

The effect of phenotypic variation on metapopulation persistence

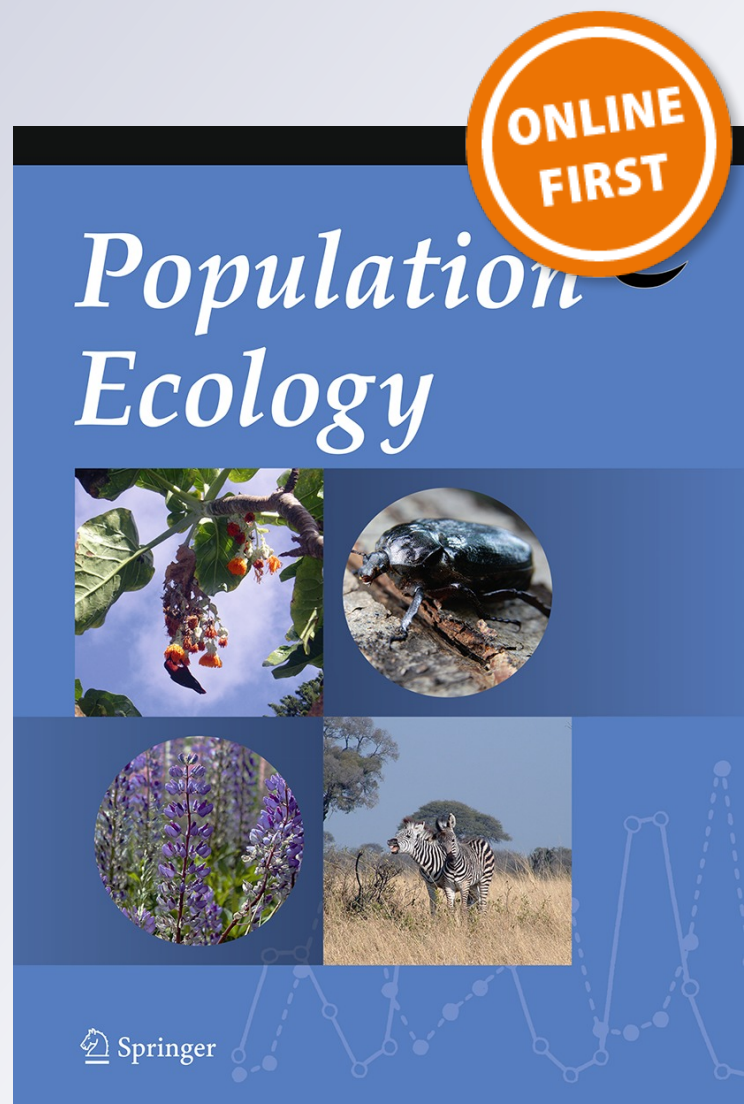
Jean P. Gibert

Population Ecology

ISSN 1438-3896

Popul Ecol

DOI 10.1007/s10144-016-0548-z



Your article is protected by copyright and all rights are held exclusively by The Society of Population Ecology and Springer Japan. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".



The effect of phenotypic variation on metapopulation persistence

Jean P. Gibert¹

Received: 27 November 2015 / Accepted: 21 April 2016
© The Society of Population Ecology and Springer Japan 2016

Abstract Demographic stochasticity (due to the probabilistic nature of the birth–death process) and demographic heterogeneity (between-individual differences in demographic parameters) have long been seen as factors affecting extinction risk. While demographic stochasticity can be independent of underlying species traits, demographic heterogeneity may strongly depend on phenotypic variation. However, how phenotypic variation can affect extinction risk is largely unknown. Here, I develop a stochastic metapopulation model that takes into account the effects of demographic stochasticity and phenotypic variation in the traits controlling colonization rates to assess what the effect of phenotypic variation may be on the persistence of the metapopulation. Although phenotypic variation can lead to a decrease in metapopulation persistence under some conditions, it also may lead to an increase in persistence whenever phenotypic mismatch—or the distance between the optimal trait value and the population mean—is large. This mismatch can in turn arise from a variety of ecological and evolutionary reasons, including weak selection or a recent history of invasion. Last, the effect of phenotypic variation has a deterministic component on colonization rates, and a stochastic component on persistence through colonization rates, but both are important to understand the overall effect. These results have important implications for the conservation of threatened species and management practices that may historically have overlooked phenotypic variation as unimportant noise around mean values of interest.

Keywords Extinction risk · Individual variation · Migration · Trait variation · Variability

Introduction

Understanding the factors leading to extinction is a central goal in ecology (e.g., Gilpin and Hanski 1991; Lande 1993; Kendall and Fox 2003; Melbourne and Hastings 2008). This understanding is crucial when it comes to making informed decisions about the management of endangered species or sets of species in threatened communities and ecosystems (Gilpin and Hanski 1991). Many factors influencing extinction risk have been identified, including abiotic factors (e.g., pollution), biotic factors (e.g., invasive species) as well as exogenous factors (i.e., that are external to the focal population) and endogenous factors (i.e., that are related to internal population level processes, Roughgarden 1975; Melbourne and Hastings 2008).

Stochasticity in population growth and dynamics has long been seen as a major factor increasing extinction risk (May 1973; Chesson 1981; Fox and Kendall 2002). The sources of this stochasticity are many, and they can be broadly divided into two classes: demographic—or stochasticity in population growth due to the random nature of the birth–death process—and environmental—or random fluctuations in environmental conditions that lead to fluctuations in the number of births and deaths—(e.g., Caswell 2001, 2009; Lande et al. 2003; Engen et al. 2005). Although both types of stochasticity can increase extinction risk, demographic stochasticity is mainly a problem for small populations (Caswell 2001), while environmental stochasticity can affect much larger populations (Caswell 2001; Melbourne and Hastings 2008).

✉ Jean P. Gibert
jeanphisth@gmail.com

¹ School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588, USA

Another source of stochasticity in population growth is demographic heterogeneity (Conner and White 1999; Fox and Kendall 2002; Kendall and Fox 2003; Fox 2005; Vindenes et al. 2008; Vindenes and Langangen 2015). This source of stochasticity occurs whenever there are actual differences among individuals (e.g., the traits they have) that lead to systematic differences in their chance of surviving and reproducing, as opposed to differences in the chance of surviving and reproducing due to the randomness of births and deaths, as it is the case in demographic stochasticity (Melbourne and Hastings 2008). How demographic heterogeneity affects extinction risk is an active area of research and has been shown to have opposite effects on extinction risk. Indeed, heterogeneity can reduce extinction risk (Conner and White 1999; Fox and Kendall 2002; Fox 2005), increase it (Robert et al. 2003) or both increase and decrease extinction risk (Kendall and Fox 2003; Vindenes et al. 2008; Melbourne and Hastings 2008).

