Spatial and spatiotemporal variation in metapopulation structure affects population dynamics in a passively dispersing arthropod

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Summary

1. The spatial and temporal variation in the availability of suitable habitat within metapopulations determines colonization–extinction events, regulates local population sizes and eventually affects local population and metapopulation stability. Insights into the impact of such a spatiotemporal variation on the local population and metapopulation dynamics are principally derived from classical metapopulation theory and have not been experimentally validated.

2. By manipulating spatial structure in artificial metapopulations of the spider mite *Tetranychus urticae*, we test to which degree spatial (mainland–island metapopulations) and spatiotemporal variation (classical metapopulations) in habitat availability affects the dynamics of the metapopulations relative to systems where habitat is constantly available in time and space (patchy metapopulations).

3. Our experiment demonstrates that (i) spatial variation in habitat availability decreases variance in metapopulation size and decreases density-dependent dispersal at the metapopulation level, while (ii) spatiotemporal variation in habitat availability increases patch extinction rates, decreases local population and metapopulation sizes and decreases density dependence in population growth rates. We found dispersal to be negatively density dependent and overall low in the spatial variable mainland–island metapopulation.

4. This demographic variation subsequently impacts local and regional population dynamics and determines patterns of metapopulation stability. Both local and metapopulation-level variabilities are minimized in mainland–island metapopulations relative to classical and patchy ones.

Key-words: dispersal, metapopulation structure, population dynamics, stochasticity, synchrony, *Tetranychus urticae*, variability

Introduction

The development of the metapopulation concept by Levins (1969) resulted in an increasing awareness of the importance of spatial habitat configuration for colonization–extinction dynamics in fragmented landscapes. This subsequently triggered research on dispersal because of its central role in metapopulation dynamics (Hanski 2004) and simultaneously opened a new perspective in conservation biology through the consideration of landscape structure as a major driving force for the persistence of populations (e.g. Fahrig 2007). While the field has moved from a patch occupancy perspective to approaches that integrate population dynamics (Benton, Lapsley & Beckerman 2001; Benton, Cameron & Grant 2004; Strevens & Bonsall 2011), most of our insights herein are derived from theory (e.g. Fronhofer *et al.* 2012). Establishing a thorough understanding of the impact of spatial and spatiotemporal variation in habitat availability in an empirical study system is therefore a central challenge in ecology and conservation biology (Benton, Lapsley & Beckerman 2002).

Populations in spatially structured habitats are expected to be regulated not only by external factors such as spatiotemporal variation in habitat and/or resource availability

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(Benton, Lapsley & Beckerman 2001; Altwegg *et al.* 2014) but also by internal density-dependent feedbacks (Turchin 1999; Benton, Lapsley & Beckerman 2001). Density-dependent processes at the local level may impact population dynamics at the metapopulation level by rescuing local populations at the brink of extinction or impacting the synchrony of the population fluctuation (Cappuccino 1995). In a constant environment, the population regulation by density-dependent population growth can lead to a stable equilibrium in population size. However, because many populations are subject to continuous disturbance, this equilibrium is unlikely to be reached in natural populations (Friedenberg 2003; Cameron & Benton 2004).

Local densities are additionally regulated by emigration and immigration (Strevens & Bonsall 2011). Dispersal is typically positively density dependent when local exploitative and interference competition are strong (Bowler & Benton 2005). A negative density dependence in dispersal may, however, also evolve when densities are directly related to local habitat quality rather than to the level of competition, especially when dispersal costs are low (Rodrigues & Johnstone 2014). Because habitat fragmentation leads to substantial dispersal costs, dispersal will be especially a density-dependent process during emigration (Poethke & Hovestadt 2002; Dytham & Travis 2006). This local density dependence will be detectable at the metapopulation level when organisms are able to move freely within the metapopulations, so when dispersal is global. When the population dynamics are strongly impacted by external forces, for instance by synchronized depletion of resources, local density dependency will not necessarily lead to density dependence at the metapopulation level (Bowler & Benton 2005).

Density dependence of population growth and emigration principally affects local population dynamics. Dispersal also affects metapopulation stability through spatial coupling. The strength and direction of the stabilizing impact depend directly on the strength and direction of the density-dependent effects and the topology of the metapopulation (Tromeur, Rudol & Gross 2013). Not too low dispersal rates not only stabilize the size of local populations (Abbott 2011) but also meanwhile enhance spatial synchrony among local populations (Liebhold, Koenig & Bjornstad 2004), thereby potentially destabilizing metapopulations persistence (Hanski 1998). Alternatively, recolonization dynamics are an important prerequisite for the existence of metapopulation dynamics. Low dispersal rates will decrease the typical rescue events of local extinct patches (e.g. Heino *et al.* 1997; Hanski 1998; Holland & Hastings 2008) and thus decrease the viability of the metapopulation as a whole. Interestingly, dispersal is subject to fast evolutionary changes to changes in patch size asymmetry and patch extinction (Bowler & Benton 2005). Fast evolu-tionary dynamics could thus (re)enforce these metapopulation-level stabilizing mechanisms (Heino & Hanski 2001).

