevant analytical measure of fitness and its most useful approximations is still ongoing in theoretical biology [23]. Measuring the adaptive value of life history adaptation in metapopulations is even more constrained because of the inherent difficulty to perform reciprocal translocation experiments at the this level. Such experiments are, however, necessary to infer the relative importance of evolutionary dynamics relative to the direct impact of the spatial setting (the level of environmental heterogeneity, variation in patch sizes, distance between patches; here-after referred to as spatial forcing). 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 [24]. The total metapopulation size will therefore be determined by spatial forcing and the joint evolution of dispersal and local adaptation.

Due to practical constraints regarding replication and spatial scale, empirical studies that aim to understand the importance of evolution for metapopulation dynamics are virtually non-existing, with the exception of the long-term research on the Glanville fritillary. Here, metapopulation surveys, genomics, combined with theoretical approaches demonstrate a prominent feedback between dispersal evolution and metapopulation dynamics [6,25–27]. 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 [28–30] or statistical partitioning based on price and breeder equations or the use of Integral Projection Matrices [31–34] in time series. An alternative, largely unexplored to date, is the use of a systems approach to forecast patterns at higher metapopulation order from lower-order individual variation in life history traits [35,36]. Because metapopulation dynamics are by definition determined by processes at lower individual hierarchy, individual-based models seem highly appropriate to perform in silico experiments in systems where sound in vivo experiments are impossible to conduct at the required detail and replication. Benton [37] for instance used such an approach to infer how life-history evolution affects population dynamics in harvested populations. Especially when data are sparse, difficult, and expensive to collect, systems approaches enable the development of a predictive ecology that embraces stochasticity [38].

We follow this philosophy with as specific aim to test how quantitative 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 the spider mite *Tetranychus urticae* [18,39]. In short, we found divergent multivariate trait evolution in metapopulations with either stable patches of variable size (*mainland-island metapopulations*) or with patch size varying in space and time (*classical metapopulation*) relative to metapopulations with equal and temporally stable patch sizes (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 expression of this stress resistance in terms of life-history reaction norms is unknown.

By following a systems approach we here show that evolved trait variation has a significant impact on local- and metapopulation level population sizes, but that most variation in metapopulation performance is related to spatial forcing. Virtual invasion experiments subsequently demonstrated the adaptive value of evolutionary change in individuals evolving in 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.

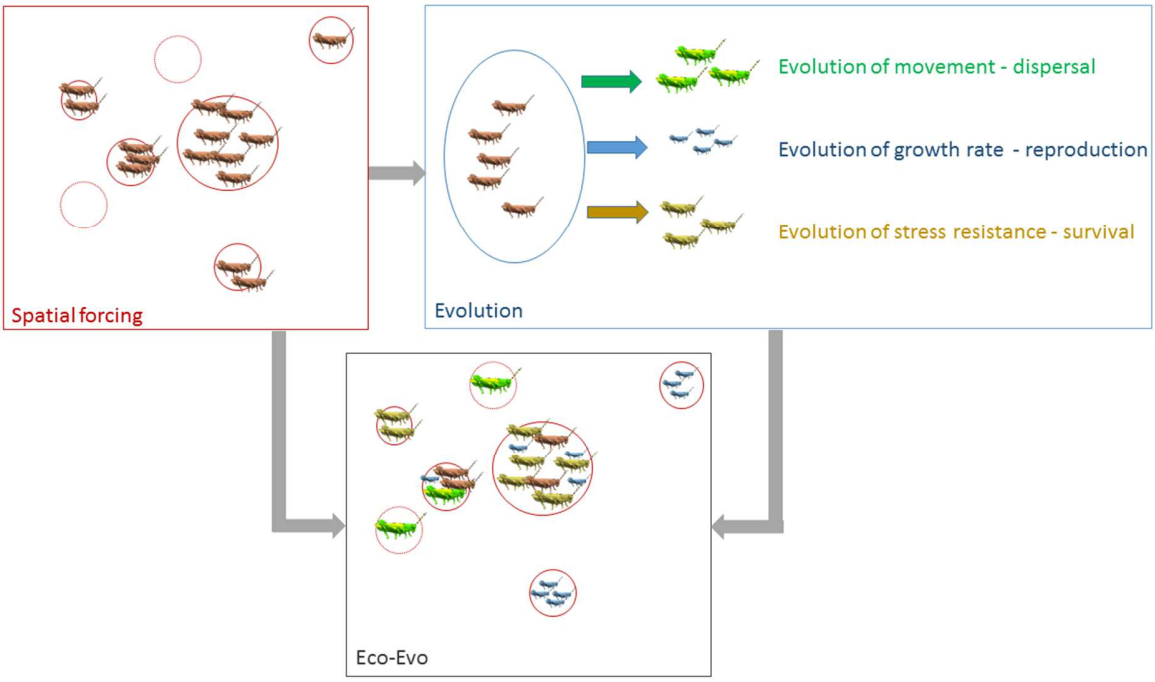

Fig. 1: Conceptual overview. Metapopulation dynamics as quantified by mean and variance of local and metapopulation size are affected by the specific spatial components of the metapopulation like patch size, connectedness and patch persistence (dashed lines versus full lines). These attributes thus induce 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

The model algorithm

The model is individual-based and simulates mite development and population dynamics as in the experiments [18,39] on a daily basis for 1200 days, after an initialization phase of 100 time steps. In the experimental evolution [18,39], 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 [39]. 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 carrying capacity as defined by the total availability of leaf surface over subsequent generations was thus identical among treatments. The evolved traits, as determined at the end of the experimental evolution (see [18] and schematic overview in 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 [18] are initialized in each metapopulation (100 individuals per patch unit). Parameterisation of feeding rates and 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. Due to experimental limitations, these experiments were 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 1,2) based on the observed local and metapopulation-level demography (see Table 1 for a schematic overview of the derived patterns in [39]), so that overall emerging metapopulation and population statistics from the model fitted the experimentally observed ones.