Demographic heterogeneity can arise from a number of factors including geographic or habitat heterogeneity (e.g., Gates and Gysel 1978; Menge et al. 1994; Landis et al. 2005), frailty effects and reproductive heterogeneity (Vaupel and Yashin 1985; Fox et al. 2006; Kendall et al. 2011), and both genetic and phenotypic variation (Chesson 1981). Ecologists have historically dismissed phenotypic variation as noise around mean trait values of interest (Lomnicki 1988). But even populations that are made of clones (i.e., individuals that share the same genetic makeup) will have slight differences in the way genes are expressed (e.g., Price et al. 2003), leading to potentially important amounts of phenotypic variation (Lomnicki 1988; Sherratt and MacDougall 1995). More importantly, there are strong reasons to expect ecological effects of variation per se whenever there exists a concave down or concave up relationship between a focal trait and the ecological process of interest through Jensen's inequality (Jensen 1906; Ruel and Ayres 1999; Gibert and Brassil 2014; Gibert and DeLong 2015). Phenotypic variation thus has the potential to alter demographic heterogeneity and stochasticity, and through that, have consequences for the persistence of populations with considerable phenotypic variation.

This paper assesses whether phenotypic variation in traits controlling ecological processes can have important effects on metapopulation persistence. Phenotypic variation has recently been shown to influence an enormous set of parameters and processes (Araújo et al. 2011; Bolnick et al. 2011; Violle et al. 2012; Gibert et al. 2015), including predator–prey interactions (through for example, attack rate, handling time and mutual interference, Okuyama 2008, 2013; Pettorelli et al. 2011; Gibert and Brassil 2014; Gibert and DeLong 2015), dietary variation (Snowberg et al. 2015), disease dynamics (Lloyd-Smith et al. 2005),

food web structure (Svanbäck et al. 2015), tri-trophic interactions (Hughes et al. 2015), as well as trait evolution (Fisher 1930; Dobzhansky 1937; Frank 2012) and eco-evolutionary dynamics (Schreiber et al. 2011; Vasseur et al. 2011). In all cases, phenotypic variation was found to be largely stabilizing and to potentially increase population persistence.

Here I address how underlying phenotypic variation in traits that control dispersal, such as wing length or body size, might affect the persistence of a metapopulation model with demographic stochasticity. I argue that this effect may be mediated through deterministic consequences of the occurrence of phenotypic variation in the parameters controlling the dynamics of the system, which in turn result in a stochastic effect on metapopulation persistence.

Methods

Generalities

In metapopulations, persistence results from the balance between two main parameters: colonization and extinction rates (Levins 1969). Because the local extinction rate is largely dependent upon patch size (MacArthur and Wilson 1967; Laurance 2005; Arroyo-Rodríguez et al. 2009), I assume that phenotypic variation will mainly affect colonization rates and have no effect on extinction rates. Colonization rates depend in turn on the distance colonizers must travel (Levins 1969; Gibert et al. 2013) and on the production of colonizers (Alonso and McKane 2002), which is a function of demographic parameters and is thus ultimately determined by phenotypic variation, as has been shown empirically in three-spined sticklebacks (Laskowski et al. 2015). To address how phenotypic variation in the traits determining colonization rates affect persistence, I used two models: the first considers external migration from a mainland only whenever the metapopulation goes extinct; the second considers migration from a mainland as a process that can occur anytime.

The models

For the first model, I reformulated an already existing stochastic metapopulation model (Gurney and Nisbet 1978) to track the total number of occupied patches over time for a species living in a space consisting of N identical patches with no spatial correlation. I later modified this model (see “Incorporating phenotypic variation”) to take phenotypic variation into account. The model assumes that at each infinitesimal time step, there is a chance for an empty patch to be colonized and for an occupied patch to become

unoccupied through local extinction. These one-step transition probabilities are independent of the state of the system at previous time steps and can be written as:

$$C(n+1|n) = cn\left(1 - \frac{n}{N}\right)dt, \quad (1)$$

$$E(n-1|n) = en dt, \quad (2)$$

where $C(n+1|n)$ is the probability that an unoccupied patch is colonized, $E(n-1|n)$ is the probability that an occupied patch becomes unoccupied, N is the total number of patches in the metapopulation, n is the number of occupied patches, c is the colonization rate and e is the extinction rate (Levins 1969; Alonso and McKane 2002). We define $C(1|0) \equiv \phi dt$, which can be seen as a chance of receiving migrants from outside the metapopulation if the metapopulation was to go extinct. As ϕ decreases, the stationary probability of extinction tends to 1. Setting $\phi \neq 0$, however, does not preclude the metapopulation from going extinct because (1) ϕ can be arbitrarily small and (2) even if ϕ is large, its final effect will depend on the relative values of all other colonization and extinction transition probabilities. I nevertheless assessed the effect of ϕ in the dynamics of the model (see “Results”) for thoroughness. This model would apply to scenarios where external migration from the continent is so negligible compared to $C(n+1|n)$ (i.e., $C(n+1|n) \gg \phi$), that effectively the only time the external migration impacts dynamics is when the metapopulation as a whole goes extinct. It could also apply in situations where humans monitor the status of a metapopulation, and supply propagules when the metapopulation goes extinct either intentionally or unintentionally, which may be of relevance in management and conservation scenarios. Last, I imposed a boundary at $n=0$, by defining $C(0|-1) = E(-1|0) \equiv 0$, since patch occupancy cannot be negative. To simplify notation, I will refer to $C(n+1|n)$ as C_n , to $C(n|n-1)$ as C_{n-1} , to $E(n-1|n)$ as E_n and to $E(n|n+1)$ as E_{n+1} from now on.

Under these conditions, the master equation controlling the change in the distribution of occupied sites ($P(n, t)$) over time can be written as:

$$\frac{dP(n, t)}{dt} = C_{n-1}P(n-1, t) + E_{n+1}P(n+1, t) - P(n, t)(C_n + E_n), \quad (3)$$

where the probability of finding n occupied patches at time t increases with the probability that a colonization event occurred multiplied by the probability of having $n-1$ occupied sites ($C_{n-1}P(n-1, t)$), increases with the probability that an extinction event occurred multiplied by the probability of having $n+1$ occupied sites ($E_{n+1}P(n+1, t)$), and decreases with the probability of having both an extinction or a colonization event

multiplied by the probability of having exactly n occupied sites ($P(n, t)(C_n + E_n)$, van Kampen 1981). The stationary distribution ($t \rightarrow \infty$) can be found by recurrence (Appendix 1), and is equal to:

$$P(n, \infty) = \frac{C_0 \dots C_{n-1}}{E_1 \dots E_n} P(0, \infty), \quad (4)$$

with

$$P(0, \infty) = \frac{1}{1 + \sum_{n=1}^N \frac{C_0 \dots C_{n-1}}{E_1 \dots E_n}}. \quad (5)$$

Using Eqs. (1) and (2) and assuming $\phi = 1$ for simplicity, the stationary distribution for the model becomes (Appendix 2):

$$P(n, \infty) = \frac{\frac{1}{ne^n} \left(\frac{c}{N}\right)^{n-1} \frac{\Gamma(N)}{\Gamma(N-n+1)}}{1 + \sum_{n=1}^N \frac{1}{ne^n} \left(\frac{c}{N}\right)^{n-1} \frac{\Gamma(N)}{\Gamma(N-n+1)}}, \quad (6)$$

where Γ is the Gamma function. The mean number of occupied patches can then be found as:

$$\langle n \rangle = \sum_{n=1}^N \frac{\frac{1}{e^n} \left(\frac{c}{N}\right)^{n-1} \frac{\Gamma(N)}{\Gamma(N-n+1)}}{1 + \sum_{j=1}^N \frac{1}{je^j} \left(\frac{c}{N}\right)^{j-1} \frac{\Gamma(N)}{\Gamma(N-j+1)}} \quad (7)$$