Not all spatially structured populations in nature are expected to be typical Levins' metapopulations, that is metapopulations consisting of equally sized patches, moderate levels of dispersal and some degree of stochastic extinctions (Baguette 2004; Fronhofer *et al.* 2012). Although we lack any empirical support, spatially structured populations in nature likely comply more to patchy or mainland–island metapopulations (Harrison & Taylor 1997). Mainland–island systems are characterized by high variation in patch size and occupancy as well as asymmetrical connectivity; patchy metapopulations are characterized by high levels of connectivity that prevent patch extinction (Fronhofer *et al.* 2012).

Substantial progress in understanding the relationship between the spatiotemporal metapopulation structure and population dynamics is hampered by the intrinsic difficulties to decouple patterns from processes in natural systems. We opted to follow an experimental approach using microcosms to study population dynamics in three types of metapopulation that approach real systems as close as possible (Benton *et al.* 2007). The objective of this research was to understand to which degree spatial and spatiotemporal variation in habitat availability affects the demographic dynamics in experimental metapopulations of a spider mite. We specifically tested the hypotheses (Figure 6) (i) that, relative to patchy metapopulations, spatial variation in habitat availability (as in mainland–island metapopulations) would increase local population size, thereby decreasing the extinction rate and temporal variability of local populations and be on average at higher densities, (ii) and that spatiotemporal variable metapopulations (classical metapopulations) would be characterized by higher patch extinction rates and subsequent variation in local population size, thereby decreasing the overall metapopulation size and average population density. Our experiments were designed to induce aerial dispersal among local patches within the artificial metapopulations. Given the overall scarce availability of habitat within the metapopulations, we expect immigration costs to be high. Metapopulation stability is therefore anticipated to be primarily driven by external factors, thereby destabilizing the spatiotemporal variable metapopulations relative to the others due to a high level of local variability and a low level of spatial synchrony. Asymmetry in patch size, and thus decreased immigration probabilities for the majority of the individuals inhabiting large patches (Poethke, Dytham & Hovestadt 2011), is additionally expected to select for lower levels of dispersal in mainland–island metapopulations, while no differences in the density-dependent population growth are *a priori* expected.

Materials and methods

EXPERIMENTAL SYSTEM OF ARTIFICIAL METAPOPULATIONS

Three types of artificial metapopulations were constructed with a varying spatial configuration of the patches but with an equal metapopulation carrying capacity. The 'LS-VL' spider mite strain was used as a base population because earlier research demonstrated its high genetic variability (Van Leeuwen *et al.* 2008; Bonte *et al.* 2010; Bitume *et al.* 2013). *Tetranychus urticae* reaches adulthood from the egg stage in on average 8 days. Freshly matured females constitute the dispersing phenotype in this species (Smitley & Kennedy 1985; Li & Margolis 1993; Bonte *et al.* 2014; Fronhofer *et al.* 2014; Van Petegem *et al.* 2015). Under standardized conditions where resources are not limiting, dispersal rates increase in relation to the density of young inseminated females (Bitume *et al.* 2013; De Roissart *et al.* 2013). Bean (*Phaseolus vulgaris* L.) leaves of standardized size were used to create patches and placed in closed boxes (71 × 44 × 31 cm). Patches were isolated from each other by a tanglefoot matrix preventing mites from dispersing by walking. Metapopulation resources were renewed weekly by adding fresh bean leafs according to the treatment. No leaves were removed before complete deterioration preventing the enforcement of extinction. A wind current (2 m s^{-1}) facilitated aerial dispersal of the mites two times a week. The wind currents were tested in a preliminary exp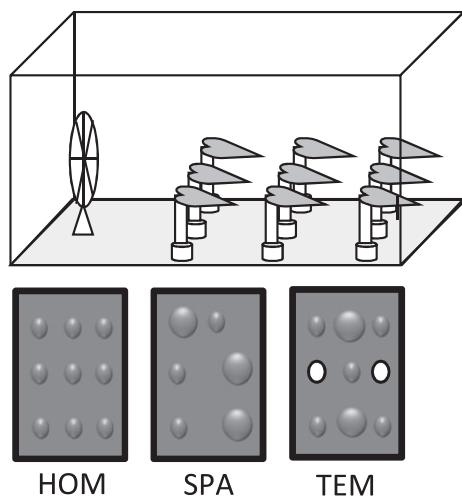eriment and ensured mite dispersal in all possible directions (see Appendix S1, Supporting Information). Artificial metapopulations with the following spatial configurations (each three times replicated) were installed (Fig. 1):

1. a homogeneous configuration: metapopulations consisting of nine equally sized bean leaf patches of 20 cm²; patches were weekly refreshed (further referred to as HOM), thereby mimicking patchy metapopulations.
2. a spatial heterogeneous configuration: metapopulations consisting of three patches of standard leaf size (20 cm²) and three double-sized patches, so corresponding to mainland–island metapopulations (further referred to as SPA). The position of the patches in the metapopulation was randomized among the three replicates but remained constant in time.
3. a spatiotemporal heterogeneous configuration: metapopulations consisting of nine patches with temporally changing leaf sizes (further referred to as TEM). Here, standard leaves of 20 cm² were every week randomly added to one of the nine patches. This resulted in a weekly changing availability of resources over the nine patches. This treatment corresponds to classical metapopulations.