(Meta)population dynamics	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 evolutionary change in life history traits in experimental classical and mainland-island metapopulations relative to patchy metapopulations (see [18]).

An overview of the parameter setting can be found in Supplementary material 2. All females in the metapopulation are expected to mate, but 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 [39]) 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 performance (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 (Fig 2A)

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 [40] in all metapopulation performance properties and for metrics related to mean values (mean population and metapopulation size, extinction probability) and variances separately (alpha, gamma variability and spatial synchrony).
b. assess to which degree metapopulations initialised with mites from the matching evolved experimental metapopulation performed better than those from the non-matching metapopulations. We interpret metapopulation performance statistics as a proxy of metapopulation fitness. 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.

2. Invasion experiment (Fig 2B)

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.

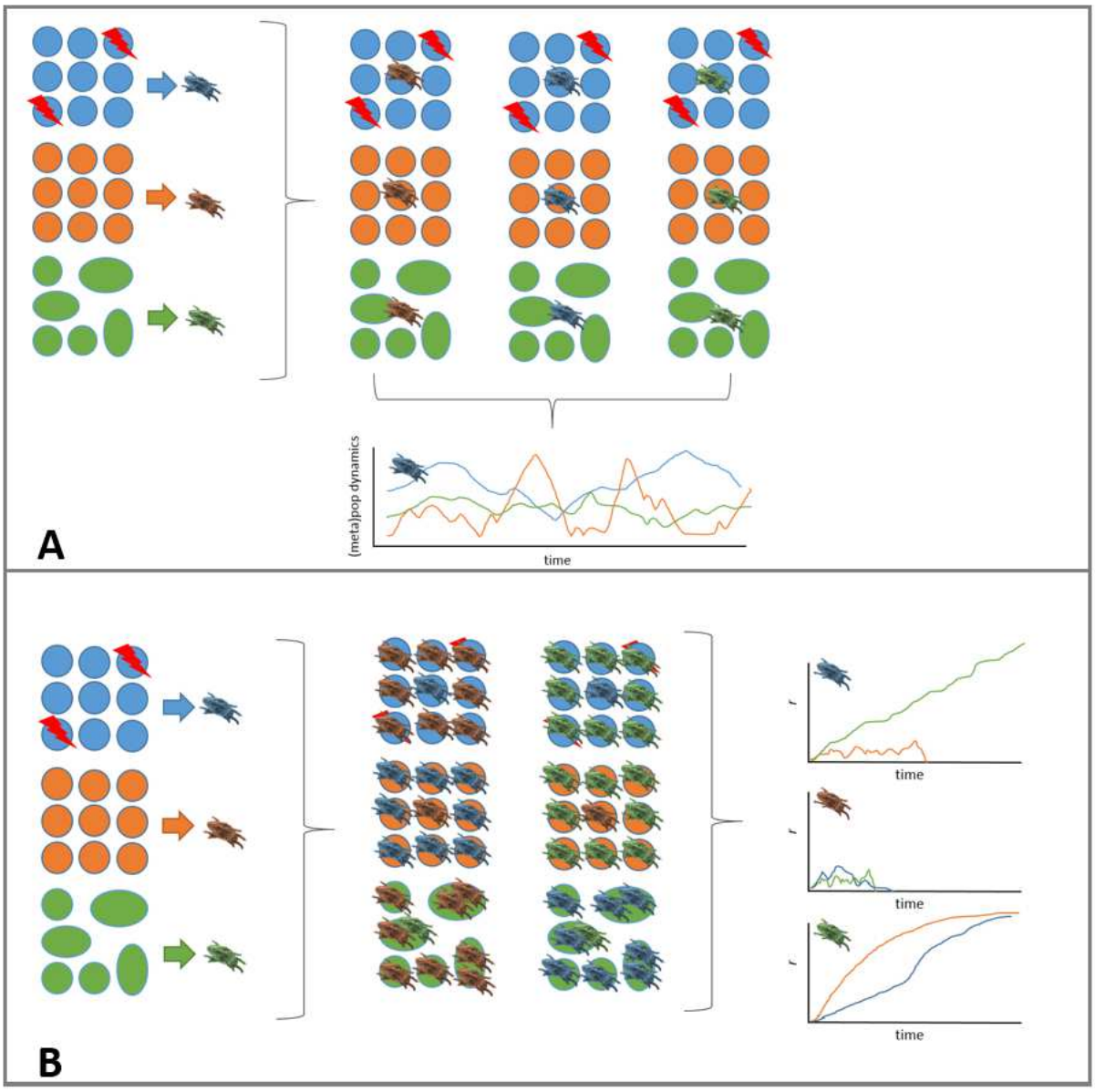

Fig 2: Schematic representation of the virtual experiments. A. Virtual translocation experiments. Individuals with traits from either metapopulation type are initiated in a matching or non-matching metapopulation (indicated by colour: blue: classical metapopulation; orange: patchy metapopulation; green: mainland island metapopulation). (Meta-) population dynamics are monitored and metrics (Table 1) are calculated. B. invasion experiment: Eventual invasion success and population growth of 90 individuals with trait distributions evolved in non-matching metapopulations (different colours). All virtual experiments are replicated 1000 times.

Results

Reciprocal metapopulation translocation experiment

Evolutionary changes in life history traits explained 12.5% of the total variation in the suite of metapopulation and population demographic metrics, while 38.9% was explained by spatial forcing (Fig 3A; Table 2).

Especially mean population sizes at the local and metapopulation-level were strongly affected by genetic trait variation (Fig 3C). More than 50% variation in metapopulation size was impacted by life-history evolution (Table 2). More specifically, mites that evolved in patchy metapopulations systematically reached high local and metapopulation densities (see Fig 4).

In contrast, metrics related to spatial and spatiotemporal variance in metapopulation size and local population size were predominantly impacted by spatial forcing (Fig 3B; up to 86% for alpha variability). Alpha and gamma variation were highest, spatial synchrony lowest in classical metapopulations (Fig 4). Spatial synchrony is highest in mainland-island 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.

