Conservation Genetics
https://doi.org/10.1007/s10592-018-1097-0

RESEARCH ARTICLE

Local and system-wide adaptation is influenced by population connectivity

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Received: 5 January 2018 / Accepted: 4 August 2018

Abstract

Complex systems can be conceptualized and studied as networks of nodes with varying connectivity between nodes. In well-connected systems, local disturbance of individual nodes can be countered by input from neighbouring nodes, buffering the system against local change. Thus, pronounced change in a well-connected system may not occur until the system hits a threshold or 'tipping point' that drives a shift to an alternative, system-wide state. In contrast, poorly connected systems are more prone to gradual node-by-node change. We use forward-in-time simulations of multi-locus evolution to test these general predictions concerning complex systems. We do so in the context of local adaptation in patchy environments comprised of many demes (i.e., nodes) of two habitat types. We vary connectivity by manipulating migration rate and the spatial clustering of habitat types. We find gradual and 'deme-by-deme' dynamics of local adaptation when connectivity is low. The dynamics transition towards more sudden, system-wide shifts as population connectivity is increased (i.e., many demes adapt more suddenly and simultaneously). Our results support a trade-off between local and system-wide resilience, and we discuss their implications for the conservation of species living in patchy and fragmented habitats.

Keywords Adaptation · Evolution · Fragmentation · Migration · Systems biology · Tipping point

Introduction

Complex systems are common in biology, and can often be characterized as networks of inter-connected nodes. For example, food webs contain interacting species, and meta-populations comprise sub-populations connected by migration, where each sub-population (i.e., 'deme') can be considered a node in the overall system (Hanski and Mononen 2011; Hanski et al. 2011, 2013; Hanski 2011). Conservation biology in particular often considers complex systems, as it aims to preserve interacting populations and species that are distributed across space in complex ways. The dynamics of such complex systems can be fundamentally affected by connectivity (or, conversely, modularity) (Leibold et al. 2004; Scheffer et al. 2012), the issue we focus on here (Fig. 1).

In a well-connected system, local disturbance of individual nodes can be countered by input from neighbouring nodes, buffering the system against local change. An example is extinction-colonisation dynamics in meta-populations, where individual sub-populations (i.e., nodes) in a well-connected meta-population can be buffered against extinction by immigration (Holyoak 2000; Hanski and Mononen 2011; Hanski et al. 2011, 2013; Hanski 2011). Thus, pronounced change in well-connected systems may not occur until the entire system hits a threshold that drives a shift to an alternative, system-wide state (Scheffer et al. 2001, 2009, 2012, 2015; Scheffer 2009, 2010). This system-wide shift, occurring at a 'tipping point', may often involve positive feedback loops that facilitate sudden, rapid change (i.e., at some critical threshold a change in the dynamic variable x can increase y, which feeds back to increase x, and so

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10592-018-1097-0) contains supplementary material, which is available to authorized users.

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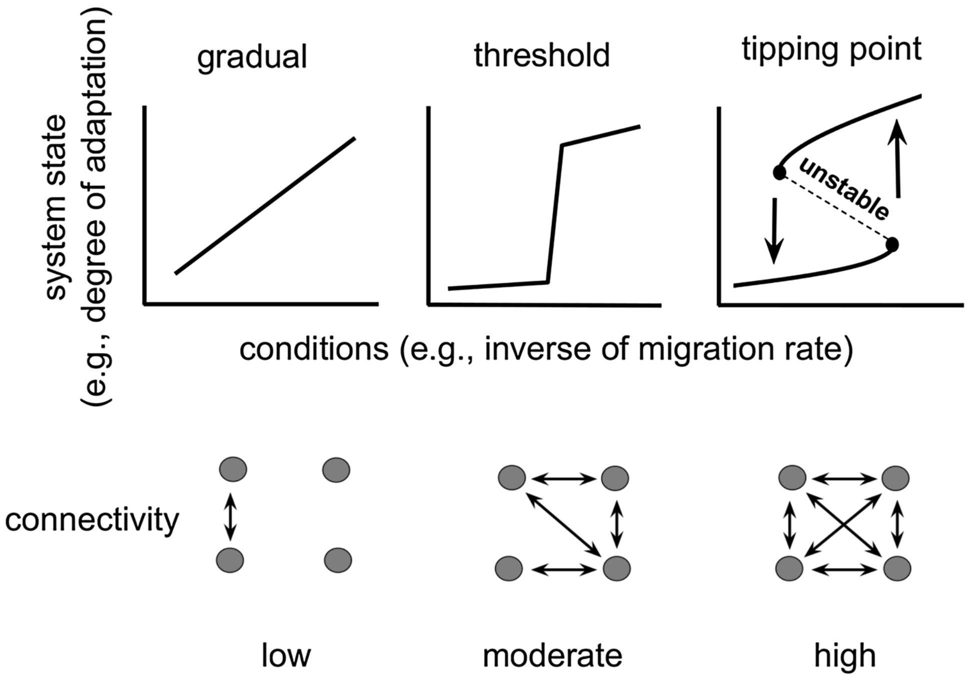