All metapopulations were thus weekly foreseen with 180-cm² leaf resources, but these were differently allocated among patches. The HOM metapopulations always consisted of nine patches with resources, and the SPA metapopulation consisted of six patches, while for the TEM metapopulations, the total number of refreshed patches was variable, though always between six and nine patches. At the beginning of the experiment, 20 randomly collected female mites from the base population were assigned to each bean leaf patch and allowed to establish populations. All metapopulations were maintained under controlled conditions (23 °C, 16:8 LD photoperiod). The experiment lasted 182 days, but demographic data were only collected when metapopulations were fully established (after *c*. 5 generations, 40 days).

LOCAL DEMOGRAPHY

Average local population densities (individuals cm^{-2}) of all the different life stages (eggs, juveniles, adult males and females) and local population extinctions were weekly quantified by counting the number of mites of all life stages (eggs, juveniles and adults) on three randomly chosen areas of 1 cm^2 of each bean leaf (thus, from each patch). Density dependence of local populations was assessed as the slope of the relationship between population growth rate [$\ln(N_{t+1}/N_t)$] and log population size [$\ln(N_t)$]. Population densities and extinctions were analysed using generalized linear mixed models (GLMM-GLIMMIX procedure SAS 9.3) (SAS Institute Inc 2006) with 'treatment' (HOM, SPA, TEM) as independent factor and each individual metapopulation as a random effect to control for dependence among replicates from each metapopulation treatment. Depending on the dependent variable, a Poisson (population density/size) or binomial error (extinction) structure was modelled with appropriate link functions. We corrected for potential overdispersion by modelling residual variation as an additional random factor. Nonsignificant contributions ($P > 0.05$) were omitted by backwards procedure and validated by model selection. Effective degrees of freedom were estimated using Kenward–Rogers procedure (Kenward & Roger 1997).

Fig. 1. Schematic representation of the experimental set-up of the invasion experiment. Top: metapopulation box containing local spider mite populations on bean leaves, bottom: metapopulation types: HOM – homogeneous configuration consisting of nine equally sized bean leaf patches; SPA – spatial heterogeneous configuration consisting of three standard size leaf patches and three double-sized leaf patches; and TEM – spatiotemporal heterogeneous configuration consisting of nine patches with temporally changing levels of resources in local populations (open patches: not refreshed at this time step). Total metapopulation carrying capacity was kept constant and equal over all treatments.

DISPERSAL AND METAPOPULATION DYNAMICS

Dispersal

Dispersal at the metapopulation level was estimated weekly by counting the number of mites on 12 rectangles (2 × 3 cm) of tanglefoot randomly placed in the metapopulation boxes. Adult females were, as foreseen, the only life stage present on the tanglefoot squares. Dispersal propensity was measured as the number of female adult mites on the total area of rectangles (12 × 6 cm^2) relative to the current estimate of the number of females on a comparable surface of leaf in the metapopulation. It was statistically analysed by means of generalized linear mixed models (GLMM) for binomially distributed data with logit link and correction for potential overdispersion. Independent factors were 'average female mite density' or 'total population density' and the 'treatment'. In order to control for possible correlation due to the common date of testing, we included 'date' as a random effect. Effective degrees of freedom were estimated using Kenward–Rogers procedure (Kenward & Roger 1997). *Post hoc* Tukey tests were performed to correct pairwise differences among treatments. All analyses were performed with SAS 9.3 (Proc Glimmix; SAS Institute, 2006).

Cross-correlation analyses of time series of dispersal propensity and total metapopulation density were performed to determine the presence of serial dependence between the different time series. Our aim was to locate density dependence and the lag between density and dispersal. Additionally, we assessed whether lags and cross-correlation coefficients differed among treatments. Cross-correlation analyses of the time series of dispersal and metapopulation density were performed using the nlme package in R 3.1-97. The autocorrelation function (ACF) was used to demonstrate the presence of periodicity in the time series. Cross-correlation coefficients of the time series were obtained by the cross-correlation function in R (CCF) and analysed using linear mixed models (MIXED procedure in SAS 9.3). 'Metapopulation replicate' was included as a random effect.

Metapopulation size/density

To estimate metapopulation size, we summed estimated local population sizes (see higher) for each replicated metapopulation for each time step they were recorded. Since the total amount of resources (total habitat availability) was equal in all metapopulations, metapopulation size is directly related to metapopulation density. Metapopulation sizes/densities were analysed using generalized linear mixed models (GLMM-GLIMMIX procedure SAS 9.3) (SAS Institute Inc 2006) with 'treatment' (HOM, SPA, TEM) as independent factor and each individual metapopulation as a random effect to control for dependence among replicates from each metapopulation treatment. A Poisson error structure was modelled with appropriate link functions. We corrected for potential overdispersion by modelling residual variation as an additional random factor (Verbeke & Molenberghs 2000). Nonsignificant contributions ($P > 0.05$) were omitted by backwards procedure and validated by model selection. Effective degrees of freedom were again estimated using Kenward–Rogers procedure. Density dependence at the metapopulation level was estimated as the slope of the relation between population growth rate ($\ln(N_{t+1}/N_t)$) and log population size ($\ln(N_t)$). With the time series of metapopula-

tion juvenile and adult density, a cross-correlation analysis was performed to determine the presence of serial dependence between the different time series. Our aim was to assess whether the ups and downs of the different time series are correlated and to locate possible lags between time series. Cross-correlation analyses of the time series of adult density and juvenile density were performed using the nlme package in R 3.1-97. Cross-correlation coefficients of the time series were analysed using general linear models (MIXED procedure in SAS 9.3) with 'metapopulation replicate' included as a random effect. *Post hoc* Tukey tests were performed to correct for pairwise differences among treatments.