Metric	Spatial forcing	Evol. Trait variation	Res
Gamma variability	0.238	0.013	0.750
Alpha variability	0.859	0.001	0.140
Spatial synchrony	0.440	0.023	0.537
Local population size	0.631	0.191	0.176
Extinction probability	0.180	0.005	0.815
Metapopulation size	0.002	0.537	0.461

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

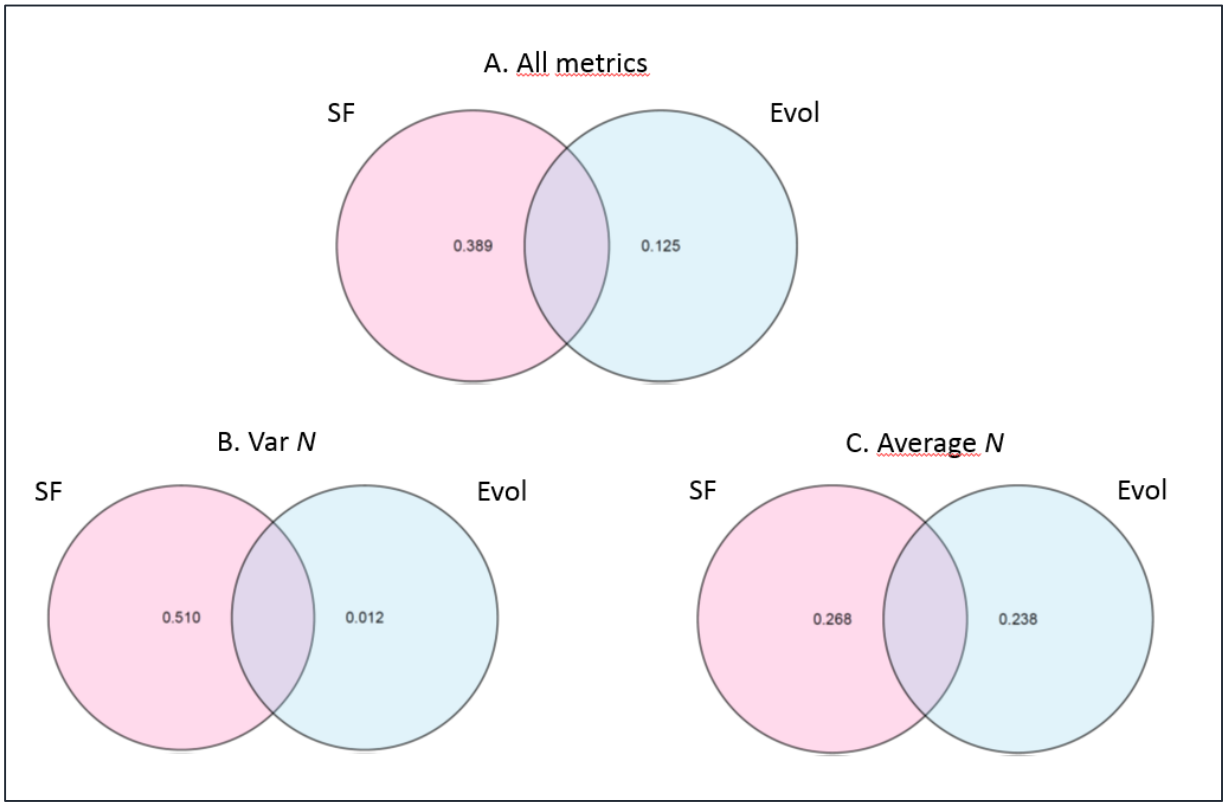

Fig. 3. Schematic representation of the variance partitioning for all metapopulation metrics (A), those related to spatiotemporal variability (B) and averages (C) in population sizes (*N*). Pink: contribution of spatial forcing; Blue: contribution of evolutionary trait variation.