The mean number of occupied patches increases in this model with increasing colonization rate (Fig. 1) and decreases with increasing extinction rate (Fig. 1), as expected from classic Levins' model (Levins 1969). This model is the continuous-time Markov chain counterpart to Gurney and Nisbet (1978) stochastic Langevin equation

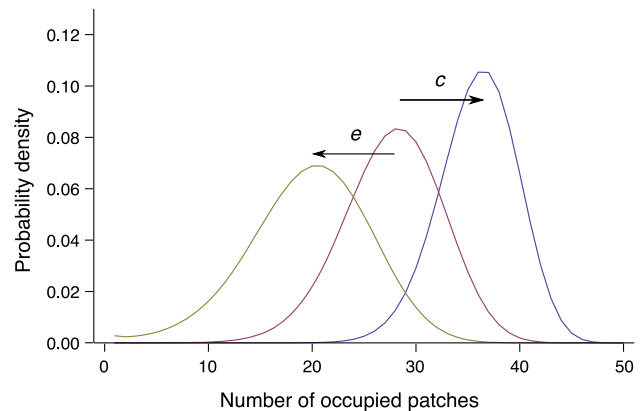


Fig. 1 Plot of the probability density associated to the number of occupied patches from Eq. (6). We can see how an increase in colonization rate (c) leads to an increase in the mean number of occupied patches while an increase in extinction rate (e) leads to a decrease in the mean number of occupied patches. The probability density curve in the center (red in color version) is our canonical set of parameters for comparison: $c = 1.4$, $e = 0.6$, and $N = 50$. In the one to the left (yellow in color version), everything is as in the one in the center but for $e = 0.8$. In the one to the right (blue in color version), everything is as in the center but for $c = 2.2$

model, based on Levins' metapopulation model (Levins 1969). Even though my particular formulation has not been explored before, its behavior should in all respects be equivalent to that of Gurney and Nisbet (1978).

The second model I explored is a continuous-time Markov chain model developed by Alonso and McKane (2002), which, contrary to the previous one, assumes that the metapopulation can receive external migration from a mainland at any time. In that case, the probability that a colonization event occurs in a time lapse dt is

$$C(n+1|n) = c n \left(1 - \frac{n}{N}\right) dt + m(N-n)dt, \quad (8)$$

where m is the migration rate from the continent, and everything else is as in the first model. The number of occupied patches is approximately (Alonso and McKane 2002):

$$\langle n \rangle \approx \frac{N}{2} \left(1 - \frac{m-e}{c} + \sqrt{\left(1 + \frac{m-e}{c}\right)^2 + 4 \frac{m e}{c^2}} \right). \quad (9)$$

This approximation is particularly useful because once I incorporate phenotypic variation the mean number of occupied patches rapidly becomes difficult if not impossible to compute numerically. In what follows, I modify these models to account for phenotypic variation in a trait that determines colonization rates.

Incorporating phenotypic variation

Building upon previous work (Schreiber et al. 2011; Gibert and Brassil 2014; Gibert and DeLong 2015), I incorporated phenotypic variation by assuming the existence of a normally distributed trait x with probability density function $p(x, \bar{x}, \sigma^2)$, that determines colonization rates in a Gaussian way:

$$c(x) = c_{\max} \exp \left[-\frac{1}{2} \frac{(\theta - x)^2}{\tau^2} \right], \quad (10)$$

where c_{\max} is the maximal colonization rate, θ represents the trait value at which colonization is optimal, and τ controls the rate at which colonization rates decrease away from the optimum value. This functional form is common in traits controlling dispersal such as body size (Manzaneda et al. 2009) or wing length (Pulido and Widmer 2005), and can arise from either stabilizing or conflicting selection in the traits controlling dispersal (Manzaneda et al. 2009). Gaussian functional forms such as the one assumed here are also common in theoretical papers studying how traits and their evolution might affect metapopulation dynamics (Hanski and Mononen 2011; Hanski et al. 2011). Notice

that colonization rates are defined at the metapopulation level, so the trait distribution considered is also defined across local populations. Using Eq. (10) it is possible to calculate the mean colonization rate as,

$$\langle c \rangle = \int_{-\infty}^{\infty} c(x) p(x, \bar{x}, \sigma^2) dx, \quad (11)$$

which convolves nicely to:

$$\langle c \rangle = \frac{c_{\max} \tau}{\sqrt{\tau^2 + \sigma^2}} \exp \left[-\frac{1}{2} \frac{d^2}{\tau^2 + \sigma^2} \right], \quad (12)$$

where $d^2 = (\theta - \bar{x})^2$, hereafter referred to as phenotypic mismatch following previous work (Raimundo et al. 2014; Gibert and Brassil 2014; Gibert and DeLong 2015). Notice that while selection can reduce mismatch, it is not certain that it will. Indeed, whether mismatch will decrease ultimately depends on a number of other factors, including, but not limited to, whether selection is strong, whether there is antagonistic selection on the trait (e.g., imposed by other interacting species or environmental differences across patches that makes moving between patches deleterious) or whether the trait is plastic. Changes in τ affect how sensitive colonization rates are to changes in both phenotypic mismatch and phenotypic variation. Because $\langle c \rangle$ is an explicit function of phenotypic variation (σ^2), it is now possible to assess the effect of the latter in the mean number of occupied sites for both models. Using Eqs. (7) and (12), $\langle n \rangle$ becomes for the first model:

$$\langle n \rangle = \sum_{n=1}^N \frac{\frac{1}{e^n} \left(\frac{\langle c \rangle}{N} \right)^{n-1} \frac{\Gamma(N)}{\Gamma(N-n+1)}}{1 + \sum_{j=1}^N \frac{1}{j e^j} \left(\frac{\langle c \rangle}{N} \right)^{j-1} \frac{\Gamma(N)}{\Gamma(N-j+1)}}, \quad (13)$$

while for the second model it becomes:

$$\langle n \rangle \approx \frac{N}{2} \left(1 - \frac{m-e}{\langle c \rangle} + \sqrt{\left(1 + \frac{m-e}{\langle c \rangle}\right)^2 + 4 \frac{m e}{\langle c \rangle^2}} \right). \quad (14)$$

Alternatively, phenotypic variation can be incorporated in a different way. For the first model, by plugging Eq. (10) into Eq. (7), and convolving the whole with the trait distribution we get:

$$\langle n \rangle = \int_{-\infty}^{\infty} \sum_{n=1}^N \frac{\frac{1}{e^n} \left(\frac{c(x)}{N} \right)^{n-1} \frac{\Gamma(N)}{\Gamma(N-n+1)}}{1 + \sum_{j=1}^N \frac{1}{j e^j} \left(\frac{c(x)}{N} \right)^{j-1} \frac{\Gamma(N)}{\Gamma(N-j+1)}} p(x, \bar{x}, \sigma^2) dx. \quad (15)$$

For the second model, the expression reads

$$\langle n \rangle \approx \int_{-\infty}^{\infty} \frac{N}{2} \left(1 - \frac{m-e}{c(x)} + \sqrt{\left(1 + \frac{m-e}{c(x)} \right)^2 + 4 \frac{me}{c(x)^2}} \right) p(x, \bar{x}, \sigma^2) dx. \quad (16)$$

Equations (15) and (16) are not always numerically computable, so in some cases I had to adjust the range of parameters studied. Comparing the two ways in which I incorporated phenotypic variation helped with assessing how robustly we can predict the effects of phenotypic variation on metapopulation persistence.

