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# Environment, but not migration rate, influences extinction risk in experimental metapopulations

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Ecological theory suggests that several demographic factors influence metapopulation extinction risk, including synchrony in population size between subpopulations, metapopulation size and the magnitude of fluctuations in population size. Theoretically, each of these is influenced by the rate of migration between subpopulations. Here we report on an experiment where we manipulated migration rate within metapopulations of the freshwater zooplankton *Daphnia magna* to examine how migration influenced each of these demographic variables, and subsequent effects on metapopulation extinction. In addition, our experimental procedures introduced unplanned but controlled differences between metapopulations in light intensity, enabling us to examine the relative influences of environmental and demographic factors. We found that increasing migration rate increased subpopulation synchrony. We failed to detect effects of migration on population size and fluctuations in population size at the metapopulation or subpopulation level, however. In contrast, light intensity did not influence synchrony, but was positively correlated with population size and negatively correlated with population fluctuation. Finally, synchrony did not influence time to extinction, while population size and the magnitude of fluctuations did. We conclude that environmental factors had a greater influence on extinction risk than demographic factors, and that metapopulation size and fluctuation were more important to extinction risk than metapopulation synchrony.

**Keywords:** extinction; metapopulation dynamics; migration rate; population fluctuation; synchrony

## 1. INTRODUCTION

Natural populations typically exhibit spatial structure, separation into subpopulations connected by migration. Collectively, these non-independent subpopulations comprise a metapopulation (Levins 1970). The considerable amount of theory addressing metapopulations suggests that one of the key factors determining metapopulation dynamics is the rate of migration between subpopulations (Hanski 1999).

Migration is predicted to influence extinction risk in several ways. Moderate migration may provide a rescue effect, renewing extinct or declining subpopulations (Allen *et al.* 1993) and ultimately resulting in population turnover (MacArthur & Wilson 1963, 1967; Brown & Kodric-Brown 1977). However, too much migration is predicted to increase extinction risk by synchronizing subpopulations, thus increasing the chance that all subpopulations within a metapopulation will be reduced to small numbers simultaneously (Earn *et al.* 2000).

Migration may also influence metapopulation size, though theory predicts that migration can have conflicting influences. Migration ultimately removes individuals from the source population, reducing its population density. While some of these migrants join other populations or

successfully initiate new populations, others are lost to mortality during migration or in unsuccessful colonization attempts (Hanski & Zhang 1993). The result is a net decrease in metapopulation size because of migration. However, under the right conditions, migration can also have the opposite effect on metapopulation size. Ives *et al.* (2004) demonstrated that migration can increase metapopulation size if the net movement of individuals is into a subpopulation when its growth rate is positive and out of a subpopulation when its growth rate is negative.

Finally, when migration is low, and thus subpopulation dynamics are asynchronous, large and small subpopulations should compensate for each other, reducing the amount of variation in metapopulation size over time, but increasing the amount of variation in subpopulation size over time. In contrast, high migration rates are predicted to have the opposite effect of increasing the overall amount of fluctuation in metapopulation size while decreasing the fluctuation in subpopulation size (Dey & Joshi 2006).

Some hypothesized effects of migration on metapopulation dynamics have been demonstrated empirically (reviewed in Griffen & Drake 2008a). For example, migration increased subpopulation synchrony in plants and fruit flies (Molofsky & Ferdy 2005; Dey & Joshi 2006) and increased fluctuations in the size of fruitfly metapopulations (Dey & Joshi 2006). Another study (Ives *et al.* 2004) demonstrated an increase in metapopulation size from migration both theoretically and empirically using a fungus. In addition to these

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demographic effects, migration within metapopulations can ameliorate heterogeneous environmental stresses (i.e. source–sink dynamics, Pulliam 1988) and genetic bottlenecks (Waite *et al.* 2005). However, while migration has been empirically linked to metapopulation dynamics that may potentially influence metapopulation persistence, an explicit causative link is lacking in these studies between migration (or a lack of migration) and metapopulation extinction from demographic effects.

Migration is not the only factor that alters metapopulation dynamics, of course; similar changes can come from other driving variables, including environmental factors. For example, habitat quality (as determined by food amount) can strongly influence the size of populations (e.g. Griffen & Drake 2008*b*) and population fluctuations (e.g. Kieth 1983). In some circumstances, migration and spatial variation in environmental factors may interact to influence metapopulation dynamics, as with source–sink populations (Pulliam 1988). Conversely, an entire metapopulation may experience similar environmental conditions. In this case, when environmental conditions are identical between subpopulations (and when migration mortality is low), we may anticipate that migration may influence synchrony between subpopulations, but may have smaller, more subtle effects on average metapopulation size or temporal fluctuations in metapopulations size that may be overshadowed by environmental influences. The relative importance of migration and environmental factors for metapopulation persistence in these cases is an important question for habitat design and environmental management, given limiting resources and the inevitable trade-offs among management strategies.