Fig. 1 Schematic of the predicted effects of connectivity on the dynamics of complex systems, i.e., increased connectivity can lead to more sudden, system-wide changes. Tipping points represent an extreme case of sudden change, where a difficult to reverse shift occurs between alternative stable states. (Reproduced with permission from Scheffer et al. 2012)

on) (Servedio and Saetre 2003; Crespi 2004; Rasanen and Hendry 2008; Schwander et al. 2010; Lehtonen and Kokko 2012).

In contrast, poorly connected systems allow gradual node-by-node change, because change of individual nodes is not buffered by input from other nodes. In terms of the capacity of a system to recover from disturbance (i.e., its resilience), highly connected systems are thus predicted to be robust to local perturbation, but prone to system-wide change. This implies a trade-off between local and system-wide resilience (Leibold et al. 2004; Scheffer et al. 2012).

This type of 'systems thinking' can be applied to the dynamics of local adaptation, speciation, and genetic differentiation. For example, Flaxman et al. (2014) modelled divergence with gene flow in terms of the per-locus strength of divergent selection (DS) between ecological environments (s), migration rates (m), and numbers of genetic loci involved (L). In the model, loci differentiate due to a combination of selection acting directly on them plus indirect effects of selection stemming from their statistical associations (linkage disequilibrium, LD) with other divergently selected loci. When migration was high ($m > s$), sudden speciation and genome-wide differentiation occurred and went hand-in-hand with a positive feedback loop. Below a critical threshold of genome wide DS and between-population LD, differentiation built very slowly due to the homogenising effect of migration. However, once a critical level of both was reached, DS and LD entered a positive feedback loop where each enhanced the other, driving a rapid reduction in gene flow and a transition from one species into two. Similar dynamics likely apply for polygenic adaptation generally (Hendry et al. 2001; Hendry 2017), and for the coupling of multi-locus clines and reproductive barriers (Barton 1983; Barton and Hewitt 1985; Barton and de Cara 2009; Bierne et al. 2011; Nosil et al. 2017).

The sudden temporal dynamics described in Flaxman et al. (2014) were dependent on two types of connectivity. First, sudden transitions from one species to two were only observed in models that allow for the build up of LD, because LD (i.e., statistical connectivity among loci) was a key component of the feedback that drives the transition. In other words, LD accentuated the effectiveness of multi-locus selection. Second, sudden transitions only occurred when the gross migration rate connecting populations (i.e., spatial connectivity between demes) was high relative to the strength of DS. When migration was low, individual loci overcame gene flow via the selection they directly experienced, and thus diverged on their own, without the need for indirect selection. In other words, genes had largely independent dynamics and gradual, 'gene-by-gene' divergence ensued. This previous work applied systems thinking in a genomic context (gradual 'gene-by-gene' versus sudden, genome-wide differentiation). Here we apply similar thinking in a different context, namely whether adaptation across space occurs gradually for individual demes/sub-populations versus more suddenly for many demes.

Specifically, the previous work of Flaxman et al. (2014) was restricted to the simple spatial setting of a single pair of populations (i.e., two demes). Here, we extend these models to a network of many sub-populations (multiple demes). This allows us to establish the conditions under which adaptation evolves gradually for individual demes ('deme-by-deme' adaptation) versus emerging as a systems-level property that affects many demes more suddenly and simultaneously. Thus, our focus is on whether adaptation occurs in a deme-by-deme or system-wide manner, not on the overall rate of adaptation per se. We describe various metrics below to quantify how 'deme-by-deme' versus system-wide the evolution of adaptation is. Our findings inform the role of migration in evolution and have implications for conservation biology, because habitat fragmentation commonly affects the connectivity of sub-populations in space (e.g., Coulon et al. 2004; Dixo et al. 2009; Barr et al. 2015).