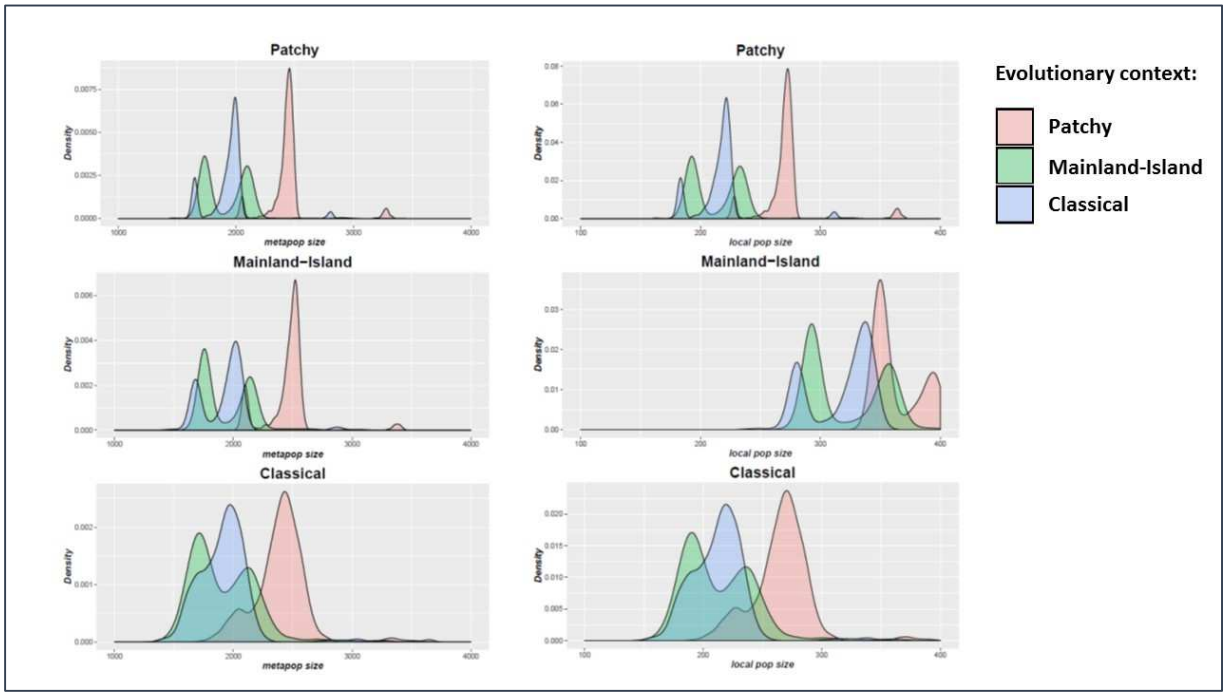

Fig 3. Results from virtual translocation experiments show highest average population and metapopulation sizes for mites with an evolutionary background from patchy populations. Population sizes are thus not maximized when genotypes match their metapopulation background.

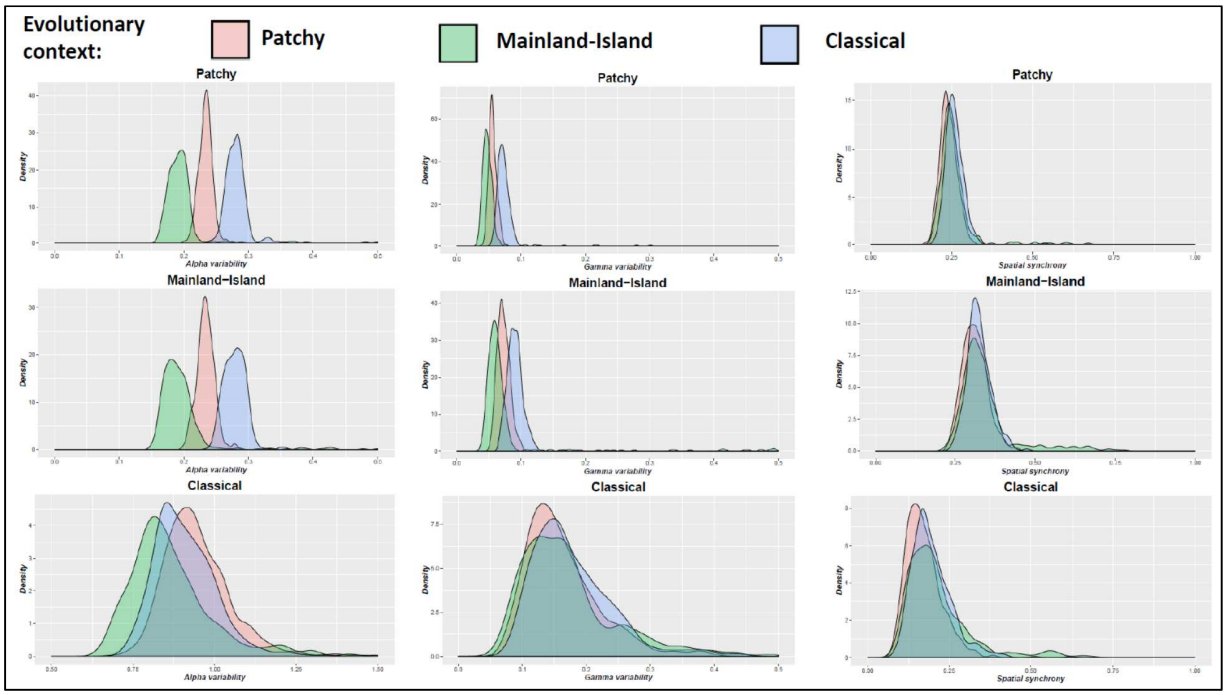

Fig. 4. Results from virtual translocation experiments show a predominant impact of the metapopulation typology (spatial forcing) for alpha, gamma variability and spatial synchrony. Note that ranges along X-axis is different for alpha variability in classical metapopulations relative to patch and mainland-island metapopulations.

Metapopulation typology accounted for 18% of the variation patch extinction (Table 2). Daily patch extinction risks varied in classical metapopulations between 0 and 0.02, but were never higher than 0.0001 in the other metapopulation types. In classical metapopulations, matching genotypes had with those from patchy metapopulations on average the lowest rates (respectively 0.00001 [0-0.0065 CI] and 0.00001 [0-0.0079 CI]) , while extinction risks were highest for individuals with an evolutionary background in the mainland-island metapopulations (0.0021 [0-0.01181 CI]).

In conclusion, metapopulation dynamics are predominantly shaped by spatial forcing, but evolved trait variation may induce shifts in metapopulation performance. 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.

Invasion experiments

The virtual invasion experiments (see Fig. 5) showed that genotype-metapopulation type matching only increased invasiveness (i.e., invasion probability and local abundance after successful invasion in all metapopulation types) for genotypes evolved in patchy populations, especially when the matching metapopulation was populated by mainland-island genotypes. Genotypes from classical metapopulation only invaded their matching metapopulation occupied by genotypes from mainland-island metapopulations. Mainland-island genotypes were not able to invade their matching metapopulation occupied by either genotypes from classical or patchy metapopulations.

Transcriptomic and physiological analyses indicated evolved stress resistance in mites from classical and mainland-island metapopulations [18]. We therefore performed additional invasion experiments for some specific scenarios by allowing 10, 25 and 50% lower mortality rate. This enabled us to test the prediction that such evolved stress resistance as translated in higher starvation tolerance would increase individual performance and invasibility. Under this condition, the previously failed invasions became successful (dashed lines in Fig. 5).