(META)POPULATION VARIABILITY AND SPATIAL SYNCHRONY

Temporal variability at both local population (α-variability) and metapopulation scales (γ-variability) was calculated following Wang & Loreau (2014). α-Variability is calculated as the square of the weighted average of the coefficient of variation (CV) across local populations; γ-variability, as the square of the CV of the metapopulations. Variability parameters were first separately analysed using general linear models (GLM procedure in SAS 9.3). *Post hoc* Tukey tests were performed to correct pairwise differences among treatments. Spatial synchrony is defined as a metapopulation-wide measure of population synchrony and equals the ratio of metapopulation γ-variability to local α-variability (see Wang & Loreau 2014 for details).

Results

LOCAL DEMOGRAPHY

Average local population size (adults, juveniles and eggs) differed among treatments ($F_{2,6.054} = 36.20$; $P = 0.0004$). Population sizes were on average larger in the spatially heterogeneous metapopulations (22.11 ± 2.32 SE individuals) than in the homogeneous (15.43 ± 1.62 SE individuals) ($t_{5.94} = -6.96$; $P = 0.0010$) and spatiotemporal heterogeneous (14.80 ± 1.55 SE individuals) ($t_{6.122} = 7.71$; $P = 0.0006$) metapopulations. Larger population size in spatially heterogeneous metapopulations was equally observed for the different life stages (adults, juveniles and eggs) separately (see Tables S1 and S2). Average local population densities differed among treatments ($F_{2,6.083} = 25.26$ $P = 0.0011$) and were lower in spatiotemporally variable metapopulations (10.50 ± 1.17 SE individuals) compared to homogeneous (15.20 ± 1.69 SE individuals) and spatially heterogeneous metapopulations (14.41 ± 1.60 SE individuals) (Fig. 2). The proportion of local populations going extinct was significantly affected by treatment ($F_{2,5.166} = 10.77$; $P = 0.0144$). The average proportion of extinctions was higher in spatiotemporal variable metapopulations (0.251 ± 0.091 SE) than in homogeneous (0.01 ± 0.006 SE) and spatial variable metapopulations (0.027 ± 0.015 SE). All treatments exhibited negative density dependence of local population growth (HOM: slope = -0.662; SPA: slope = -0.7611; TEM: slope = -0.5219), and density dependence was lowest in the TEM metapopulations ($F_{2,1630} = 37.61$; $P < 0.0001$) (Fig. 3a).
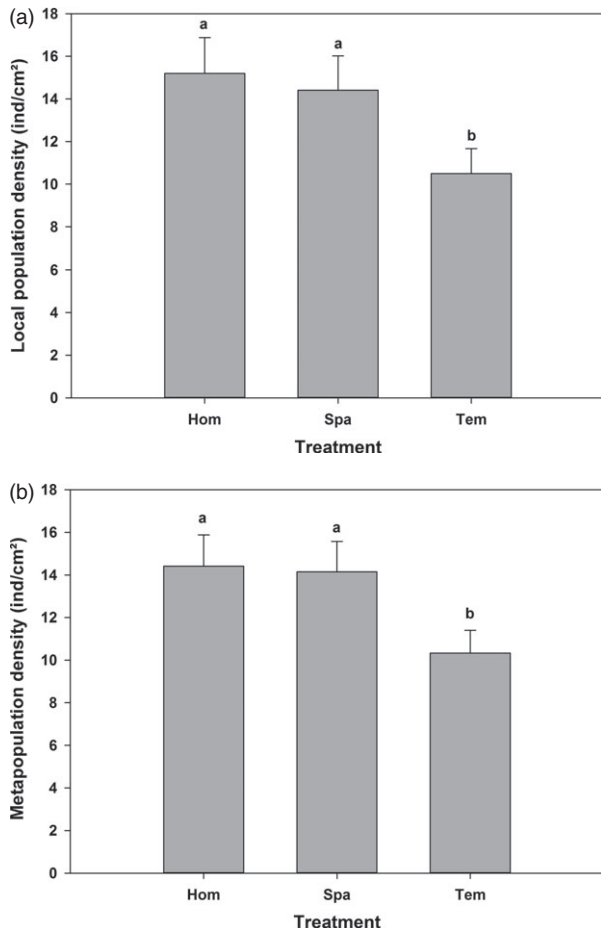
Fig. 2. Effects of metapopulation structure on density. (a) effect on local population density, (b) metapopulation density. Densities comprise average number of females, males, juveniles and eggs/cm². Equal notations indicate nonsignificant contrast for the respective measurements. Error bars represent one standard error.