Results

I explored two different scenarios, one where phenotypic mismatch is zero ($d^2 = 0$), and one where phenotypic mismatch is larger than zero ($d^2 > 0$). In the first model, it can be seen that, for $d^2 = 0$, the mean number of occupied patches goes down with phenotypic variation (Fig. 2a–d). This is true for both ways of incorporating phenotypic variation (Fig. 2a, b vs c, d), different metapopulation sizes (Fig. 2a, c) and values of the parameter τ (Fig. 2b, d). The effect of phenotypic variation on mean occupancy, however, is different when phenotypic mismatch is large ($d^2 > 0$): mean occupancy increases at first, and then decreases (Fig. 2e–h). These results also hold for the Alonso and McKane model (Fig. 3). When exploring the effect of variation using Eq. (16), however, it was not possible to analyze all the scenarios explored for the first model, which is why I do not show results on how varying τ affects mean occupancy for that model, or why the range of values analyzed for phenotypic variation is slightly smaller in this case as well (i.e., Fig. 3c, f).

Last, I explored how joint changes in parameters could affect metapopulation persistence. When phenotypic variation and phenotypic mismatch vary together in the first model, mean occupancy decreases as they jointly increase, and is maximal when there is no phenotypic variation or mismatch (Fig. 4a). This shows that phenotypic mismatch may be detrimental for metapopulation persistence in a case where underlying traits control colonization rates in a gaussian fashion, as is assumed here. This effect of variation and mismatch is not qualitatively affected by considering external migration (as in the second model, Fig. 4b, c), and is not qualitatively affected by the value of ϕ either (external migration when metapopulation goes extinct as explained for the first model, Fig. 4d). Even in the range of values where ϕ has a strong effect ($\phi \approx 0$), phenotypic variation generally decreases occupancy if phenotypic mismatch is small.

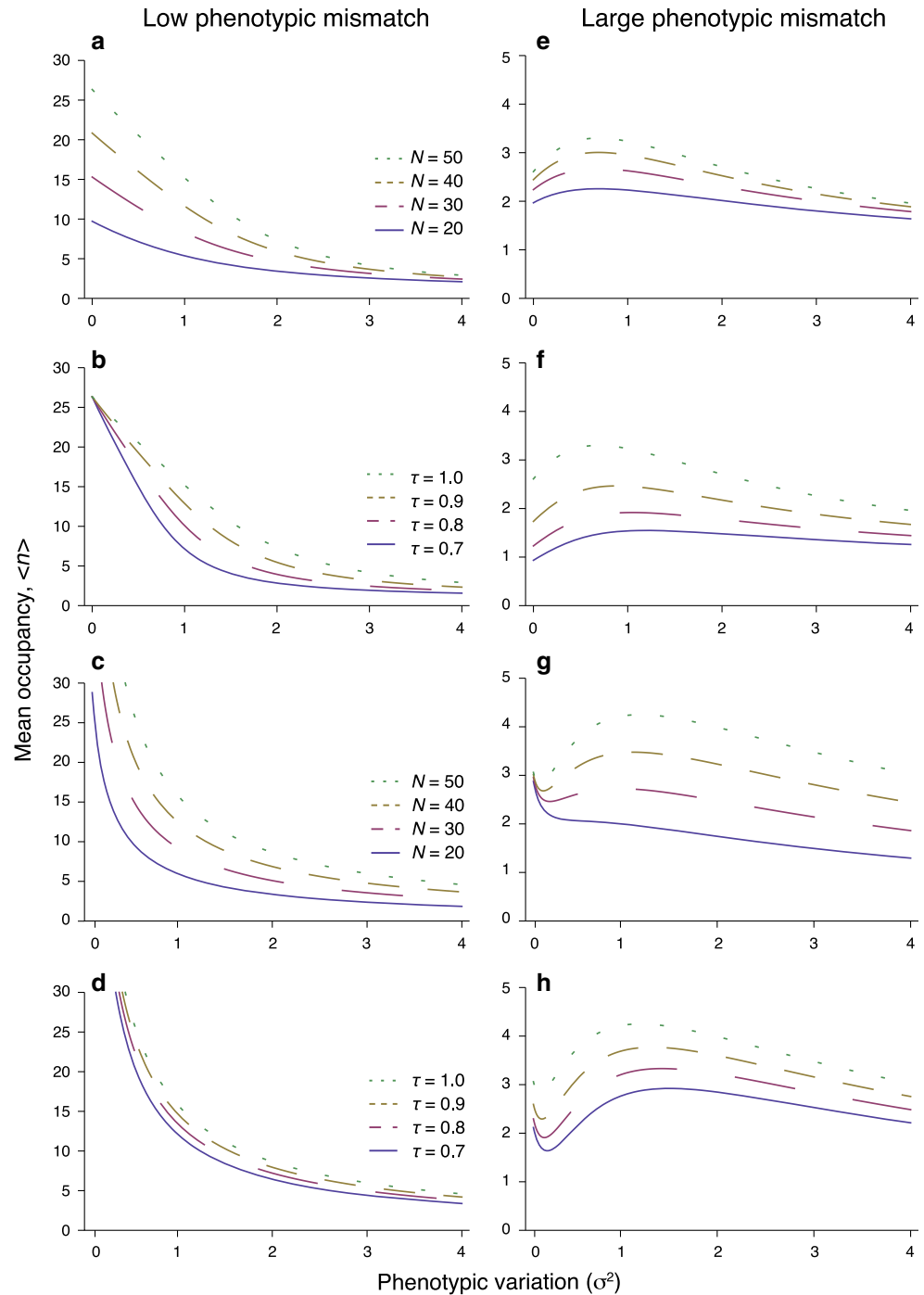
Discussion

My results show that phenotypic variation can have both negative and positive impacts on extinction risk in metapopulations, which is consistent with what past studies have shown about the effect of demographic heterogeneity (Chesson 1981; Conner and White 1999; Fox and Kendall 2002; Kendall and Fox 2003; Fox 2005; Vindenes et al. 2008; Melbourne and Hastings 2008). Regarding the positive effect of phenotypic variation, my results are also in line with what others have shown in deterministic models (Schreiber et al. 2011; Vasseur et al. 2011; Gibert and Brassil 2014; Gibert and DeLong 2015). These results also suggest that the effect of phenotypic variation can strongly depend on other important factors, such as, phenotypic mismatch, which is ultimately controlled by past and present selection acting on the traits controlling dispersal. Indeed, it is this parameter that ultimately determines whether the effect of phenotypic variation is positive or negative. Hence, to fully understand the effect of phenotypic variation on extinction risk, we may need to also understand how it interplays with past and current selection acting on the traits that control the process of interest, as recent studies argue (Hairston et al. 2005; Hanski et al. 2011; Schreiber et al. 2011; Gibert et al. 2015).