Here we report results from a laboratory experiment that examined the importance of migration and environmental drivers of metapopulation dynamics and extinction. We established simple metapopulations, each consisting of two subpopulations of the freshwater cladoceran *Daphnia magna*. We manipulated the degree of migration between subpopulations by varying the number and size of holes in partitions that separated subpopulations. Unplanned but controlled differences in environmental factors between metapopulations were introduced into the experiment inadvertently as a result of our experimental procedures, but provided a serendipitous opportunity to contrast the influence of migration and environmental drivers. We show that increasing migration between subpopulations increased synchrony, but that this was not a factor in determining extinction risk. Conversely, metapopulation size and fluctuations were strongly correlated with extinction risk, but were driven largely by environmental factors rather than by migration.

## 2. MATERIAL AND METHODS

### (a) *Model system*

Our model system consisted of a single clone of the freshwater cladoceran *D. magna* reared on a food resource of pulverized blue–green algae (*Spirulina* spp.). *Daphnia* are a standard model for ecological studies (Lampert 2006) and we have previously used this consumer–resource system to study extinction dynamics (Griffen & Drake 2008*b*). This system is particularly useful because inactivated *Spirulina*

cannot grow and reproduce, allowing us to examine the effects of migration on metapopulation dynamics, independent of complex dynamics that can occur because of tight coupling between consumers and resources. Further, migration can benefit metapopulations both demographically and genetically (Shirley & Sibly 2001). The clonal nature of *Daphnia* allowed us to isolate demographic components of migration to determine how these effects influence metapopulation dynamics and subsequent extinction risk independent of genetic effects.

We conducted the experiments described below within small laboratory microcosms (31.5 × 21.7 × 2 cm) made of clear Plexiglas and filled with synthetic freshwater medium (USEPA 2002). Each microcosm was divided into two halves by a partition running down the middle. Holes connecting the two subchambers were located in the partition. We manipulated migration rates by varying the number and size of these holes, thus altering the total cross-sectional area (*A*) of holes connecting the two subchambers. Specifically, we used six combinations of hole number and hole size as follows (arranged in order from greatest cross-sectional area to least): two 3 mm holes (total area: 14.1 mm<sup>2</sup>), four 2 mm holes (total area: 12.6 mm<sup>2</sup>), one 3 mm hole (total area: 7.1 mm<sup>2</sup>), two 2 mm holes (total area: 6.3 mm<sup>2</sup>), one 2 mm hole (total area: 3.1 mm<sup>2</sup>) and no holes (control without migration). We varied both hole size and number because preliminary evidence indicated that hole size was more effective in controlling migration rate of adults, while hole number was more effective in controlling migration rate of juveniles. (We functionally define adults in this study as individuals ≥ 1 mm in length, based on size at reproduction of this clone when fed *Spirulina*, B. Griffen 2008, unpublished data.)

### (b) *Migration rate experiment*

We first conducted an experiment to quantify the migration rates within experimental chambers. A single adult and a single juvenile *D. magna* were placed into one side of each of our five migratory chamber types (we did not use the no-migration control chambers for this experiment). We checked the chambers every 24 h for 6 days, recording the location of each individual to determine whether migration had occurred. We replicated this 15 times for each of the five chamber types in three blocks of five replicates each. We pooled the data from each of the 15 replicates and determined the transition probability for each chamber type, or the probability that migration between subchambers occurred over a 24 h period. Because we sampled at 24 h intervals, migration could have occurred without our knowledge (e.g. an individual could have moved from side 1 of the chamber to side 2, and back to side 1 between sampling intervals). To account for this, we determine transition probabilities using a hidden Markov model (R package *hmm.discnp* v. 0.07).

A hidden Markov model is a statistical model, commonly used in temporal pattern recognition, in which the model system is assumed to be a Markov process, transitioning between a finite set of states (Durbin *et al.* 1999; Cappé *et al.* 2005). Transitions among states are governed by a set of transition probabilities. All states in standard Markov models are directly observable, allowing simple derivation of transition probabilities. In a hidden Markov model, some states are not directly observable. The model uses the set of observable states, together with the set of potential

hidden states and a probability distribution to derive transition probabilities using maximum likelihood. Migration probabilities were determined for both adults and juveniles and we then analysed these probabilities together using analysis of covariance (ANCOVA) with age as a factor (adult or juvenile, as defined above) and hole area connecting subchambers as a continuous predictor variable.

Migration rates can be density-dependent (e.g. Rosenberg *et al.* 1997). Results of this experiment therefore may not reflect absolute migration rates that occurred in our metapopulation experiment, but rather, provide an indication of the *relative* migration rates that occurred in our experimental chambers with different numbers and sizes of holes for migration.

### (c) *Metapopulation experiment*

We conducted a second experiment to determine how varying migration rate influenced metapopulation dynamics. Each of the six migration treatments was replicated 10 times, yielding a total of 60 metapopulations. Both subpopulations of each metapopulation were inoculated with five individuals of a single *D. magna* clone (one non-gravid adult and four juveniles) on 1 August 2007 or 2 August 2007 (five replicates of each treatment were randomly selected to start each day). Each metapopulation was censused every week by counting the number of adults and the number of juveniles within each subpopulation using a hand tally counter. Under these experimental conditions, the generation time was approximately two weeks (B. Griffen 2008, unpublished data). This sampling interval therefore provided approximately two samples per generation. Each count was repeated six times to estimate sampling error (see electronic supplementary material, appendix A). The experiment ended when all populations had become extinct (168 days). Resting eggs were produced periodically and were removed at monthly intervals when we exchanged 50 per cent of the medium to prohibit build-up of metabolites that might be toxic to *D. magna*. Resting eggs in natural populations can hatch after long periods of dormancy, providing a buffer against extinction. However, for the purpose of this study, we considered populations to be extinct when no adult or juvenile individuals remained alive.