Fig. 3. Effects of metapopulation structure on density dependence. (a) local population growth rate in relation to local population density (Ln N_t) and metapopulation structure, (b) metapopulation growth rate in relation to the metapopulation density (Ln N_t) and structure. Densities comprise average number of females, males, juveniles and eggs per cm². Full, dashed and dotted lines represents the modeled values.

DISPERSAL AND METAPOPULATION DYNAMICS

Dispersal

Dispersal propensity was negatively affected by the average total (adults, juveniles and eggs) and female density in the metapopulation over treatments (total: $F_{1,177} = 68·66$; $P < 0·0001$; female: $F_{1,177} = 165·13$; $P < 0·0001$). The strength of density dependence of dispersal differed between treatments, with a steeper decline in the spatiotemporal heterogeneous metapopulations ($F_{2,177} = 20·91$; $P < 0·0001$) (Fig. 4). Overall, average dispersal propensity differed among treatments ($F_{2,10·99} = 20·91$; $P = 0·0002$) and was lowest in spatial heterogeneous metapopulations ($0·063 \pm 0·01$SE SE) compared to the other two treatments (HOM: $0·29 \pm 0·004$SE; TEM: $0·20 \pm 0·003$SE). Obviously, because the slopes of TEM differ from those from SPA en HOM, only the differences among the latter are meaningful in the context of this study. Cross-correlation analysis of the time series of dispersal propensity and metapopulation density revealed no differences of cross-correlation coefficients among treatments ($F_{2,54} = 0·11$; $P = 0·8945$). Neither did we find differences
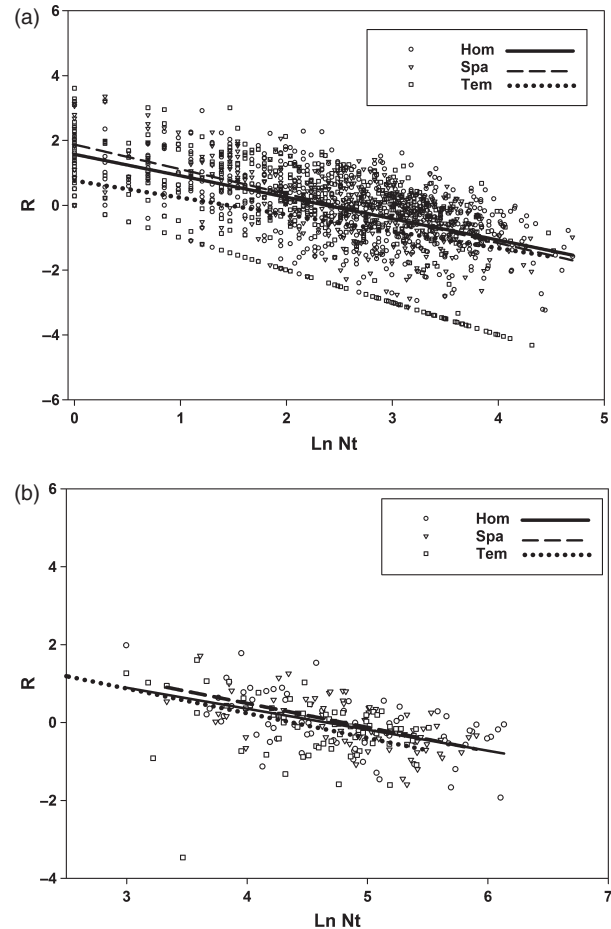
among lags (lag unit = 1 week) ($F_{9,54} = 1·28$; $P = 0·2679$) nor did the lags between both time series differ among all treatments ($F_{18,54} = 1·11$; $P = 0·3694$).

Metapopulation size/density

Metapopulation density differed among treatments ($F_{2,181} = 27·19$; $P < 0·0001$). Metapopulation density of spatiotemporal heterogeneous metapopulations ($10·33 \pm 1·07$ SE individuals) was on average lower than of homogenous ($14·42 \pm 1·46$ SE individuals) and spatially heterogeneous metapopulations ($14·15 \pm 1·44$ SE individuals) (Fig. 2b). The same results hold for metapopulation size. All treatments exhibited negative density dependence of metapopulation growth (HOM: slope = $-0·54$; SPA: slope = $-0·65$; TEM: slope = $-0·63$), but density dependence at this level of organization did not differ among all treatments ($F_{2,181} = 0·42$: $P = 0·6545$) (Fig. 3b). Cross-correlation coefficients of the time series of juvenile density and adult density did not differ statistically among treatments ($F_{2,54} = 0·66$;
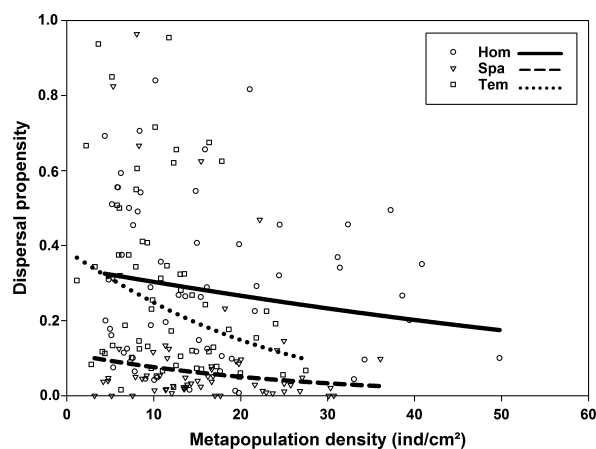
Fig. 4. Effects of metapopulation density and structure on dispersal. Dispersal propensity (number of dispersive mites/metapopulation density) in relation to the experienced metapopulation density and the metapopulation structure. Densities comprise average number of females, males, juveniles and eggs/cm^2. Full, dashed and dotted lines represents the modeled values.