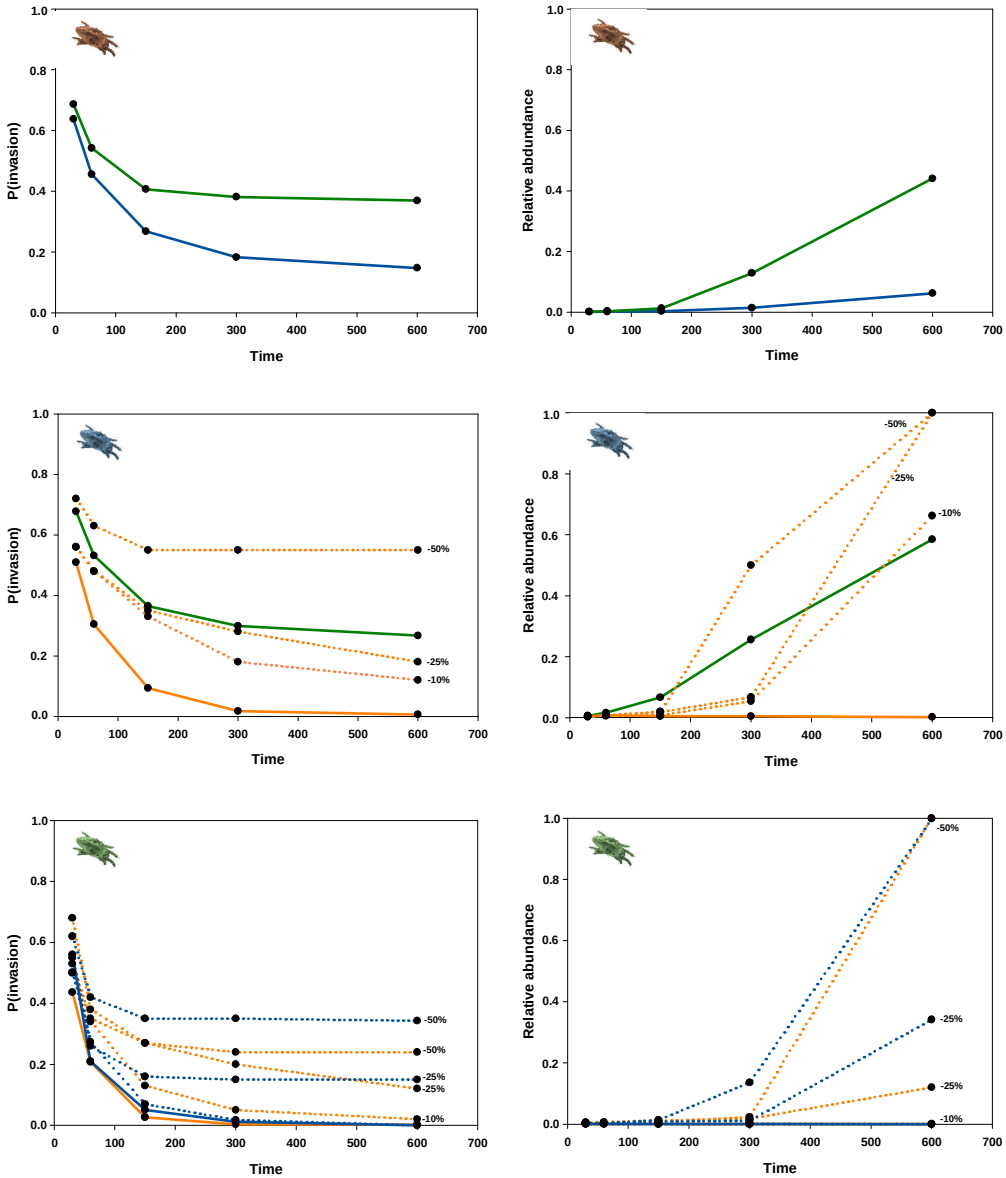

Fig 5. Graphical representation of the virtual invasion experiments. Colour of the mites indicate the matching metapopulation (genotype origin and metapopulation type to invade). Lines depict either temporal changes in the probability of invasion (left panels) or relative abundance during successful invasion (right panels) of genotypes in their matching metapopulation type occupied by genotypes with traits evolved in different metapopulation contexts. Line colours indicate the genetic background of the invaded population. Dashed lines show results from invasion experiments in those combinations were invasion failed in the base model, when starvation tolerance is implemented at different rates (relative decrease in mortality rate under starvation). All data are based on 1000 independent invasion experiments. Colour codes: Orange: patchy metapopulation; blue: classical metapopulation; green: mainland-island metapopulation.

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 [6,8,41]. 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 and eventually lead to evolutionary rescue or suicide [9]. Because different populations are connected by dispersal in metapopulations, dispersal is expected to be a central life history trait for these eco-evolutionary dynamics [5]. Many theoretical, but also experimental studies using bacterial and protist populations confirm this view [42,43]. 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 [18]. By building further on this experimental work, 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 [44].

Evolutionary changes in life history explained between 20% and 50% of all variation in population sizes among the three experimental metapopulation types. Although this quantification is conditional to the imposed variation in metapopulation typology, it nevertheless demonstrates the potentially strong impact of evolution on metapopulation viability. Metapopulations occupied by genotypes evolved in patchy metapopulations reached highest local and metapopulation sizes overall. Life history evolution in mainland-island and classical metapopulations consequently did not optimise population sizes. Because demographic variability was predominantly determined by spatial forcing, no indications of enhanced metapopulation performance, either increased population sizes, lower variability and spatial synchrony, due to evolutionary dynamics were found. 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 forcing and only relevant in classical metapopulations, a reduced rate was found for matching genotypes. Life-history evolution thus improves metapopulation performance to some degree only in classical 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. The predicted population and metapopulation sizes are in line with those

empirically derived (see Table 2) 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 [18]. 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 by up to 50%, as 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 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. 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 [43].

While the link between life-history evolution and metapopulation performance 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. Mutants 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, which were in line with insights from –omic approaches [18], were key to optimality. This also implies that our estimate of the contribution of evolutionary change to metapopulation dynamics 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 3).