Methods

Description of the model

We developed an individual-based model to test the hypothesis that increased connectivity among demes, either through higher migration rates or by increased spatial connectivity of the same patch type, causes demes to differentiate and adapt in a more system-wide rather than 'deme-by-deme' manner. We modeled a 10 × 10 matrix of demes, with each deme having one of two equally common habitat or patch types. We refer to these patch types as ancestral and novel habitats. Habitat types were arranged in either: (1) a highly regular patchwork (i.e., checkerboard) configuration in which neighboring demes were always of different types (i.e., there was low connectivity among the same patch type; landscape aggregation index = 0) (sensu He et al. 2000) or (2) a random configuration in which neighboring demes were equally likely to be of the same or different types, resulting in higher connectivity of patches of the same type across the system relative to the checkerboard configuration (each replicate simulation used a different random configuration; average landscape aggregation index = 0.50) (Fig. S1).

Each deme had a set carrying capacity of K diploid hermaphroditic individuals (see Table 1 for a summary of all parameters). Each individual's genome contained a set of L bi-allelic loci that were evenly spaced along a single chromosome having an assumed recombination length of 100 centi-Morgans. We assumed discrete, non-overlapping generations. Each generation comprised three steps: (1) dispersal, (2) viability selection, and (3) reproduction (including mutation) of surviving individuals until reaching carrying capacity (i.e., there were thus no long-term extinction events, see Discussion for further consideration).

Dispersal occurred probabilistically based on the migration rate, m, which gives the probability that an individual disperses. Dispersal only occurred into neighboring demes, and the dispersal direction (up, down, left or right) was chosen at random and with equal probability. Dispersal out of the meta-population (i.e., off the 10 × 10 deme matrix) was allowed, and resulted in instant death. The population size (N) was allowed to exceed the carrying capacity (K) at this stage in the simulation. Dispersal was followed by *viability selection*. We assumed fitness was determined by the individual's genotype at the L loci, with an ancestral allele that was beneficial in one habitat type (the ancestral habitat type) and deleterious in the other (the novel habitat type), and a derived allele with equal but opposite effects on fitness (i.e., habitat-related fitness trade-offs for alternate alleles).

Fitness was assumed to be multiplicative, such that the absolute total fitness of an individual was $w = (1 - s)^n$, where n was the number of maladaptive alleles it possessed given the habitat type it resided in (across loci) and s was the selection coefficient, which was set equal for all loci. There were no dominance or epistatic interactions affecting fitness. Survival was then treated as a Bernoulli random variable (survival = 1, death = 0) with $p = w$ (that is, absolute fitness).

We then modeled *reproduction* for all surviving individuals in each deme. Pairs of parents were chosen at random to produce offspring (one at a time), until the offspring

Table 1 Definitions of model parameters and data summaries

Symbol	Definition
K	Deme carrying capacity (100)
N	Current deme population size
m	Migration rate or probability out of a deme (0.001–0.3)
L	Number of loci affecting fitness (20)
s	The per locus strength of selection against locally deleterious alleles (0.04)
w	Absolute fitness, that is an individual's survival probability
p_i	The mean frequency of derived alleles (across loci) in deme i
$\mu_{nov,}$ μ_{anc}	The mean frequency of derived allele across all demes in ancestral or novel patch types
σ_{anc}, σ_{nov}	The standard deviation of the mean frequency of derived allele across all demes in ancestral or novel patch types
$\Delta\sigma$	Our overall measure of 'deme-by-deme' (versus system-wide) adaptation = $\sigma_{anc} - \sigma_{nov}$

Values (when kept constant) or ranges are given for parameters in parentheses population size was equal to the carrying capacity. We chose a chromosome copy at random for each parent to pass down, and allowed mutations with probability $1e^{-6}$ per locus and recombination (which was modeled as a Poisson process with an expectation of 1). Computer software implementing these simulations was written by the authors in C++ and using the Gnu Scientific Library (source code and a compiled Linux binary are available from Dryad, https://doi.org/10.5061/dryad.2qg02qq).