Microcosms were located on a laboratory bench top, in a room with 24 h fluorescent light and the temperature held constant at  $22.8 \pm 0.6^\circ\text{C}$ . Microcosms were placed on their sides and were stacked on top of each other, randomly ordered into stacks of ten. This arrangement was used to simplify experimental maintenance, but at the same time it inadvertently introduced environmental variation between the different metapopulations, as shading from tanks higher in stacks reduced light available to the metapopulations situated below. This in turn influenced the potential for population growth as described below.

We fed *D. magna* a solution of processed, dried *Spirulina* spp. (JEHM Co., Inc.), prepared by mixing 0.05 g *Spirulina* (a blue-green alga, 10.16% N, 44.96% C) into 25 ml of deionized water. We fed each subpopulation 400  $\mu\text{l}$  of food solution per day. Some metapopulations (24 of the 60) developed algal growths on the sides of their chambers as a result of aerial contamination. This alga provided additional food and resulted in increased population sizes. Because of the shading within stacks described above, chambers with algal growth were not randomly distributed, but were correlated with height within a stack. For analyses, we removed these

metapopulations from the experiment at the point when algal growth was first detectable during metapopulation censoring. Accordingly, we analysed our experimental results using Cox proportional hazards models (R package *survival* v. 2.32) that account for censored observations. We first tested for effects of experimentally manipulated migration rates on time to extinction. We then mechanistically explored the effects of migration by examining its effects on metapopulation synchrony, metapopulation size, and both metapopulation and subpopulation fluctuations. Finally, we explored how each of these measures correlated with time to extinction. For each of these analyses, we also included chamber height as a continuous variable to test for effects of environmental factors. Each of these analyses is described in detail below.

Two other artefacts of the experimental procedure had the potential to influence our results: the start of our experiment was blocked over 2 days, and replicate chambers were randomly assigned to stacks. Starting day and stack number were each initially included in the analyses. However, neither explained a significant amount of the variation (all  $p > 0.2$ ), and these factors were therefore not included in any of the final analyses.

#### (i) *Effects of chamber height*

We noted throughout the experiment that algal growth was more common in chambers higher up in stacks. We hypothesized that this was owing to increased availability of light. We therefore explored the effects of chamber height by examining two factors. First, we examined how chamber height influenced metapopulation censoring (the removal of a metapopulation from the experiment when algal growth was detected) using logistic regression (we used a generalized additive model, hereafter GAM, with a binomial family and logit link function). Second, we measured light intensity at each of the 10 heights within a single stack. We then tested the hypothesis that light attenuated with decreasing height in a stack because of shading using linear regression of measured light intensity on height within the stack.

#### (ii) *Extinction and rescue events*

We examined how migration influenced rescue events. Migration between subpopulations has the potential to rescue subpopulations that have gone extinct. We counted the number of these rescue events for each of the six treatments (i.e. the number of times that one of the two subpopulation went extinct and was subsequently re-populated) and determined how migration rate influenced the number of rescue events using linear regression with the regression line forced through the origin (because no rescue events can occur when migration is not possible). The number of observed rescue events is a conservative estimate, as extinctions and rescue events could have occurred between sampling intervals without detection.

In addition to survival analysis, we also tested for an effect of our experimental treatment (migration rate as influenced by hole area) and chamber height on time to metapopulation extinction using Cox proportional hazards. With this and all other survival analyses described below, we ensured that the proportional hazards assumption was met by verifying that the slope of the residuals for each predictor variable plotted against time was not different from zero using a  $\chi^2$ -test (Grambsch & Therneau 1994).

(iii) *Subpopulation synchrony*

We estimated the amount of synchrony between subpopulations by calculating the single score two-way intraclass correlation coefficient (R package *irr* v. 0.7) for each metapopulation (McGraw & Wong 1996; Fontaine & Gonzalez 2005). This method is recommended when comparing two sets of data with the same metric and variance, but that cannot be designated as dependent and independent variables (Zar 1984). The intraclass correlation (ICC) is calculated using mean squares from an analysis of variance as:

$$ICC = \frac{MS_S - MS_E}{MS_S + (k - 1)MS_E}, \quad (2.1)$$

where  $MS_S$  is the subpopulation mean square,  $MS_E$  the mean square error and  $k$  the number of subpopulations (McGraw & Wong 1996). This coefficient ranges between  $-1$  and  $1$ , approaching  $1$  as subpopulations become increasingly synchronous. We then used linear regression to examine how subpopulation synchrony (response variable) changed with the amount of migration (hole area as predictor variable) and with height within a stack of metapopulation chambers. Finally, we used Cox proportional hazards regression to examine whether time to metapopulation extinction was influenced by metapopulation synchrony or chamber height.