Phenotypic mismatch, or the difference between the optimal and the mean trait value in the population can result from selection acting on a focal trait (Fellowes et al. 1998; Nuismer et al. 2010). Indeed, low levels of phenotypic mismatch may result from strong stabilizing selection constantly pushing to maintain the trait on or near an optimal value (Nuismer et al. 2010). Large levels of mismatch may result from weak selection (Nuismer et al. 2010), or from a recent history of invasion of the species to its current habitat or location (Jones and Gomulkiewicz 2012). Here, we show that this phenotypic mismatch can have important consequences for the survival of a metapopulation, since at low levels of mismatch, phenotypic variation decreases mean occupancy and increases the chance that the metapopulation will go extinct, while at larger levels of mismatch, phenotypic variation can have the opposite effect. Because phenotypic mismatch may change over time through rapid evolutionary change of the traits controlling dispersal, these results suggest the possibility that eco-evolutionary feedbacks may have important consequences for metapopulation persistence, as other studies stressed (Hanski and Mononen 2011; Hanski et al. 2011).

It is possible that selection may reduce phenotypic mismatch over time, which eventually would lead to a scenario that could gradually erode phenotypic variance. It

Fig. 2 **a–d** Plots of the mean number of occupied patches ($\langle n \rangle$) in the first model against phenotypic variation (σ^2) for varying levels of the total number of patches (N) (**a**, **c**), varying levels of the parameter τ (**b**, **d**), and low phenotypic mismatch ($d^2 = 0$). Plots **a**, **b** were obtained using Eq. (13) and plots **c**, **d** were obtained using Eq. (15). **e–h** same as in **a–d** but for large phenotypic mismatch ($d^2 = 1.3$). Other parameters: $c_{\max} = 2.2$, $e = 0.6$, $\phi = 1$ and $\tau = 1.0$ (unless otherwise stated), $N = 50$ (unless otherwise stated)

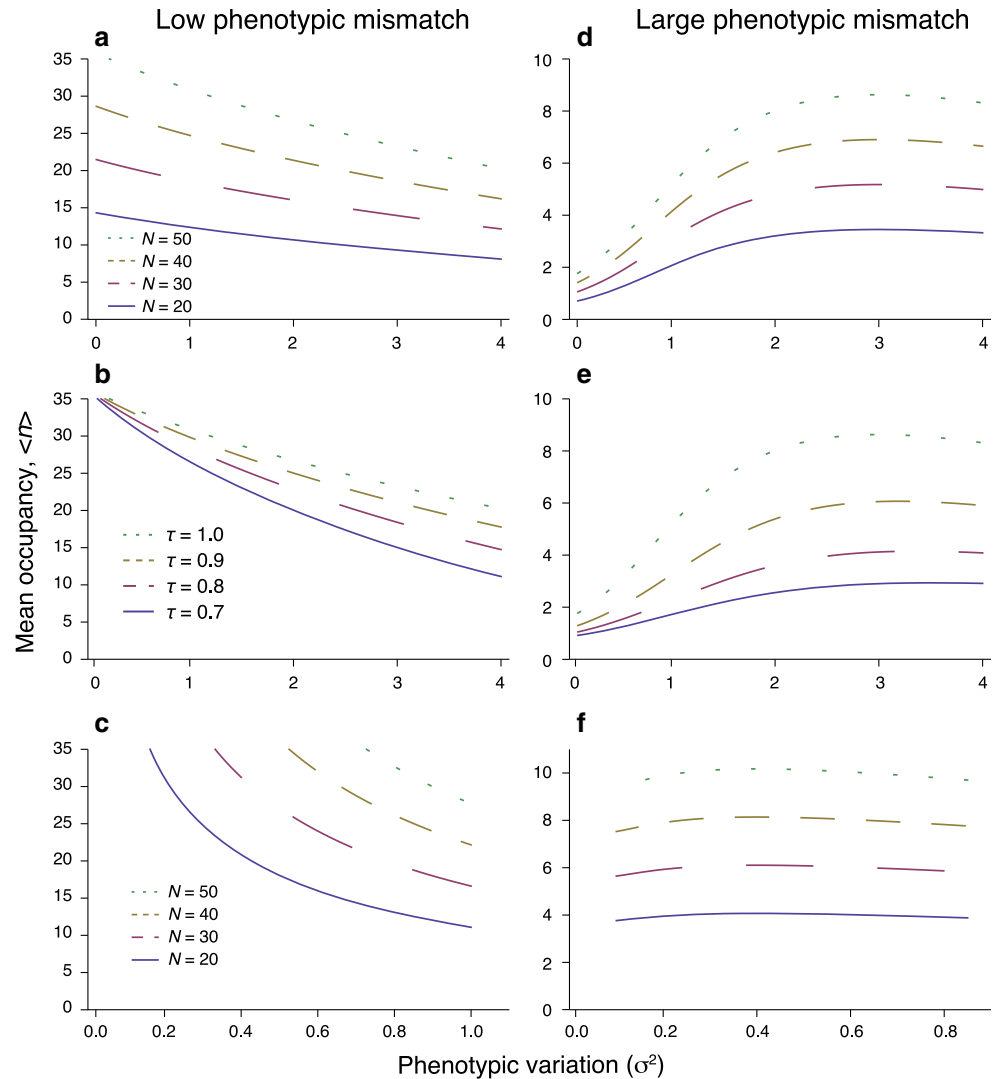


is thus important to contemplate mechanisms that could maintain phenotypic variation over time for the results of this paper to hold for metapopulations under strong stabilizing selection. Such possible mechanisms include all classic evolutionary processes such as gene flow from outside the metapopulation, mutation and pleiotropy (e.g., Mitchell-Olds et al. 2007). However, depending on how heritable the traits are, it is possible that some if not most of the variation in the traits controlling dispersal might arise

through phenotypic plasticity, which will not be eroded by selection, even though it can fuel evolutionary change as well (Price et al. 2003). Thus, even in scenarios under strong stabilizing selection, it is possible to still find core levels of irreducible phenotypic variation and phenotypic mismatch, with potentially important ecological effects on the persistence of metapopulations.