Simulations

Simulation parameters were chosen to illustrate how migration affects the spatial and temporal dynamics of local adaptation, rather than to represent any particular real biological system. Future work tailored to specific circumstances is warranted, but our approach here represents a reasonable starting point for exploring the dynamics of adaptation. We began the simulations with all demes fixed for ancestral alleles at all loci; the ancestral alleles were beneficial in what we hereafter refer to as the ancestral habitat type. In other words, we assumed no initial standing genetic variation. Simulations were run for a fixed amount of time of 100,000 (random configuration) or 500,000 (patchwork configuration) generations, as this was the time required to observe pronounced, system-wide adaptation in each case. In all simulations, we assumed $K = 100$ per deme and $L = 20$ fitness affecting loci. We set the strength of selection as $s = 0.04$ or 0.02. We observed qualitatively similar results for these two s values and thus focus on $s = 0.04$ in the main text, and report results from $s = 0.02$ in the Electronic Supplementary Materials (see Figs S2–S6). Thus, an individual with all maladaptive alleles (20 loci * 2 gene copies = 40 alleles total) would have an absolute fitness (survival probability) of $(1–0.04)^{40} = 0.195$. Perfectly adapted individuals thus had a survival probability of 1.0. We initially focus on contrasting simulation results generated from using a relatively low migration rate (m) of 0.01 versus a relatively high rate of 0.10. We then expand our treatment of migration rate variation to quantitatively span rates from 0.001 to 0.10. Ten replicate simulations were conducted for all combinations of parameters, for each of the two landscape configurations (i.e., ten for random and ten for patchwork).

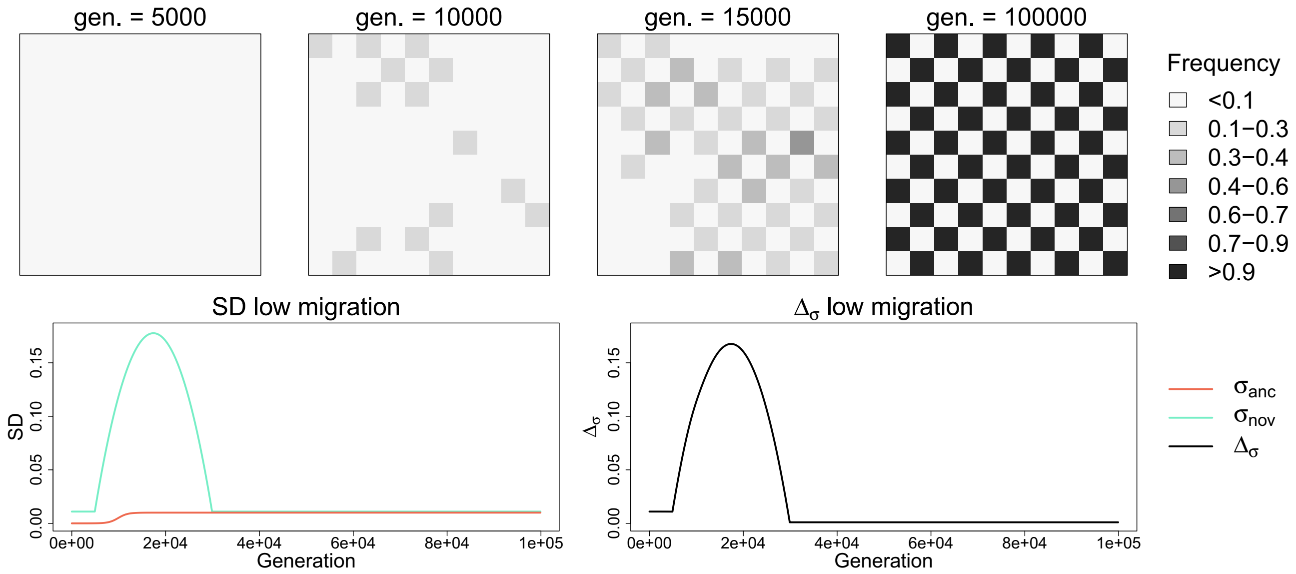
Metrics of 'deme-by-deme' versus system-wide change

Our simulations output the allele frequencies for each of the L loci for each deme every 10 generations. We summarized these results using a series of metrics that quantify the extent to which adaptation occurred for individual demes (i.e., in a 'deme-by-deme' fashion) versus more suddenly and simultaneously for many or all demes (i.e., the system) (Table 1). As an overall measure of degree of adaptation for each deme, we considered the mean frequency of derived alleles (across loci) in each deme (p_i, where $i = \{1, 2,\ldots, 100\}$ denotes the index of the deme). Thus, in patches of the ancestral type, $p_i = 0$ would denote perfect adaptation, whereas in patches of the novel type $p_i = 1$ would denote perfect adaptation. We analyzed evolutionary dynamics in terms of the derived allele frequencies rather than fitness to avoid non-linear dynamics in time that would necessarily arise from the non-linear relationship between genotype and fitness specified by the multiplicative fitness model. With that said, given our assumption that all loci had equal effects on fitness, derived allele frequencies and mean fitness are closely related.