(iv) *Metapopulation size*

We examined the hypothesis that migration increases metapopulation size as follows. We calculated the average metapopulation size by summing subpopulations at each sample time and averaging across the entire time series for each metapopulation. We then used linear regression to determine whether average metapopulation size changed with migration rate (hole area) or chamber height. Finally, we used Cox proportional hazards to determine how average metapopulation size and chamber height influenced time to metapopulation extinction.

(v) *Metapopulation and subpopulation fluctuations*

We quantified metapopulation and subpopulation fluctuations using an index introduced by Dey & Joshi (2006):

$$\text{Flux} = \frac{1}{\bar{N}} \sum_{t=0}^{T-1} \text{abs}(N_{t+1} - N_t), \quad (2.2)$$

where  $\bar{N}$  is the mean population size over  $T$  sample times. We then used separate linear regression analyses to determine how  $\text{Flux}_{\text{metapopulation}}$  and  $\text{Flux}_{\text{subpopulation}}$  changed with migration rate (hole area) and chamber height. Finally, we examined how fluctuation influenced extinction using separate Cox proportional hazards with time to metapopulation extinction as response variable and  $\text{Flux}_{\text{metapopulation}}$  and chamber height or with  $\text{Flux}_{\text{subpopulation}}$  and chamber height as predictors.

**3. RESULTS****(a) Migration rates in different chambers**

Relative migration rates (transition probabilities) from one side of our experimental chamber to the other increased proportionally with the total area of holes in partitions between subchambers (ANCOVA covariate, parameter estimate =  $0.012 \pm 0.003 \text{ mm}^{-2}\text{d}^{-1}$ ,  $F_{1,8} = 64.57$ ,  $p < 0.001$ , figure 1). However, the transition probabilities were generally higher for juveniles than for adults

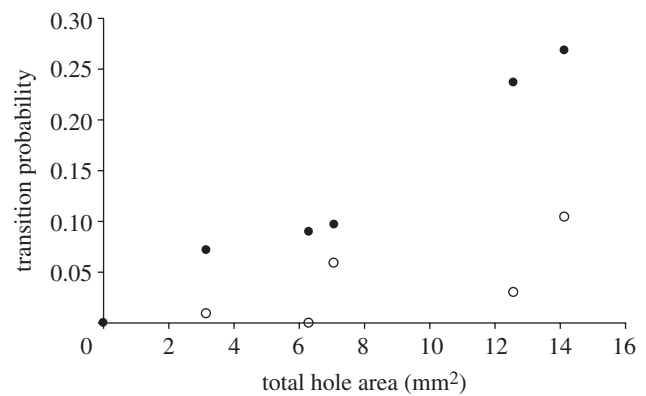


Figure 1. Daily transition probabilities of juvenile and adult *D. magna* from one subchamber to the other as a function of the total surface area of holes in partitions that separated subchambers. Results are from migration rate experiment. Filled circles, juveniles; open circles, adults.

(ANCOVA main effect,  $F_{1,8} = 38.22$ ,  $p < 0.001$ , figure 1), and increased faster with hole size for juveniles than for adults (ANCOVA interaction term,  $F_{1,8} = 18.14$ ,  $p = 0.002$ ). For juveniles, the transition probabilities ranged from *ca* 0.07 to *ca* 0.27 per day, depending on the area of holes, while for adults the range of daily transition probabilities was from  $<0.01$  to 0.11 (figure 1).

**(b) Migration impacts on metapopulation dynamics****(i) Effects of chamber height**

Algal growth, and thus population censoring, increased in our experiment with chamber height (GAM, deviation explained = 14.6%,  $z = 3.07$ ,  $p = 0.002$ ). This was probably influenced by light intensity, which was directly related to height in the stack due to shading. The relationship between light intensity and height within a stack was approximately linear ( $F_{1,8} = 67.23$ ,  $p < 0.001$ ,  $R^2 = 0.88$ ), so that light intensity at the top of chamber stacks (lux = 287) was more than double than at the bottom (lux = 130).

**(ii) Extinction and rescue events**

Population turnover, the extinction of subpopulations that were subsequently repopulated via migration, significantly increased with total hole area ( $F_{1,5} = 70.72$ ,  $p < 0.001$ , figure 2a). However, we failed to detect an effect of migration on metapopulation extinction time, after controlling for effects of chamber height within a stack (overall likelihood ratio = 6.57 on 2 d.f.,  $p = 0.04$ ; effect of hole area: coefficient =  $-0.04 \pm 0.04$  (s.e.),  $z = -0.99$ ,  $p = 0.32$ , figure 2b; effect of chamber height: coefficient =  $0.20 \pm 0.09$ ,  $z = 2.91$ ,  $p = 0.03$ , figure 2c).