$P = 0.5219$). Significant differences among lags (lag unit = 1 week) were detected ($F_{9,54} = 5.13$; $P < 0.0001$), and a significant interaction between lag and treatment was detected ($F_{18,54} = 2.76$; $P = 0.0021$). Cross-correlation coefficients were significantly different from 0 for lags 1, 7, 8, 9 and 10 (Table S3). Over all treatments cross-correlation coefficients differed significantly between lags 1 and 2, 3, 4, 5, 6, 8 and between lags 3 and 10 (Table S4).

(META)POPULATION VARIABILITY AND SPATIAL SYNCHRONY

Treatment affected local population variability (α-variability) ($F_2 = 46.14$; $P = 0.0002$). Local population variability was lowest in spatially variable metapopulations (0.56 ± 0.09 SE), followed by homogeneous (0.93 ± 0.08 SE) and spatiotemporal variable metapopulations (1.71 ± 0.08 SE) (Fig. 5a). Metapopulation variability (γ-variability) differed significantly among treatments ($F_{2,7} = 5.50$; $P = 0.044$) (Fig. 5b). Metapopulation variability was lower in spatially variable metapopulations (0.27 ± 0.07 SE) and spatiotemporally variable metapopulations (0.29 ± 0.06 SE) compared to homogeneous metapopulations (0.53 ± 0.06 SE). Pairwise contrasts are, however, marginally not-significant and only indicating trends (HOM–SPA $t_6 = 3.01$ $P = 0.054$; $t_6 = 2.71$ HOM–TEM $P = 0.078$). Over all treatments, metapopulation variability was found to be lower than local population variability ($t_6 = 33$ $P < 0.0001$). Spatial synchrony differed significantly among treatments ($F_{2,7} = 22.47$; $P = 0.0016$) (Fig. 5c). Synchrony was lowest in metapopulations with spatiotemporal variation (0.17 ± 0.04 SE) compared to homogeneous (0.57 ± 0.04 SE) ($t_6 = 6.43$ $P = 0.0016$) and spatially variable metapopulations (0.47 ± 0.04 SE) ($t_6 = 4.85$ $P = 0.0068$).
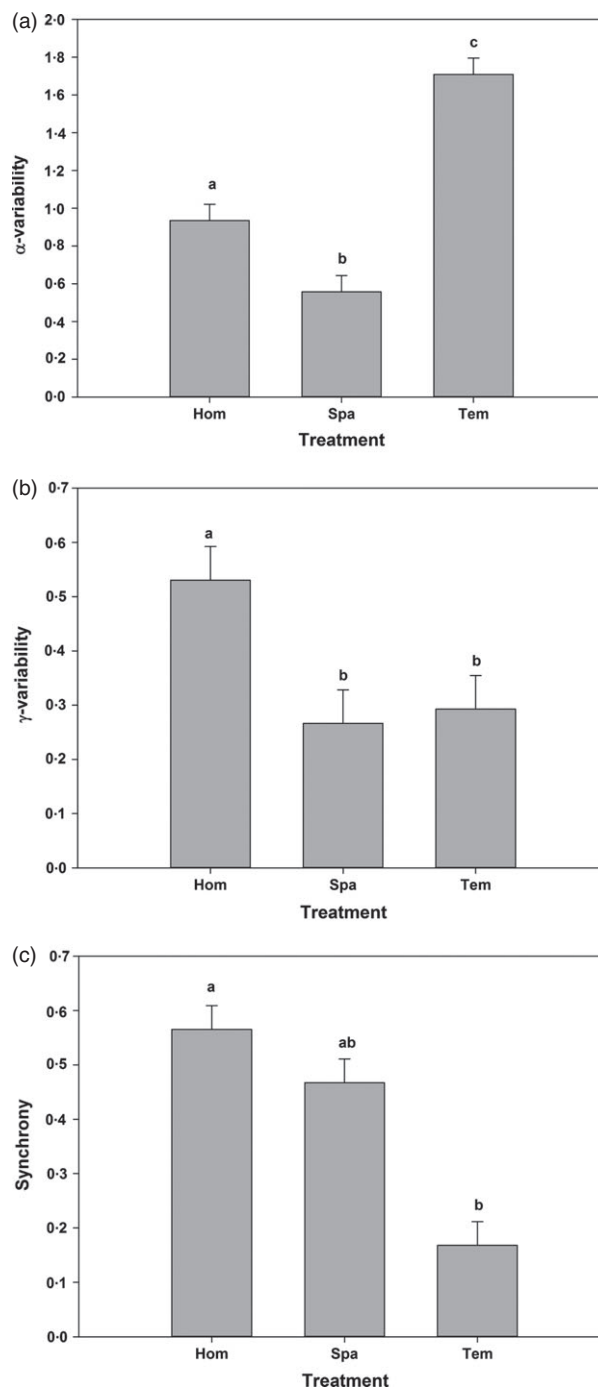