To measure adaptation at the system or meta-population level, for each patch type, we calculated the mean of the p_i, that is, the grand mean frequency of derived alleles, which we denote μ_{anc} and μ_{nov}, for the ancestral and novel patch types, respectively. This metric shows how well, on average, demes are adapted to each patch type; $\mu_{\mathrm{anc}} = 0$ denotes perfect adaptation in the ancestral habitat type and $\mu_{\mathrm{nov}} = 1$ denotes perfect adaptation in the novel habitat type. For our focus on the potential for deme-by-deme dynamics, this metric is preferred over other common metrics of metapopulation adaptation that provide a single (rather than patch/deme specific) measure of local adaptation (summarized in Blanquart et al. 2013).

Similarly, for each habitat type we calculated the standard deviation of the p_i across demes ($\sigma_{\mathrm{anc}} = \sqrt{(\Sigma_{i=1}^{J}(p_i - \mu_{\mathrm{anc}})^2/J)}$ and $\sigma_{\mathrm{nov}} = \sqrt{(\Sigma_{i=1}^{J}(p_i - \mu_{\mathrm{nov}})^2/J)}$ where the summation is over the J demes of the relevant habitat type, that is the ancestral or novel patch types. This metric captures, at the meta-population level, the extent to which demes occupying a given patch type are uniformly or heterogeneously adapted to that patch type (Fig. 2). Higher standard deviations denote greater heterogeneity *among demes* in levels of adaptation (i.e., higher standard deviation = greater among-deme variation in local adaptation). This standard deviation metric thus generally captures the degree to which adaptation to the novel patch type occurred in a 'deme-by-deme' versus system-wide way. The exception was for high values of m, where this metric is sometimes misleading because under these conditions the simulations can give rise to a generalist metapopulation with some variation rather than two locally adapted types (see "Results" and "Discussion"). Thus, we defined a second metric of 'deme-by-deme' local adaptation as $\Delta\sigma = \sigma_{\mathrm{nov}} - \sigma_{\mathrm{anc}}$, that is the difference in the standard deviation of the p_i between the novel and ancestral patch types (Fig. 2). We summed this difference across generations for a final metric of the degree to which adaptation and differentiation occurred in a 'deme-by-deme' manner.

(a) Low migration (m = 0.01)



(b) High migration (m = 0.1)