**(iii) Subpopulation synchrony**

Synchrony between subpopulations within a metapopulation increased with the amount of migration ( $F_{1,57} = 7.89$ ,  $p = 0.007$ , figure 3a), but was not influenced by chamber height ( $F_{1,57} = 0.83$ ,  $p = 0.37$ , figure 3b). However, while migration increased subpopulation synchrony, synchrony did not influence time to metapopulation extinction (overall likelihood ratio = 5.57 on 2 d.f.,  $p = 0.06$ ; effect of synchrony: coefficient =  $-0.09 \pm 0.83$ ,

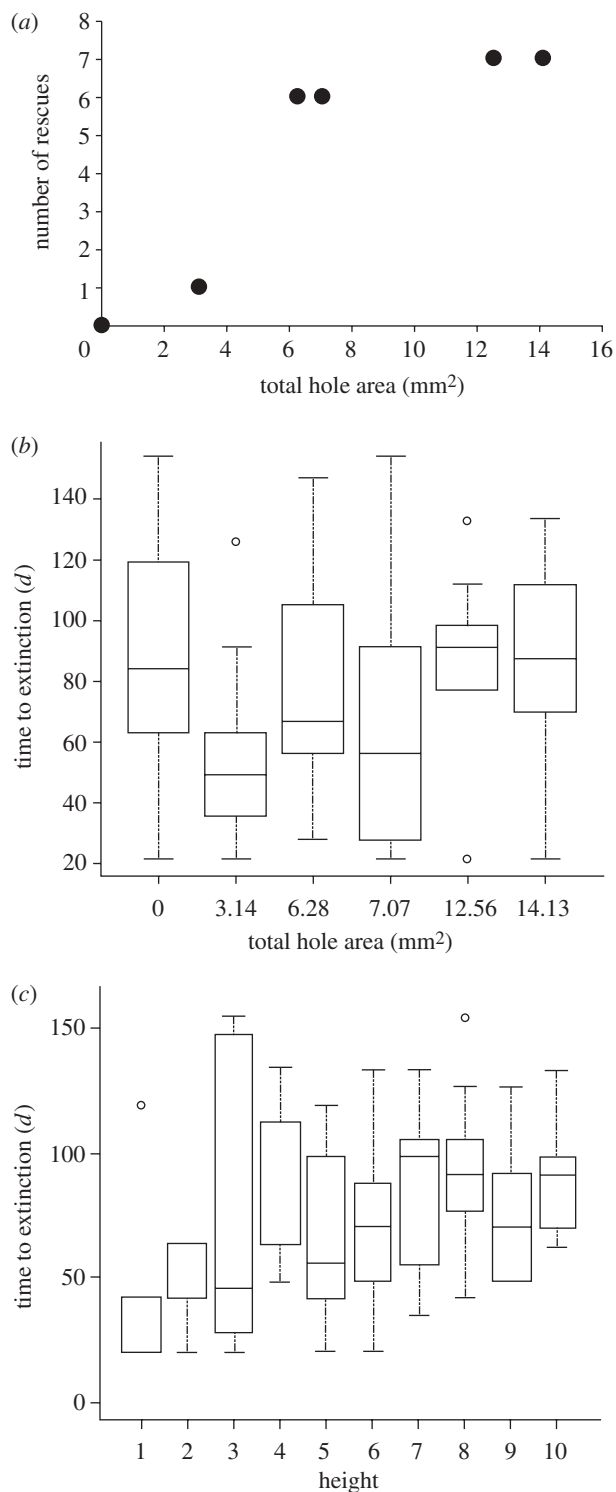


Figure 2. (a) Total number of rescue events observed in treatments with different hole areas available for migration between subchambers. (b) Time to extinction as a function of total area of migratory holes. (c) Time to extinction as a function of chamber height within a stack on the laboratory bench.

$z = -0.11$ ,  $p = 0.91$ , figure 3c; effect of chamber height: coefficient =  $0.2 \pm 0.09$ ,  $z = 2.22$ ,  $p = 0.03$ ).

(iv) Population size

The average size of metapopulations ranged from 5 to 40 individuals and size was not influenced by the amount of migration between subpopulations ( $F_{1,57} = 0.34$ ,  $p =$