It has also been empirically shown that phenotypic variation controls dispersal capacity in the three-spine

Fig. 3 **a–c** Plots of the mean number of occupied patches ($\langle n \rangle$) in the second model against phenotypic variation (σ^2) for varying levels of the total number of patches (N) (**a**, **c**), varying levels of the parameter τ (**b**), and low phenotypic mismatch ($d^2 = 0$). Plots **a**, **b** were obtained using Eq. (14) and plot **c** was obtained using Eq. (16). **d–f** same as in **a–c** but for large phenotypic mismatch ($d^2 = 1.3$). All other parameters as in Fig. 1. Horizontal axis scale is different in panels **c**, **f**



stickleback *Gasterosteus aculeatus* (Laskowski et al. 2015). Together with my findings, these results suggest that individual phenotypic variation may be a key yet largely overlooked factor when it comes to devising conservation and management plans for threatened metapopulations. For example, by not taking phenotypic variation into account, the probability of extinction of a metapopulation might be largely underestimated if the phenotypic mismatch is small, or largely overestimated if the mismatch is large. Moreover, the increasing temperatures associated with global warming are likely to affect the mean body size of some if not most ectothermic species (Daufresne et al. 2009; Sheridan and Bickford 2011), with important consequences for food web body size structure (Gibert and DeLong 2014). Yet, little is known as to how warming may affect variation in body size even though there are strong reasons to believe that both the mean and variance of body size can change with temperature, as it was empirically

shown in a protist system (DeLong 2012). Together, these results further emphasize the need for a deeper understanding of the effect of phenotypic variation upon ecological processes, and how these effects may be potentially mediated by environmental temperature.

Importantly, the effect described here occurs through two distinct components: first, there is a deterministic effect of phenotypic variation on colonization rates, then this deterministic effect leads to a stochastic effect of phenotypic variation on metapopulation persistence through colonization rates (which determines demographic stochasticity in these models). Our results thus highlight the importance of considering the joint effect of both deterministic and stochastic factors in regulating the fate of natural populations. Notice, however, that we may not be able to separately quantify their effects in nature, as the deterministic effect of phenotypic variation on colonization rates is a prerequisite for the stochastic effect of phenotypic

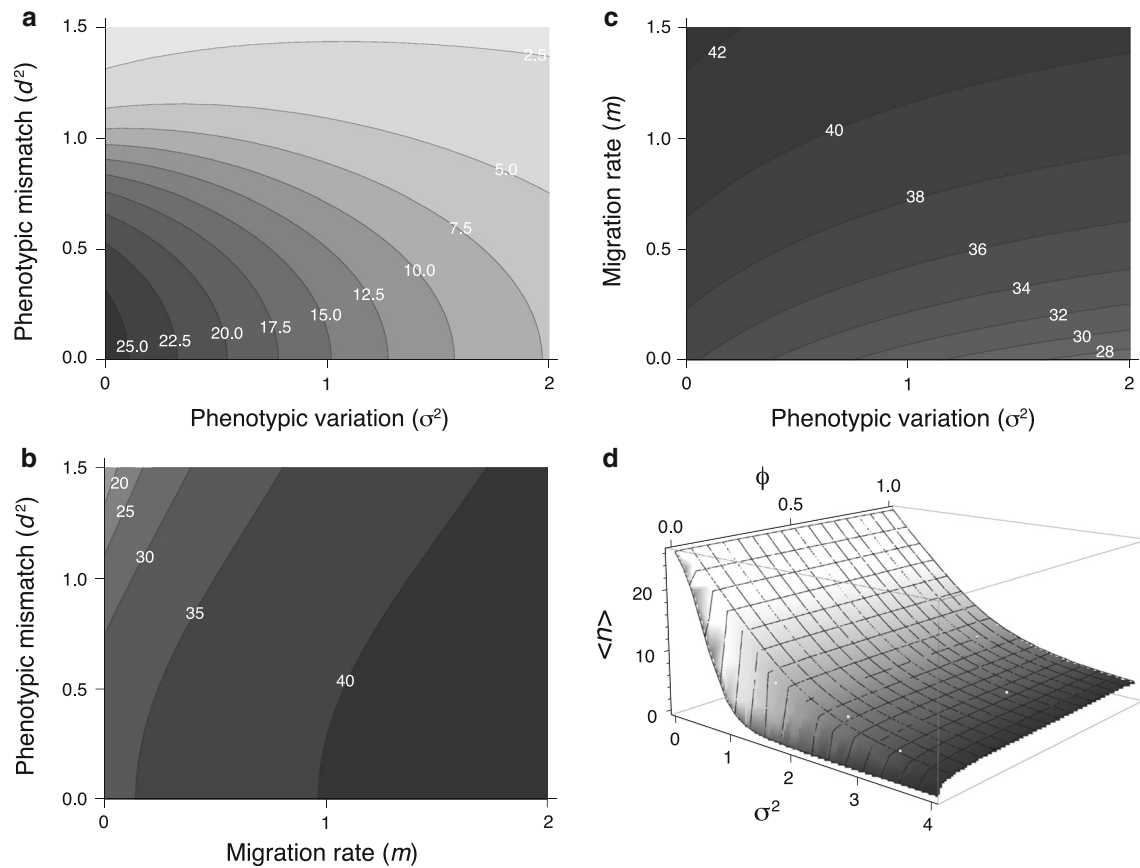


Fig. 4 **a** Contour plot of how the mean number of occupied patches (grey tones, white numbers), changes as a function of phenotypic mismatch (d^2) and phenotypic variation (σ^2) for the first model. **b** Same as in **a** but for migration rate (m) and phenotypic variation for

the second model. **c** Same as in **b** but for phenotypic mismatch and migration rate. **d** Surface showing how the effect of phenotypic variation on mean occupancy changes with ϕ , for low phenotypic mismatch ($d^2 = 0$). All other parameters as in previous figures

variation on metapopulation persistence. These two components of the overall effect of phenotypic variation occur sequentially and are fundamentally linked, which makes their separate quantification potentially challenging. Both ought to be considered together as a complex pathway through which phenotypic variation affects persistence.

It is important to notice as well that my models depend on a number of parameters whose values will affect the results shown here. For example, the value of τ , the parameter that controls the sensitivity of the colonization rates to changes in phenotypic variation, is arbitrary in my models, and larger values of the parameter will lead to scenarios where no effect of phenotypic variation may be observed. Also, the effects described here strongly depend on the total number of patches considered (Figs. 2, 3), with larger populations needing larger levels of phenotypic mismatch to show a similar change in the total number of occupied sites. Last, it is interesting to notice that the two models explored showed qualitatively similar but quantitatively different responses to phenotypic variation (Figs. 2 vs 3). In Levins' model (Eqs. 13, 15), the effect of

phenotypic variation was much stronger than in Alonso and McKane's (Eqs. 14, 16). This is because of the way both models depend on c : the Levins' model can be roughly seen as parabolic function of c of the form $\frac{\sum_{i=1}^N c^i}{1 + \sum_{i=1}^N c^i}$, thus tending faster and faster to 1 with increasing N ; Alonso and McKane's model, on the other hand, goes to 1 as $1 - \frac{1}{c}$, which does so at a slower pace. This difference in the concavity of both functions with respect to c leads to a difference in how much they respond to variation in the parameter. The faster the function tends to 1, the stronger their concavity with respect to c and the stronger they respond to variation in that parameter, as a previous study also suggested (Inouye 2005).