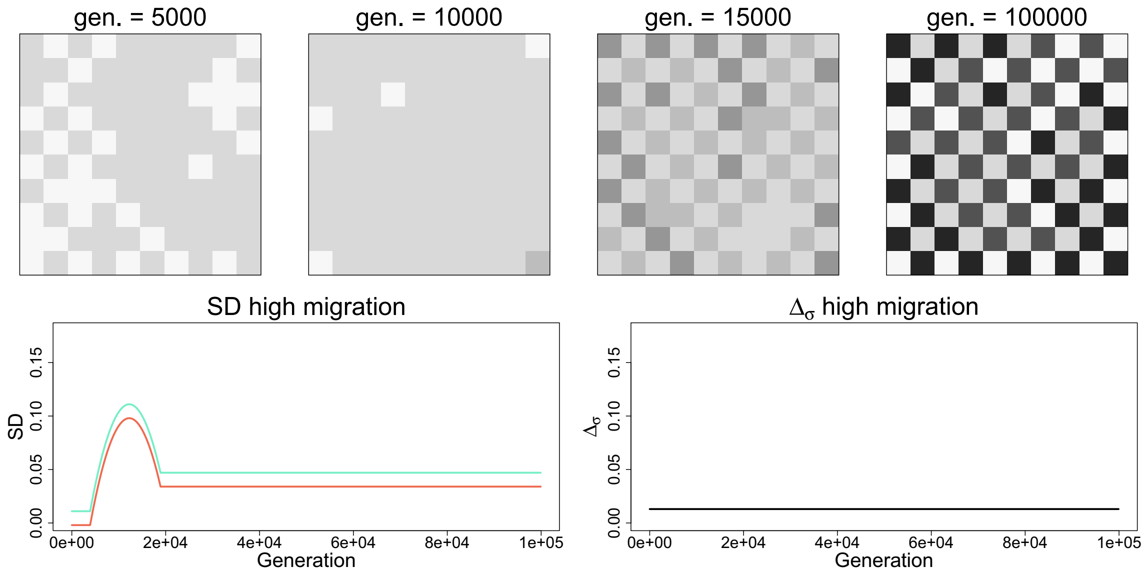
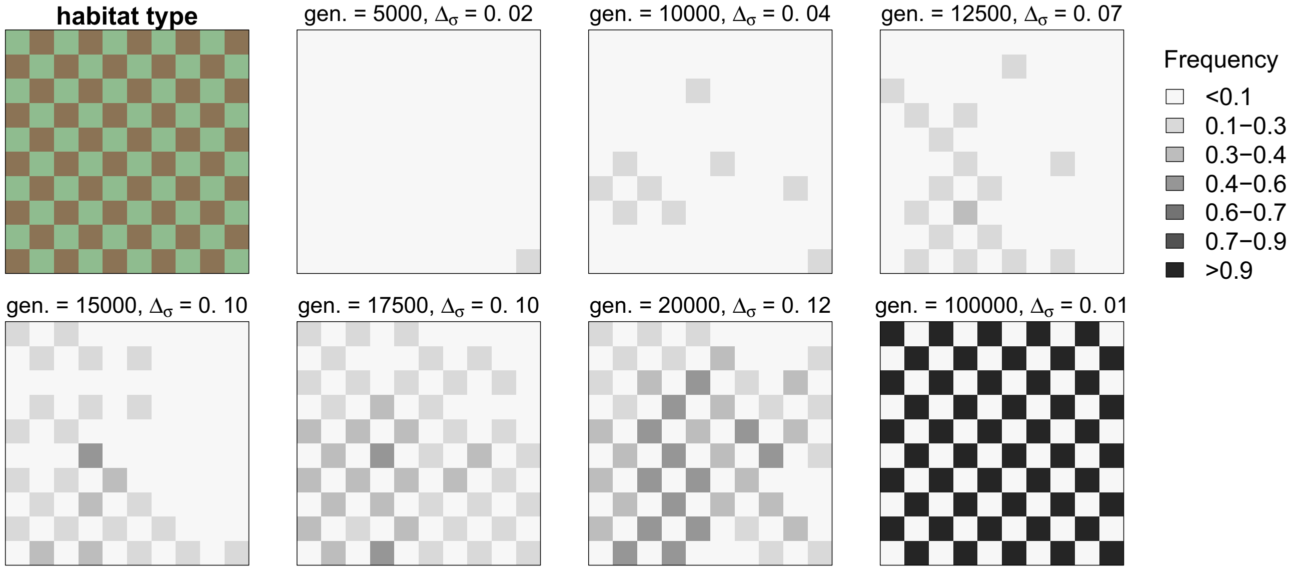


Fig. 2 This series of conceptual plots shows predicted patterns of adaptation with a patchwork patch configuration (habitat type) and low (**a**) or high (**b**) migration (connectivity) among demes. In the checkerboard plots, grey-scale is used to denote mean allele frequencies in each patch and 'gen.' denotes generation number. With low migration, derived alleles spread mostly across novel patch types and do so in a deme-by-deme manner, giving rise to an elevated standard deviation SD in mean derived allele frequencies across novel patch types (σ_{nov}) relative to ancestral patch types (σ_{anc}). This generates high values of $\Delta\sigma$. In contrast, with high gene flow, derived alleles spread across the entire meta-population before increasing in frequency in the novel patches across the entire system. During the period when derived alleles spread, the SD in mean derived alleles increases to a similar extent in novel and ancestral patches resulting in near zero values of $\Delta\sigma$

Results

Representative results are shown in Figs. 3, 4, 5, 6. Figures 3 and 4 show deme allele frequencies in specific generations, whereas Figs. 5 and 6 show summary metrics of deme-by-deme versus system-wide adaptation (compare these figures to expectations shown in Fig. 2). Demes exhibited higher overall levels of local adaptation when migration rates were low (contrast panels (a) and (b) in Figs. S7 and S8). As this result is expected from numerous past treatments

(a) low migration (m = 0.01)



(b) high migration (m = 0.1)