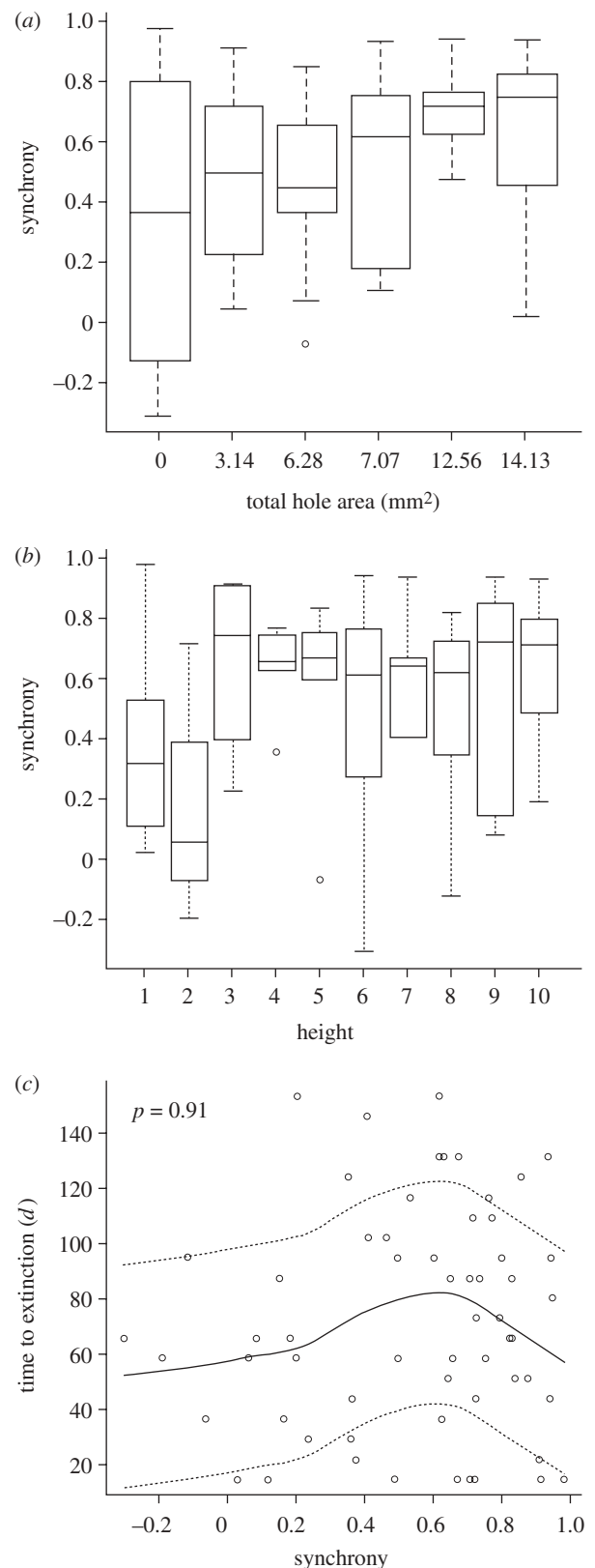


Figure 3. Effect of (a) hole area and (b) chamber height on subpopulation synchrony, and (c) the subsequent effect of subpopulation synchrony on time to metapopulation extinction. Line in (c) is the Lowess smoothed fit ( $\pm 1$  s.e.) based on 75 per cent of the data.

0.56, figure 4a), but increased with chamber height ( $F_{1,57} = 9.09$ ,  $p = 0.004$ , figure 4b). Further, time to metapopulation extinction increased with average metapopulation size and chamber height (overall likelihood

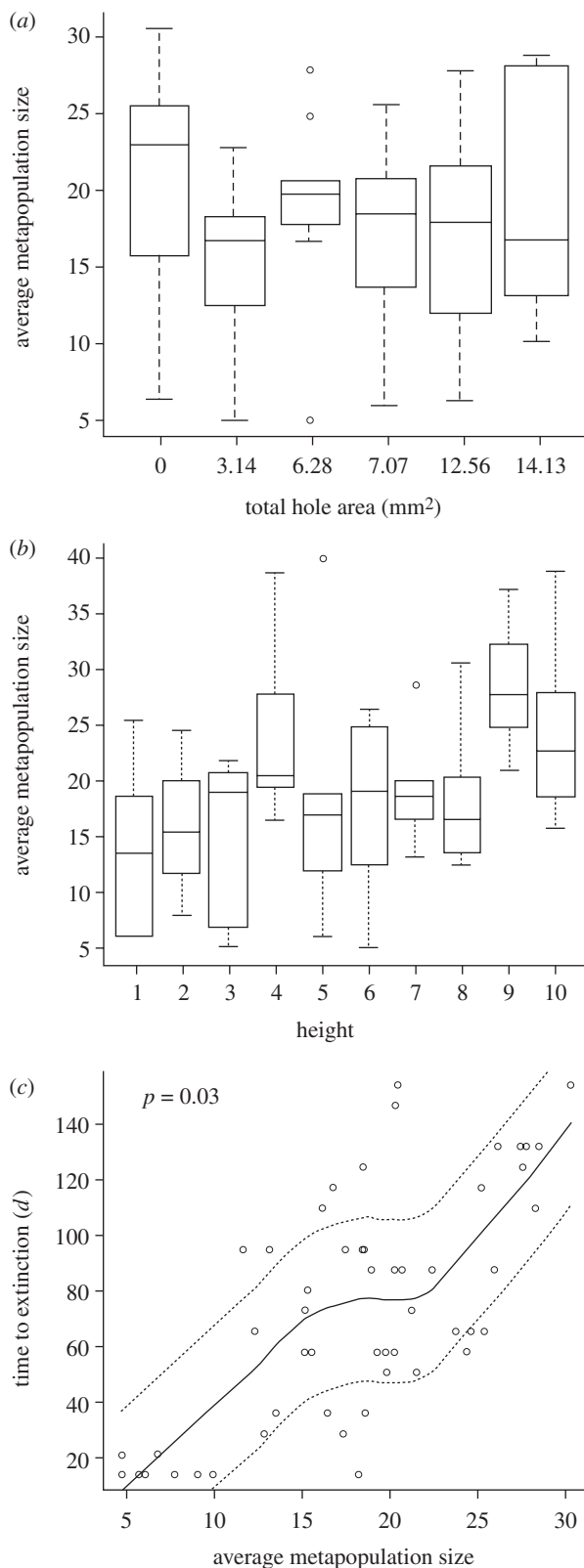


Figure 4. Effect of (a) hole area and (b) chamber height on average metapopulation size, and (c) the subsequent effect of metapopulation size on time to metapopulation extinction. Line in (c) is the Lowess smoothed fit ( $\pm 1$  s.e.) based on 75 per cent of the data.

ratio = 9.78 on 2 d.f.,  $p = 0.008$ ; effect of average metapopulation size: coefficient =  $0.11 \pm 0.05$ ,  $z = 2.18$ ,  $p = 0.03$ , figure 4c; effect of chamber height: coefficient =  $0.30 \pm 0.11$ ,  $z = 2.70$ ,  $p = 0.007$ ).