We show that in our 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 [2,45]. 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. 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 histories 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

1. Fahrig L. Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst. 2003;34: 487–515. doi:DOI 10.1146/annurev.ecolsys.34.011802.132419

2. Wang S, Haegeman B, Loreau M. Dispersal and metapopulation stability. PeerJ. 2015;3: e1295. doi:10.7717/peerj.1295

3. Cheptou PO, Hargreaves AL, Bonte D, Jacquemyn H. Adaptation to fragmentation: Evolutionarydynamics driven by human influences. Philos Trans R Soc B Biol Sci. 2017;372. doi:10.1098/rstb.2016.0037

4. Olivieri I, Couvet D, Gouyon PH. The genetics of transient populations: Research at the metapopulation level. Trends Ecol Evol. 1990;5: 207–210. doi:10.1016/0169-5347(90)90132-W

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

6. Hanski I, Mononen T. Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. Ecol Lett. 2011;14: 1025–34. doi:10.1111/j.1461-0248.2011.01671.x

7. Hanski I. Eco-evolutionary dynamics in a changing world. Ann N Y Acad Sci. 2012;1249: 1–17. doi:10.1111/j.1749-6632.2011.06419.x

8. Kinnison MT, Hairston NG. Eco-evolutionary conservation biology: Contemporary evolution and the dynamics of persistence. Funct Ecol. 2007;21: 444–454. doi:10.1111/j.1365-2435.2007.01278.x

9. Delgado M del M, Ratikainen II, Kokko H. Inertia: the discrepancy between individual and common good in dispersal and prospecting behaviour. Biol Rev Camb Philos Soc. 2011;86: 717–32. doi:10.1111/j.1469-185X.2010.00167.x

10. Olivieri I, Tonnabel J, Ronce O, Mignot A. Why evolution matters for species conservation: perspectives from three case studies of plant metapopulations. Evol Appl. 2016;9: 196–211. doi:10.1111/eva.12336

11. Hanski I. Metapopulation dynamics. Nature. 1998;396: 41–49.

12. Molofsky J, Ferdy J-B. Extinction dynamics in experimental metapopulations. Proc Natl Acad Sci. 2005;102: 3726–3731. doi:10.1073/pnas.0404576102

13. Laiolo P, Obeso JR, Goodnight C, Stevens L, C JG, Schwartz J, et al. Multilevel Selection and Neighbourhood Effects from Individual to Metapopulation in a Wild Passerine. Waterman JM, editor. PLoS One. Public Library of Science; 2012;7: e38526. doi:10.1371/journal.pone.0038526

14. Aspi J, Jäkäläniemi A, Tuomi J, Siikamäki P. Multilevel phenotypic selection on morphological characters in a metapopulation of Silene tatarica. Evolution. 2003;57: 509–17. Available: http://www.ncbi.nlm.nih.gov/pubmed/12703940

15. Bonte D, Vandenbroecke N, Lens L, Maelfait J-P. Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. Proc Biol Sci. 2003;270: 1601–1607.

16. Bonte D, Bossuyt B, Lens L. Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. Behav Ecol. 2007;18: 438–443. doi:10.1093/beheco/arl103

17. Duplouy A, Ikonen S, Hanski I. Life history of the Glanville fritillary butterfly in fragmented versus continuous landscapes. Ecol Evol. 2013;3: 5141–5156. doi:10.1002/ece3.885

18. De Roissart A, Wybouw N, Renault D, Van Leeuwen T, Bonte D, Pfrender M. Life history evolution in response to changes in metapopulation structure in an arthropod herbivore. Pfrender M, editor. Funct Ecol. 2016;30: 1408–1417. doi:10.1111/1365-

2435.12612

19. Arnold SJ, Bürger R, Hohenlohe PA, Ajie BC, Jones AG. Understanding the evolution and stability of the G-matrix. Evolution. NIH Public Access; 2008;62: 2451–61. doi:10.1111/j.1558-5646.2008.00472.x

20. Walsh B, Blows MW. Abundant Genetic Variation + Strong Selection = Multivariate Genetic Constraints: A Geometric View of Adaptation. Annu Rev Ecol Evol Syst. 2009;40: 41–59. doi:10.1146/annurev.ecolsys.110308.120232

21. Barrett RDH, Schluter D. Adaptation from standing genetic variation. TRENDS Ecol Evol. 2008;23: 38–44. doi:10.1016/j.tree.2007.09.008

22. Ronce O. How Does It Feel to Be Like a Rolling Stone? Ten Questions About Dispersal Evolution. Annual Review of Ecology, Evolution, and Systematics. 2007. pp. 231–253. doi:10.1146/annurev.ecolsys.38.091206.095611

23. Metz JAJ, Gyllenberg M. How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionarily stable dispersal strategies. Proc R Soc B Biol Sci. 2001;268: 499–508. doi:10.1098/rspb.2000.1373

24. Zhang B, Kula A, Mack KML, Zhai L, Ryce AL, Ni W-M, et al. Carrying capacity in a heterogeneous environment with habitat connectivity. Ovaskainen O, editor. Ecol Lett. 2017;20: 1118–1128. doi:10.1111/ele.12807

25. Hanski I, Mononen T, Ovaskainen O. Eco-evolutionary metapopulation dynamics and the spatial scale of adaptation. Am Nat. 2011;177: 29–43. doi:10.1086/657625

26. Hanski I, Saccheri I. Molecular-level variation affects population growth in a butterfly metapopulation. PLoS Biol. 2006;4: 719–726. doi:10.1371/journal.pbio.0040129

27. Fountain T, Nieminen M, Sirén J, Wong SC, Hanski I. Predictable allele frequency changes due to habitat fragmentation in the Glanville fritillary butterfly. Proc Natl Acad Sci U S A. 2016;113: 1600951113-. doi:10.1073/pnas.1600951113

28. Becks L, Ellner SP, Jones LE, Hairston NG, Hairston Nelson G. JG. Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics. Ecol Lett. 2010;13: 989–997. doi:10.1111/j.1461-0248.2010.01490.x