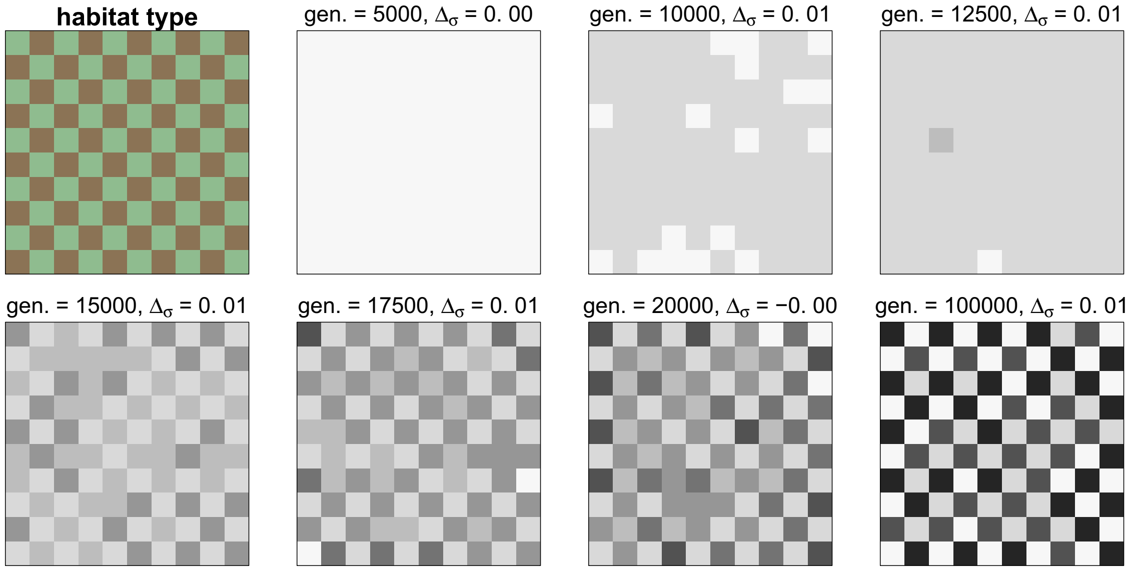
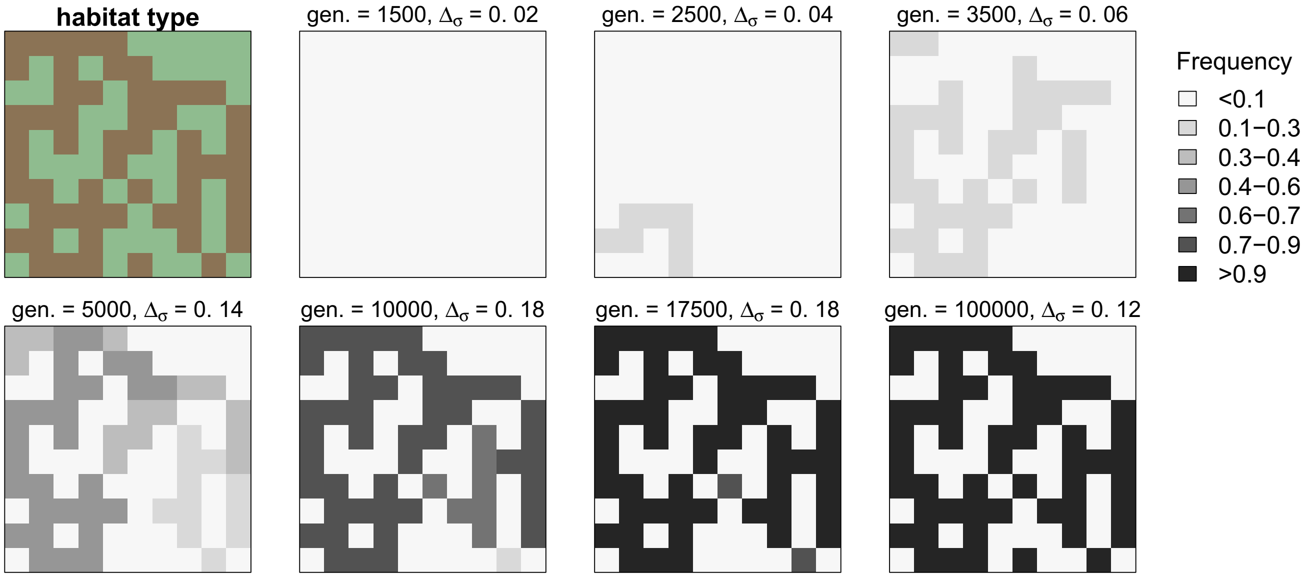


Fig. 3 This series of plots shows results from an example patchwork patch configuration (habitat type) where the different colors denote patch types, followed by mean deme derived allele frequencies (p_i) at seven time points from one representative simulation with $m=0.01$ (**a**) and one for $m=0.10$ (**b**). Colors in the top-left panel for each migration rates denote habitat type and grey-scale is used to denote mean allele frequencies. *Gen.* generation number. The difference in the standard deviation of the p_i between the novel and ancestral patch types ($\Delta\sigma$) is higher when adaptation occurs with low migration than with high migration. (Color figure online)

of selection-migration balance, we focus less below on this outcome, and more on the temporal and spatial dynamics of adaptation, and particularly on whether adaptation occurred in a deme-by-deme or system-wide manner.