(v) *Metapopulation and subpopulation fluctuations over time* Metapopulation size fluctuations varied considerably ( $\text{Flux}_{\text{metapopulation}} = 0.25\text{--}1.74$ ). The degree of fluctuations was not influenced by migration ( $F_{1,57} = 1.35$ ,  $p = 0.25$ , figure 5a), but decreased strongly with chamber height ( $F_{1,57} = 20.26$ ,  $p < 0.0001$ , figure 5c). Increasing metapopulation fluctuation greatly decreased the time to extinction, even after accounting for the significant effects of chamber height (overall likelihood ratio = 14.1 on 2 d.f.,  $p = 0.0009$ ; effect of  $\text{Flux}_{\text{metapopulation}}$ : coefficient =  $-3.35 \pm 1.12$ ,  $z = -3.00$ ,  $p = 0.003$ , figure 5e; effect of chamber height: coefficient =  $0.27 \pm 0.10$ ,  $z = 2.82$ ,  $p = 0.005$ ).

Identical trends were observed with fluctuation in the size of subpopulations ( $\text{Flux}_{\text{subpopulation}} = 0.36\text{--}1.50$ ). Indeed, there was a strong correlation between  $\text{Flux}_{\text{metapopulation}}$  and  $\text{Flux}_{\text{subpopulation}}$  (Pearson's correlation = 0.91, 95% CI = 0.86–0.94). As with metapopulations, subpopulation fluctuation was not influenced by migration ( $F_{1,57} = 0.43$ ,  $p = 0.51$ , figure 5b), but decreased with chamber height ( $F_{1,57} = 10.79$ ,  $p = 0.002$ , figure 3d). Increasing subpopulation fluctuation also decreased the time to extinction, along with the effects of chamber height (overall likelihood ratio = 15.0 on 2 d.f.,  $p = 0.0006$ ; effect of  $\text{Flux}_{\text{subpopulation}}$ : coefficient =  $-3.71 \pm 1.21$ ,  $z = -3.07$ ,  $p = 0.002$ , figure 5f; effect of chamber height: coefficient =  $0.29 \pm 0.10$ ,  $z = 2.96$ ,  $p = 0.003$ ).

#### 4. DISCUSSION

We found that increasing migration rate increased the synchrony between subpopulations, but did not influence population size or fluctuations at the metapopulation or subpopulation level. However, synchrony did not influence time to extinction, while population size and the magnitude of fluctuation did. Thus, for the most part, migration in our experiment did not play a large role in metapopulation extinction. The exception was that increasing migration rate increased the number of rescue events that were observed.

The increase in synchrony with migration in our experiment is consistent with previous laboratory (Molofsky & Ferdy 2005) and field (Roland & Matter 2007) studies. However, our study does not directly support the theory that metapopulation extinction risk increases with synchrony, even though the mechanism underlying this theoretical relationship (the potential for rescue of extinct subpopulations when metapopulation dynamics are asynchronous) was upheld in our experiment (figure 3). The failure to detect a relationship between synchrony and time to extinction therefore suggests that the driving variable behind extinction was environmental (i.e. light intensity or another factor associated with chamber height) rather than demographic (i.e. migration). The lack of importance of migration for metapopulation extinction is contrary to a previous study with *Drosophila* spp. (Forney & Gilpin 1989); however, their study examined migration in the absence of environmental differences. Our results do not necessarily suggest that migration is unimportant for population persistence, but rather, that in this system the influence of migration was subtle and was overshadowed by the influence of environmental quality. This suggestion deserves