29. Turcotte MM, Reznick DN, Daniel Hare J. Experimental test of an eco-evolutionary dynamic feedback loop between evolution and population density in the green peach aphid. Am Nat. 2013;181 Suppl: S46-57. doi:10.1086/668078

30. Turcotte MM, Reznick DN, Hare JD. The impact of rapid evolution on population dynamics in the wild: Experimental test of eco-evolutionary dynamics. Ecol Lett. 2011;14: 1084–1092. doi:10.1111/j.1461-0248.2011.01676.x

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

32. Smallegange IM, Coulson T. Towards a general, population-level understanding of eco-evolutionary change. Trends in Ecology and Evolution. 2013. pp. 143–148. doi:10.1016/j.tree.2012.07.021

33. Coulson T, MacNulty DR, Stahler DR, vonHoldt B, Wayne RK, Smith DW. Modeling Effects of Environmental Change on Wolf Population Dynamics, Trait Evolution, and Life History. Science (80-). 2011;334: 1275–1278. doi:10.1126/science.1209441

34. Vindenes Y, Langangen Ø. Individual heterogeneity in life histories and eco-evolutionary dynamics. Ecol Lett. 2015;18: 417–432. doi:10.1111/ele.12421

35. Evans MR, Bithell M, Cornell SJ, Dall SRX, Díaz S, Emmott S, et al. Predictive systems ecology. Proc Biol Sci. 2013;280: 20131452. doi:10.1098/rspb.2013.1452

36. Evans MR, Norris KJ, Benton TG. Predictive ecology: systems approaches. Philos Trans R Soc Lond B Biol Sci. 2012;367: 163–169. doi:10.1098/rstb.2011.0191

37. Benton TG. Individual variation and population dynamics: lessons from a simple system. Philos Trans R Soc Lond B Biol Sci. The Royal Society; 2012;367: 200–10. doi:10.1098/rstb.2011.0168

38. Travis JMJ, Delgado M, Bocedi G, Baguette M, Bartoń K, Bonte D, et al. Dispersal and species' responses to climate change. Oikos. 2013;122: 1532–1540. doi:10.1111/j.1600-0706.2013.00399.x

39. De Roissart A, Wang S, Bonte D. Spatial and spatiotemporal variation in metapopulation structure affects population dynamics in a passively dispersing arthropod. Coulson T, editor. J Anim Ecol. 2015;84: 1565–1574. doi:10.1111/1365-2656.12400

40. Oksanen J, Blanchet F, Kindt R, Legendre P, O'Hara R. Vegan: community ecology package. R Packag 23-3. 2016; Available at: https://cran.r-project.org/web/packa. doi:10.4135/9781412971874.n145

41. Ezard THG, Côté SD, Pelletier F. Eco-evolutionary dynamics: disentangling phenotypic, environmental and population fluctuations. Philos Trans R Soc Lond B Biol Sci. 2009;364: 1491–8. doi:10.1098/rstb.2009.0006

42. Bell G, Gonzalez A. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. Science. 2011;332: 1327–1330. doi:10.1126/science.1203105

43. Fronhofer EA, Altermatt F. Eco-evolutionary feedbacks during experimental range expansions. Nat Commun. 2015;6: 6844. doi:10.1038/ncomms7844

44. Ellner SP, Geber MA, Hairston NG. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. Ecology Letters. 2011. pp. 603–614. doi:10.1111/j.1461-0248.2011.01616.x

45. Walter JA, Sheppard LW, Anderson TL, Kastens JH, Bjørnstad ON, Liebhold AM, et al. The geography of spatial synchrony. Blasius B, editor. Ecol Lett. 2017; doi:10.1111/ele.12782

46. Van Petegem K, Boeye J, Stoks R, Bonte D. Spatial selection and local adaptation jointly shape life-history evolution during range expansion. Am Nat. Cold Spring Harbor Labs Journals; 2016;188: 485–498. doi:10.1101/031922

47. Wang S, Loreau M. Ecosystem stability in space: ??, ?? and ?? variability. Ecol Lett. 2014;17: 891–901. doi:10.1111/ele.12292

48. van der Vaart E, Beaumont MA, Johnston ASA, Sibly RM. Calibration and evaluation of individual-based models using Approximate Bayesian Computation. Ecol Modell. 2015;312: 182–190. doi:10.1016/j.ecolmodel.2015.05.020

49. van der Vaart E, Johnston ASA, Sibly RM. Predicting how many animals will be where: How to build, calibrate and evaluate individual-based models. Ecol Modell. 2016;326: 113–123. doi:10.1016/j.ecolmodel.2015.08.012

Supplementary material 1: model specifics

The model is individual-based, object oriented and coded in Python 3.5. Code, including parameterization for the three metapopulation types, is provided on Github https://github.com/dbonte/Eco-evo-metapopulations.git.

life cycle and population dynamics

The life cycle of the mites is coded as close as possible to realistic mites inhabiting the experimental metapopulations (see also [46]). Individuals mature according to experimentally derived growth rates, and each of the stages is characterised by experimentally quantified feeding rates, expressed as mm^2/leaf chlorophyll consumption per day. Individuals compete randomly for food and are assumed to forage on the entire leaf. These dynamics create a lottery competition for resources, and feedback on resource availability within the patch. When resources are below a predefined threshold level, individuals have a predefined probability to die. Mortality and feeding rates are age-dependent. The following life histories are specific to the evolutionary background and determined by a single allele: DAILY FECUNDITY, SEX RATIO, DISPERSAL PROPENSITY [intercept of the reaction norm with starvation], BASELINE JUVENILE and ADULT DAILY MORTALITY RATE, DEVELOPMENTAL SPEED for males and females and ADULT LONGEVITY. Reproduction is only possible for >2 days old adult females when sufficient resources [set to 20% of a single leaf] are available; sex of the offspring is assigned according to a sex ratio allele. We assigned the empirically derived mean trait values, allowed them to be conditional to resource state (survival) and implemented genetic variation by sampling the trait values from the appropriate Gaussian distribution. Individual variation is thus generated by both ontogenetic (innate) and developmental plasticity (age, nutritional condition) See Supplementary Material 2 for an overview of the mean traits.