Fig. 5. Effects of metapopulation structure on the local, spatial and metapopulation-level variability. (a) local α-variability, (b) metapopulation γ-variability, (c) spatial synchrony. Different notations indicate significant contrast for the respective measurements (for figure b, the differences indicate a borderline nonsignificant pairwise difference; $P < 0.1$; see text) Error bars represent one standard error.

Discussion

Using artificial metapopulations of the spider mite *Tetranychus urticae*, we demonstrate that, compared to spatially homogeneous metapopulations consisting of equally sized
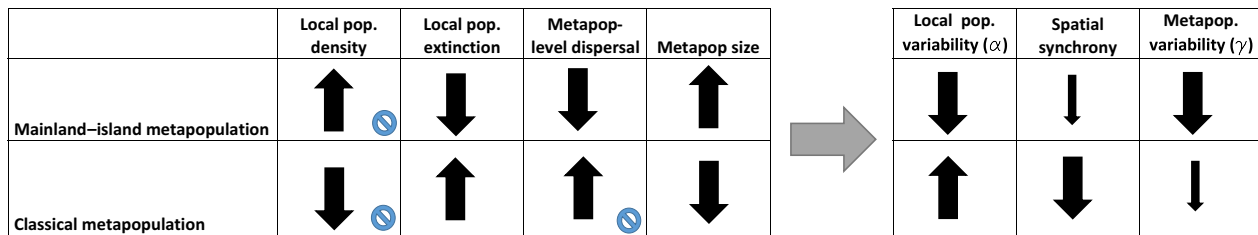
Fig. 6. Prediction on the expected changes in demography and population dynamics in the mainland–island (SPA) and classical (TEM) metapopulations relative to the patchy metapopulations (HOM). Arrows indicate the expected direction and sizes of the effect. Nonvalidated predictions are indicated by the Ø sign

patches, spatial variation in habitat availability decreases variability in metapopulation size and density-dependent dispersal at the metapopulation level. Spatiotemporal variation in habitat availability induced higher patch extinction rates, thereby lowering average local population and metapopulation sizes. Such spatiotemporal variation simultaneously increased variability in local population size, decreased the magnitude of density dependence in growth rates and decreased the synchrony of the local population dynamics. Overall, metapopulation variability was found to be lower than local population variability and increased population variability in spatiotemporal variable metapopulations reduced variability at the scale of the metapopulation (Figure 6).

A range of empirical as well as theoretical studies (Benton, Lapsley & Beckerman 2002; Drake & Lodge 2004) already demonstrated higher population extinction rates in temporally fluctuating relative to constant environments. These are predominantly caused by bottom-up effects of increased stochasticity in the form of fluctuating resource levels (Bull *et al.* 2007). External forcing of temporal variation in patch size by the manipulation of resources significantly increased variance in local population sizes and patch extinction rates. Evidently, such catastrophic events where extinct patches are colonized by few emigrants at lagged time intervals decreased the average population sizes.

Local population sizes of all stages were on average 50% higher in spatially heterogeneous metapopulations than those in other treatments. This increase resulted from the increased resource abundance in the double-sized patches (Fahrig 2007; Strevens & Bonsall 2011) and corresponds with previous studies on closed populations where the number of individuals is linked to the amount and distribution of available resources (Cameron & Benton 2004). Increases in local population sizes follow a linear response towards the availability of resources and are thus not associated with increased densities. Population growth under conditions where food resources are more abundant could be expected to lead to an extended period of time until density dependence kicks-in, thereby leading to higher local population densities and overshooting of the local carrying capacity. The absence of such a pattern indicates that population regulation occurs among all life stages and that competition among the life stages is less

asymmetrical than anticipated by higher per capita consumption rates in adult females. Alternatively, individuals may have evolved slower individual growth rates under repetitive stress as expected under high population densities and experience lower maximal per capita growth rate to improve environmental tolerance or the efficiency of resource use (Dey *et al.* 2008; Monro & Marshall 2014). Moreover, the very low extinction rates for HOM relative to SPA do not induce lower densities in HOM over generations because of lagged colonization dynamics.