Overall, this paper shows that the effect of phenotypic variation may be more complex than meets the eye. Indeed, phenotypic variation underlies demographic heterogeneity, but its effects on metapopulation persistence depends on other factors such as phenotypic mismatch as well as its deterministic effects on the parameters controlling the dynamics of interest. At low levels of mismatch,

phenotypic variation decreases persistence, but at larger levels of mismatch, the pattern can be reversed. This paper emphasizes the fact that both phenotypic variation and phenotypic mismatch may need to be taken into account when devising conservation plans of endangered species living in patches connected by migration in a context of global change.

Acknowledgments I am indebted to John DeLong for his advice, constant support and insightful comments. I am grateful with Volker Grimm and two anonymous reviewers for helpful suggestions. I was supported by a National Science Foundation Doctoral Dissertation Improvement Grant (DEB-1501668).

Appendix 1

In this appendix, I show how Eq. (4) of the main text can be derived from Eq. (3). Assuming that as $t \rightarrow \infty$, the system will go to a stationary distribution $P(n, \infty)$, we can set $\frac{dP(n, \infty)}{dt} = 0$ and solve:

$$C_{n-1}P(n-1, \infty) + E_{n+1}P(n+1, \infty) - P(n, \infty)(C_n + E_n) = 0. \quad (17)$$

At $n = 0$, $C_{-1}P(-1, \infty) + E_1P(1, \infty) - P(0, \infty)(C_0 + E_0) = 0$. Because $C_{-1} = 0$ and $E_0 = 0$ (see main text), we obtain:

$$P(1, \infty) = \frac{C_0}{E_1}P(0, \infty). \quad (18)$$

At $n = 1$, we obtain:

$$P(2, \infty) = \frac{C_1C_0}{E_2E_1}P(0, \infty). \quad (19)$$

So, by recurrence, we obtain:

$$P(n, \infty) = \frac{C_0 \dots C_{n-1}}{E_1 \dots E_n}P(0, \infty). \quad (20)$$

Now, $P(0, \infty)$ can be determined from the normalization condition, $\sum_{n=0}^N P(n, \infty) = 1$:

$$P(0, \infty) + \sum_{n=1}^N P(n, \infty) = 1. \quad (21)$$

Then, we replace with Eq. (20) to obtain:

$$P(0, \infty) + P(0, \infty) \sum_{n=1}^N \frac{C_0 \dots C_{n-1}}{E_1 \dots E_n} = 1, \quad (22)$$

which reduces to,

$$P(0, \infty) = \frac{1}{1 + \sum_{n=1}^N \frac{C_0 \dots C_{n-1}}{E_1 \dots E_n}}. \quad (23)$$

Appendix 2

In this appendix, I show that by replacing Eqs. (1) and (2) from the main text in Eqs. (4) and (5) we can obtain the stationary distribution in Eq. (6) of the main text. Replacing Eqs. (1) and (2) on Eq. (20), and assuming $\phi = 1$ we obtain:

$$P(n, \infty) = \frac{c(1 - \frac{1}{N}) \times 2c(1 - \frac{2}{N}) \times \dots \times (n-1)c(1 - \frac{n-1}{N})}{e \times 2e \times \dots \times ne} P(0, \infty). \quad (24)$$

Which can be rearranged as follows:

$$\begin{aligned} P(n, \infty) &= \frac{1}{e^n} \frac{c(N-1) \times 2c(N-2) \times \dots \times c(N-n+1)}{1 \times 2 \times \dots \times n} P(0, \infty) \\ \Leftrightarrow P(n, \infty) &= \frac{1}{e^n} \left(\frac{c}{N}\right)^{n-1} \frac{(N-1) \times (N-2) \times \dots \times (N-n+1)}{n} P(0, \infty) \\ \Leftrightarrow P(n, \infty) &= \frac{1}{ne^n} \left(\frac{c}{N}\right)^{n-1} \frac{(N-1) \times (N-2) \times \dots \times 1}{(N-n+2) \times \dots \times 1} P(0, \infty) \\ \Leftrightarrow P(n, \infty) &= \frac{1}{ne^n} \left(\frac{c}{N}\right)^{n-1} \frac{\Gamma(N)}{\Gamma(N-n+1)} P(0, \infty). \end{aligned} \quad (25)$$

By replacing $P(0, \infty)$ by Eq. (23) we obtain Eq. (6) of the main text.

References

- Alonso D, McKane AJ (2002) Extinction dynamics in mainland-island metapopulations: an N -patch stochastic model. *Bull Math Biol* 64:913–958
- Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. *Ecol Lett* 14:948–958
- Arroyo-Rodríguez V, Pineda E, Escobar F, Benítez-Malvido J (2009) Value of small patches in the conservation of plant-species diversity in highly fragmented rainforest. *Conserv Biol* 23:729–739
- Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. *Trends Ecol Evol* 26:183–192
- Caswell H (2001) *Matrix population models*, 2nd edn. Sinauer Associates, Sunderland, Massachusetts
- Caswell H (2009) Stage, age and individual stochasticity in demography. *Oikos* 118:1763–1782
- Chesson PL (1981) Models for spatially distributed populations: the effect of within-patch variability. *Theor Popul Biol* 19:288–325
- Conner MM, White GC (1999) Effects of individual heterogeneity in estimating the persistence of small populations. *Nat Resour Model* 12:109–127
- Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small. *Proc Natl Acad Sci* 106:12788–12793
- DeLong JP (2012) Experimental demonstration of a “rate–size” trade-off governing body size optimization. *Evol Ecol Res* 14:343–352
- Dobzhansky T (1937) *Genetics and the origin of species*. Columbia University Press, New York