Metapopulation dynamics

Only young 1-2 day-adult females disperse when sufficient resources are available (RESOURCE THRESHOLD; starved females do not invest in aerial dispersal and during two days a week, according to the implemented experimental setup (see [39]). Dispersal is conditional with probability following the empirical derived function DISPERSAL.ALLELE + 0.122 * log(RESOURCE AVAILABILITY). The reaction norm is independent of the evolutionary background. Dispersing individuals experience immigration costs as a 95% mortality cost. If successful, dispersing females immigrate in a randomly chosen patch (see [39]).

Resources are refreshed every 7 days according to the implemented metapopulation structure. Metapopulation dynamics thus depend on the trait initialisation and spatial setting. This allowed us to monitor metapopulation dynamics in a full factorial design metapopulation TYPE OF ORIGIN (evolutionary background) * METAPOPULATION TYPE (arena of population dynamics). Three matching and six mismatching scenarios are consequently modelled. For the invasion experiment, a small number (10 individuals/patch unit; 90 individuals/metapopulation) of matching genotypes are introduced after 600 time steps in a mismatched scenario to quantify invasion probability as a measure of fitness (invasion criterion approach).

Metrics

We measured local and metapopulation size at the end of each simulation. Temporal variability at both local population (alpha-variability) and metapopulation scales (gamma-variability) was calculated following [2,47]. Alpha-variability is calculated as the square of the weighted average of the coefficient of variation (CV) across local populations; gamma-variability, as the square of the CV of the metapopulations. Spatial

synchrony is quantified as a metapopulation-wide measure of population synchrony and equals the ratio of metapopulation gamma-variability to local alpha-variability. The patch extinction probability was measured for each run by dividing the number of extinction event by the total number of patches screened over all time steps.

Model parameterization and parameter sensitivity

Because life traits were either measured at the individual level under optimal conditions (single mites on fresh resources), from population-level dynamics (density dependency) or from single experiments neglecting both density dependency and variation among the experimental populations (feeding rates) we applied Approximate Bayesian Computation for individual based models (ABC4IBM; [48,49] to determine to which degree these empirically derived parameters deviated from those posteriori expected based on pattern oriented modelling using flat and broad priors centred around the observed ones.

A total of 100000 simulations were run with randomly selected trait values x_t sampled from a uniform prior distribution $[\bar{x}_t - 0.5\bar{x}_t, \bar{x}_t + 0.5\bar{x}_t]$ with $\bar{x}_t$ the mean observed trait value from that specific experimental setting (De Roissart et al. 2016). The resulting emerging metapopulation performance metrics (see Table 1) were calculated for each of these simulations. The deviance from observed values was calculated after z-transforming all statistics using the prior mean. Deviances of metapopulation pattern parameter D(p)were summed per simulations and provided the Goodness of Fit (GoF) for the simulation initialized with prior mean life traits

$$GoF = \sum_{p=1}^{p=n} (S_p - O_p)^2$$

From the 100000 calculates GoF /experimental scenario, the 100 with lowest deviance were chosen, verified whether they matches the observed metapopulation patterns for each of the specific metapopulation treatment in De Roissart et al. 2015), after which the posterior distributions of the matching trait distributions were calculated median and 95CI. All posteriori distributions included the experimentally determined prior distribution (see Supplementary Material 2), so we considered the model as robust for further use in the virtual experiments.

Supplementary material 2: model parameterisation

Parameters used in the model. Parameters were either derived from experimental evolution or from independent experiments (not taking into account the evolutionary context). The posterior distributions from ABC are provided for the individually measured traits and do largely overlap among scenarios.

Measured at the individual level	Classical		Mainland-island		patchy	
	Mean (sd)	posterior	Mean (sd)	posterior	Mean (sd)	posterior
Female age at maturity (from egg to adult) (days)	8.31	6.2-10.8	8.58	6.2-10.8	8.25	6.2-10.8
Male age at maturity (from egg to adult) (days)	7.98	6-10.5	8.21	6.1-10.5	7.98	6.1-10.8
Sex ratio (mm/tot)	0.28 (0.04)	0.21-0.36	0.34	0.16-0.5	0.26	0.16-0.41
Juvenile baseline mortality (/day)	0.124	0.06-0.17	0.156	0.08-0.21	0.124	0.07-0.18
Adult baseline survival (/days)	0.10	0.08-0.21	0.11	0.08-0.23	0.14	0.13-0.23
Dispersal propensity (intercept of the density dependent reaction norm)	0.7	0.35-1.0	0.58	0.31-0.82	0.7	0.35-1.0
Daily fecundity (eggs)	5.59	3.3-7.8	5.41	3.2-7.5	4.31	2.9-8.1
Measured in independent experiments at the population level						
Density dependency of dispersal (slope)	0.122 [0.07-0.17]					
Measured in independent experiments at the individual level						
Feeding rate larvae – nymph - adult (mm^2 consumed)	0.31 – 0.616 – 4.12					
Starvation tolerance larvae – nymph – adult (mortality rate under starvation)	1 – 0.99 – 0.37					

Supplementary material 3: Sensitivity of variance partitioning to unmeasured stress resistance

As for the variance partitioning of the model using the empirically quantified life history data, we additionally implemented the same procedure on models where mites from the mainland-island and the classical metapopulations received a starvation mortality of -50%, -25% and -10%. The results are summarised below:

Sensitivity Starvation mortality	-10%		-25%		-50%	
Metric	Spatial forcing	Evolved trait variation	Spatial forcing	Evolved trait variation	Spatial forcing	Evolved trait variation
All metapopulation statistics	0.405	0.120	0.409	0.147	0.401	0.134
Variability statistics	0.582	0.011	0.732	0.019	0.571	0.034
Population size statistics	0.229	0.229	0.251	0.276	0.231	0.235