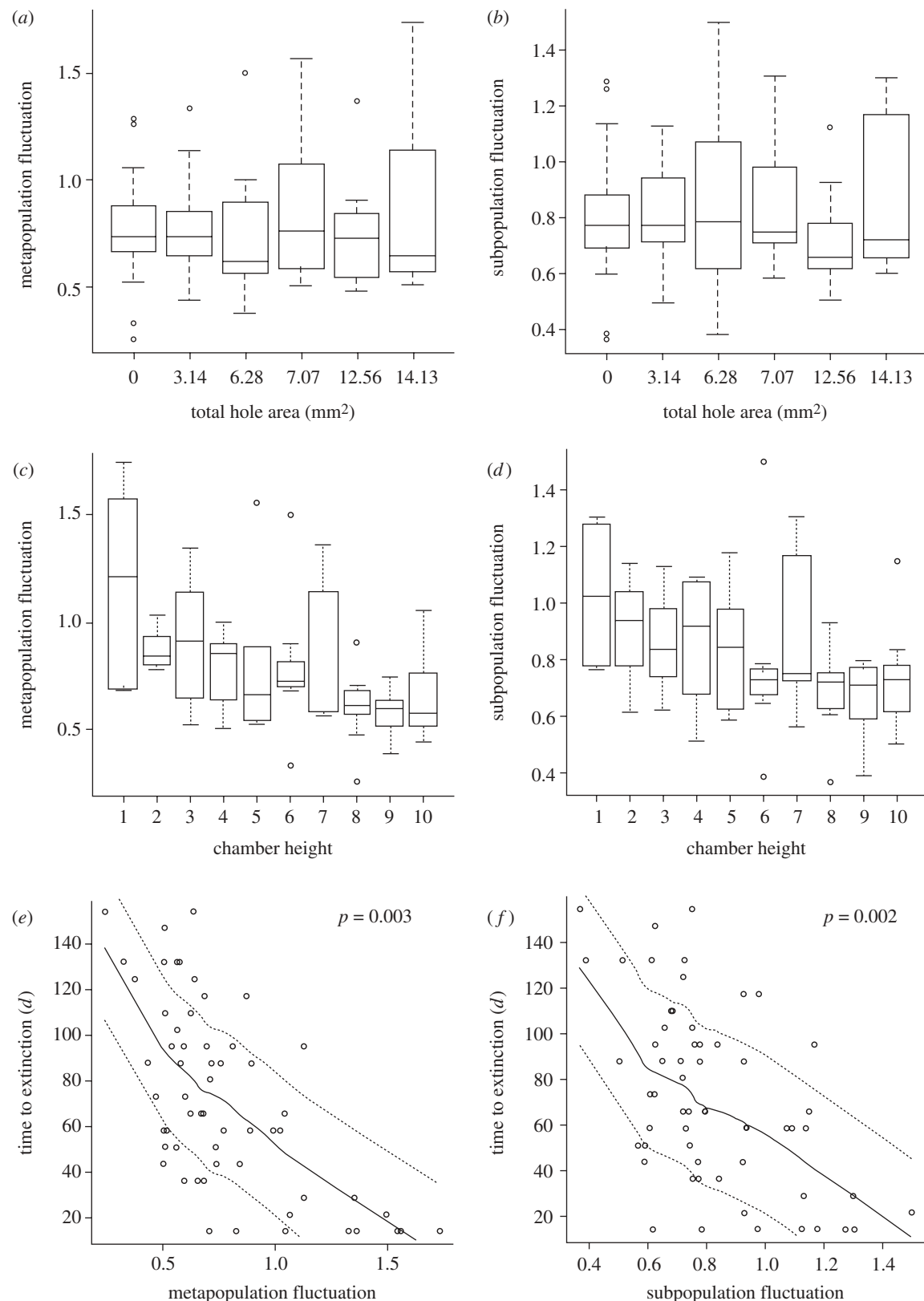


Figure 5. (a) Metapopulation and (b) subpopulation fluctuation as a function of (c) migration between subpopulations, and (d) as a function of height. (e) Time to extinction as a function of metapopulation and (f) subpopulation fluctuation. Lines in (e) and (f) are the Lowess smoothed fits ( $\pm 1$  s.e.) based on 75 per cent of the data.

further investigation using experiments that explicitly manipulated both migration rate and environmental quality.

Population size increased with chamber height (figure 4b) and fluctuation in subpopulation and

metapopulation size decreased with chamber height (figure 5c,d). Each of these factors were correlated with longer times to extinction. This also implicates the importance of environmental factors in metapopulation extinction. *Daphnia* population demographics react

strongly to both food availability and light intensity (Kleiven *et al.* 1992; Griffen & Drake 2008b), and both of these were influenced in our experiment by chamber height. The predominance of environmental factors over demographic factors has previously been noted (Andrewartha & Birch 1954; Belovsky *et al.* 1999). And while environment was more important than migration in this experiment as well, the two cannot always be separated and may interact to influence population extinction (Shirley & Sibly 2001). Results here also demonstrate that environmental factors may provide the ultimate force driving proximate demographic factors that influence population extinction (i.e. population size and fluctuations, figures 4c and 5e,f). Finally, if environmental influences consistently outweigh demographic factors in determining extinction risk, then reducing extinction risk by improving conditions within habitats (i.e. restoration) may be more effective than by facilitating migration between poor habitats (i.e. corridors).

Our results also indicate that metapopulation synchrony may be less important for extinction risk than anticipated. Recent theoretical research has focused on the importance of metapopulation synchrony and its role in extinction risk (e.g. Heino *et al.* 1997; Matter 2001; Liebhold *et al.* 2004). However, we found that although metapopulations displayed a large range of synchronous dynamics ( $-0.31$  to  $0.97$ ), synchrony was not correlated with time to extinction (figure 3c). However, while synchrony was not correlated with extinction time, extinction time showed a strong positive correlation with population size (figure 4c) and a strong negative correlation with both metapopulation (figure 5e) and subpopulation fluctuation (figure 5f). Thus, these factors may be more important to metapopulation persistence than the extent to which subpopulation dynamics are synchronized. This hypothesis warrants further investigation in studies that compare extinction risk to each of these aspects of population dynamics.

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