We observed overall a negative density dependence in population growth over the duration of the experiment, but a significant lower population growth in the spatiotemporal variable metapopulations. This accords with work of Strevens & Bonsall (2011), who indicated that the dynamics of homogenous and spatially variable systems were best described by density-dependent population dynamical models, while spatiotemporal variable systems were best described by density-independent models. They attributed this result to elevated levels of dispersal reducing the competition for resources at the local scale (Strevens & Bonsall 2011). We did not observe overall higher levels of dispersal in the spatiotemporal variable metapopulations, especially not at high densities. We instead attribute the absence of density dependence to the lagged colonization of empty patches. Indeed, slopes of the density dependence became significantly different from zero when extinct populations were excluded (HOM: slope = −0·89; SPA: slope = −0·95; TEM: slope = −1·09; $F_{2,1264} = 3·17$ $P = 0·0425$). Because local population sizes in the spatiotemporally variable metapopulations were on average lower than those in the other metapopulation types, changes in density dependence did not increase population growth rates and neither compensated for the externally induced variation in habitat availability.

Contrary to expectations and earlier work focusing at the local population level (De Roissart *et al.* 2013), we witnessed negative dependence of dispersal propensity in the metapopulation for all treatments. Rodrigues & Johnstone (2014) demonstrated that a negative density dependence of dispersal can be selected for in temporally stable environments where local differences in resource quality persist over multiple generations. In their theoretical work, density is not scaled to *K,* and evolved dispersal strategies relate more to heterogeneity in habitat quality or carrying capac-

ity. Translated to our experimental set-up, Rodrigues & Johnstone (2014) document patch size-dependent emigration strategies, rather than local density-dependent strategies. In the absence of any adaptive explanation, we therefore attribute our observed negative relationship towards changes in body condition. In the mite metapopulations where dispersal was only made possible within limited time windows, large population densities lead to increased competition, resource depletion and subsequently an expected poorer body condition. Parallel work on more actively dispersing invertebrates and vertebrates has demonstrated that individuals in poor body condition can be constrained in dispersal due to lack of sufficient reserves to levy the costs and remain philopatric (Debeffe et al. 2014; O'Sullivan, Benton & Cameron 2014). Generally, such a correlation is linked to energetic reserves to move between patches (energetic costs; Bonte et al. 2012). As for the spider mites and other passively dispersing organisms, larger amounts of reserves may also facilitate habitat selection (Bonte, De Meester & Matthysen 2011) and thus affect dispersal by changing cost–benefit balances during the immigration phase (Delgado et al. 2014).

Our results revealed a lower level of spatial synchrony of the patches in spatiotemporally variable metapopulations relative to the other metapopulation types. Dispersal stochasticity and regional stochasticity are the two prominent factors that influence spatial synchrony. It is generally difficult to establish whether spatial synchrony is due to dispersal or regional stochasticity, but which one is case makes an important difference to metapopulation dynamics (Hanski & Woiwod 1993; Bjornstad, Ims & Lambin 1999). If synchrony is due to high dispersal, high recolonization rates will facilitate metapopulation persistence and may more than compensate for the negative effect of synchronous dynamics in generating correlated local extinctions. In contrary, if synchrony is due to regional stochasticity, metapopulation persistence time is necessarily decreased, in the same manner as the expected lifetime of a local population is decreased by increasing environmental stochasticity (Hanski & Woiwod 1993). Over all treatments, in our system, synchrony was observed to increase with dispersal (slope: 8·9; $P = 0.036$). However, for the different treatments separately, dispersal levels were lowest in homogeneous and spatial variable metapopulations and were coupled with higher synchrony relative to the spatiotemporal variable metapopulations, evidently caused by the spatially correlated resource renewals.

Metapopulation variability is significantly larger in homogeneous metapopulations than in spatially heterogeneous and spatiotemporal heterogeneous metapopulations. Metapopulation variability is determined by the product of local population variability and spatial synchrony among populations (Wang & Loreau 2014). Thus, the stabilizing effects can result from lower local variability, lower spatial synchrony or both. In spatially heterogeneous metapopulations, patches with double resource abundance (i.e. carrying capacity) have larger population size and lower variability compared to smaller patches as also found in Strevens & Bonsall (2011). This results in lower average local population variability. Resource supply in the HOM and SPA metapopulations is highly synchronous and causes high synchrony in population dynamics in both treatments. Therefore, SPA decreases metapopulation variability by reducing local population variability. In contrast, TEM decreases metapopulation variability through reducing spatial synchrony. The resource supply in TEM is highly variable both in time and in space. On the one hand, the large temporal variation results in high temporal variability of local population dynamics. On the other hand, the large spatial variation substantially reduces spatial synchrony. The latter effect is so strong that although TEM generates higher local alpha variability and local extinction rates, the metapopulation variability is significantly lower than HOM. In consequence, an island–mainland metapopulation structure minimizes both local and regional variabilities and thus extinction risk at these two scales. We suggest to take this important insight as a starting point to explain the potential dominance of such metapopulations relative to more classical ones in nature.

Acknowledgements

Data accessibility

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).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Testing random flow of dispersing mites.

Appendix S2. Density estimates and cross correlations among life stages.

Fig. S1. Representation of the distribution of drifted mites into the box.

Table S1. Estimates of local population densities of the different stages.

Table S2. Contrasts of local population densities of different life stages among the different metapopulation treatments.

Table S3. Cross-correlation coefficients between time series of juvenile and adult densities for the different lags.

Table S4. Estimates of significant differences of cross-correlation coefficient between lags of the time series of juvenile and adult density (over all treatments).