- Engen S, Lande R, Sæther BE, Weimerskirch H (2005) Extinction in relation to demographic and environmental stochasticity in age-structured models. *Math Biosci* 195:210–227
- Fellowes MD, Kraaijeveld AR, Godfray HC (1998) Trade-off associated with selection for increased ability to resist parasitoid attack in *Drosophila melanogaster*. *Proc Biol Sci* 265:1553–1558
- Fisher RA (1930) The genetical theory of natural selection. Clarendon Press, Oxford
- Fox GA (2005) Extinction risk of heterogeneous populations. *Ecology* 86:1191–1198
- Fox GA, Kendall BE (2002) Demographic stochasticity and the variance reduction effect. *Ecology* 83:1928–1934
- Fox GA, Kendall BE, Fitzpatrick JW, Woolfenden GE (2006) Consequences of heterogeneity in survival probability in a population of Florida scrub-jays. *J Anim Ecol* 75:921–927
- Frank SA (2012) Natural selection. IV. The Price equation. *J Evol Biol* 25:1002–1019
- Gates JE, Gysel LW (1978) Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871
- Gibert JP, Brassil CE (2014) Individual phenotypic variation reduces interaction strengths in a consumer-resource system. *Ecol Evol* 4:3703–3713
- Gibert JP, DeLong JP (2014) Temperature alters food web body-size structure. *Biol Lett* 10:20140473
- Gibert JP, DeLong JP (2015) Individual variation decreases interference competition but increases species persistence. *Adv Ecol Res* 52:45–64
- Gibert JP, Pires MM, Thompson JN, Guimarães PR (2013) The spatial structure of antagonistic species affects coevolution in predictable ways. *Am Nat* 182:578–591
- Gibert JP, Dell AI, DeLong JP, Pawar S (2015) Scaling-up trait variation from individuals to ecosystems. *Adv Ecol Res* 52:1–17
- Gilpin M, Hanski I (1991) Metapopulation dynamics: empirical and theoretical investigations. Academic Press, San Diego
- Gurney WSC, Nisbet RM (1978) Single-species population fluctuations in patchy environments. *Am Nat* 112:1075
- Hairston NG Jr, Ellner SP, Geber MA, Yoshida T, Fox JA (2005) Rapid evolution and the convergence of ecological and evolutionary time. *Ecol Lett* 8:1114–1127
- Hanski I, Mononen T (2011) Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. *Ecol Lett* 14:1025–1034
- Hanski I, Mononen T, Ovaskainen O (2011) Eco-evolutionary metapopulation dynamics and the spatial scale of adaptation. *Am Nat* 177:29–43
- Hughes AR, Hanley TC, Orozco NP, Zerebecki RA (2015) Consumer trait variation influences tritrophic interactions in salt marsh communities. *Ecol Evol* 5:2659–2672
- Inouye BD (2005) The importance of the variance around the mean effect size of ecological processes: comment. *Ecology* 86:262–265
- Jensen J (1906) Sur les fonctions convexes et les inégalités entre les valeurs moyennes. *Acta Math* 30:175–193 (in French)
- Jones EI, Gomulkiewicz R (2012) Biotic interactions, rapid evolution, and the establishment of introduced species. *Am Nat* 179:E28–E36
- Kendall BE, Fox GA (2003) Unstructured individual variation and demographic stochasticity. *Conserv Biol* 17:1170–1172
- Kendall BE, Nogueira TM, Fox GA, Fujiwara M (2011) Demographic heterogeneity, cohort selection, and population growth. *Ecology* 92:1985–1993
- Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am Nat* 142:911–927
- Lande R, Engen S, Sæther BE (2003) Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford
- Landis RM, Gurevitch J, Fox GA, Fang W, Taub DR (2005) Variation in recruitment and early demography in *Pinus rigida* following crown fire in the pine barrens of Long Island, New York. *J Ecol* 93:607–617
- Laskowski KL, Pearish S, Bensky M, Bell AM (2015) Predictors of individual variation in movement in a natural population of threespine stickleback (*Gasterosteus aculeatus*). *Adv Ecol Res* 52:65–90
- Laurance WF (2005) When bigger is better: the need for Amazonian mega-reserves. *Trends Ecol Evol* 20:645–648
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull Entomol Soc Am* 15:237–240
- Lloyd-Smith JO, Schreiber SJ, Kopp PE, Getz WM (2005) Super-spreading and the effect of individual variation on disease emergence. *Nature* 438:355–359
- Lomnicki A (1988) Population ecology of individuals. Princeton University Press, Princeton
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton
- Manzaneda AJ, Rey PJ, Alcántara JM (2009) Conflicting selection on diaspora traits limits the evolutionary potential of seed dispersal by ants. *J Evol Biol* 22:1407–1417
- May RM (1973) Qualitative stability in model ecosystems. *Ecology* 54:638–641
- Melbourne BA, Hastings A (2008) Extinction risk depends strongly on factors contributing to stochasticity. *Nature* 454:100–103
- Menge BA, Berlow EL, Blanchette CA, Navarete SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a Rocky Intertidal Habitat. *Ecol Monogr* 64:249–286
- Mitchell-Olds T, Willis JH, Goldstein DB (2007) Which evolutionary processes influence natural genetic variation for phenotypic traits? *Nat Rev Genet* 8:845–856
- Nuismer SL, Gomulkiewicz R, Ridenhour BJ (2010) When is correlation coevolution? *Am Nat* 175:525–537
- Okuyama T (2008) Individual behavioral variation in predator–prey models. *Ecol Res* 23:665–671
- Okuyama T (2013) Consequences of variation in foraging success among predators on numerical response. *Ecol Evol* 3:4039–4043
- Petorelli N, Coulson T, Durant SM, Gaillard J-M (2011) Predation, individual variability and vertebrate population dynamics. *Oecologia* 167:305–314
- Price TD, Qvarnström A, Irwin DE (2003) The role of phenotypic plasticity in driving genetic evolution. *Proc Biol Sci* 270:1433–1440
- Pulido F, Widmer M (2005) Are long-distance migrants constrained in their evolutionary response to environmental change? Causes of variation in the timing of autumn migration in a blackcap (*S. atricapilla*) and two garden warbler (*Sylvia borin*) populations. *Ann N Y Acad Sci* 1046:228–241
- Raimundo RLG, Gibert JP, Hembry DH, Guimarães PR (2014) Conflicting selection in the course of adaptive diversification: the interplay between mutualism and intraspecific competition. *Am Nat* 183:363–375
- Robert A, Sarrazin F, Couvet D (2003) Variation among individuals, demographic stochasticity, and extinction: response to Kendall and Fox. *Conserv Biol* 17:1166–1169
- Roughgarden J (1975) A simple model for population dynamics in stochastic environments. *Am Nat* 109:713–736
- Ruel JJ, Ayres MP (1999) Jensen's inequality predicts effects of environmental variation. *Trends Ecol Evol* 14:361–366
- Schreiber SJ, Bürger R, Bolnick DI (2011) The community effects of phenotypic and genetic variation within a predator population. *Ecology* 92:1582–1593

- Sheridan JA, Bickford D (2011) Shrinking body size as an ecological response to climate change. *Nat Clim Change* 1:401–406
- Sherratt T, MacDougal AD (1995) Some population consequences of variation in preference among individual predators. *Biol J Linn Soc* 55:93–107
- Snowberg LK, Hendrix KM, Bolnick DI (2015) Covarying variances: more morphologically variable populations also exhibit more diet variation. *Oecologia* 178:89–101
- Svanbäck R, Quevedo M, Olsson J, Eklöv P (2015) Individuals in food webs: the relationships between trophic position, omnivory and among-individual diet variation. *Oecologia* 178:103–114
- van Kampen NG (1981) Stochastic processes in physics and chemistry. Elsevier, Amsterdam
- Vasseur DA, Amarasekare P, Rudolf VHW, Levine JM (2011) Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. *Am Nat* 178:E96–E109
- Vaupel JW, Yashin AI (1985) Heterogeneity's ruses: some surprising effects of selection on population dynamics. *Am Stat* 39:176–185
- Vindenes Y, Langangen Ø (2015) Individual heterogeneity in life histories and eco-evolutionary dynamics. *Ecol Lett* 18:417–432
- Vindenes Y, Engen S, Saether B-E (2008) Individual heterogeneity in vital parameters and demographic stochasticity. *Am Nat* 171:455–467
- Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J (2012) The return of the variance: intraspecific variability in community ecology. *Trends Ecol Evol* 27:244–252