With low migration ($m=0.01$) relative to selection ($s=0.04$) and either patchwork or random habitat type configurations, the standard deviation and mean degree of adaptation in the novel patch types rose together (Figs. 3, 4, 5a, 6a, S7a, c and S8a, c). This rise in σ_{nov} peaked around generation 20,940 for the patchwork configuration (mean max. σ_{nov} 0.14) and around generation 17,480 for the random configuration (mean max. σ_{nov} 0.18), and often persisted for many generations (i.e., > 10,000 generations). During that same period, μ_{anc} and σ_{anc} remained

(a) low migration (m = 0.01)



(b) high migration (m = 0.1)

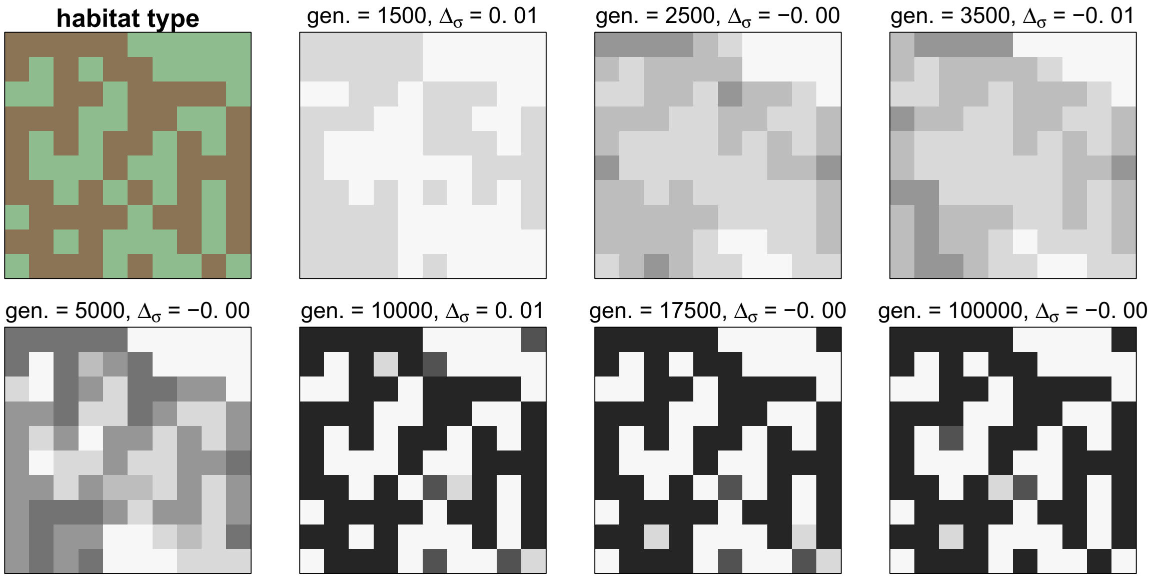


Fig. 4 This series of plots shows results from an example random patch configuration (habitat type) where the different colors denote patch types, followed by mean deme derived allele frequencies (p_i) at seven time points from one representative simulation with $m = 0.01$ and one for $m = 0.10$. Colors in the top-left panel for each migration rates denote habitat type and grey-scale is used to denote mean allele frequencies. *Gen.* generation number. The difference in the standard deviation of the p_i between the novel and ancestral patch types ($\Delta\sigma$) is higher when adaptation occurs with low migration than with high migration. (Color figure online)

low (despite a continual input of new mutations), as demes in ancestral patch types remained mostly or nearly fixed for ancestral alleles (e.g., μ_{anc} never rose above 0.028 or 0.018 in the patchwork and random configurations, respectively). The observed differences in σ_{nov} and σ_{anc} gave rise to positive values of $\Delta\sigma$, that is to deme-by-deme adaptation (Figs. 3, 4, 5c and 6c). Qualitatively similar results were obtained for weaker selection ($s = 0.02$; Figs. S2, S3, S4c and S5c).

In contrast, with high migration ($m = 0.10$), σ_{nov} increased for a briefer period during the adaptation process, and did so roughly to the same degree as σ_{anc} (Figs. 3, 4, 5b, 6b, 7b, d and S8b,d). For example, with the random habitat configuration, the mean (across replicates) maximum

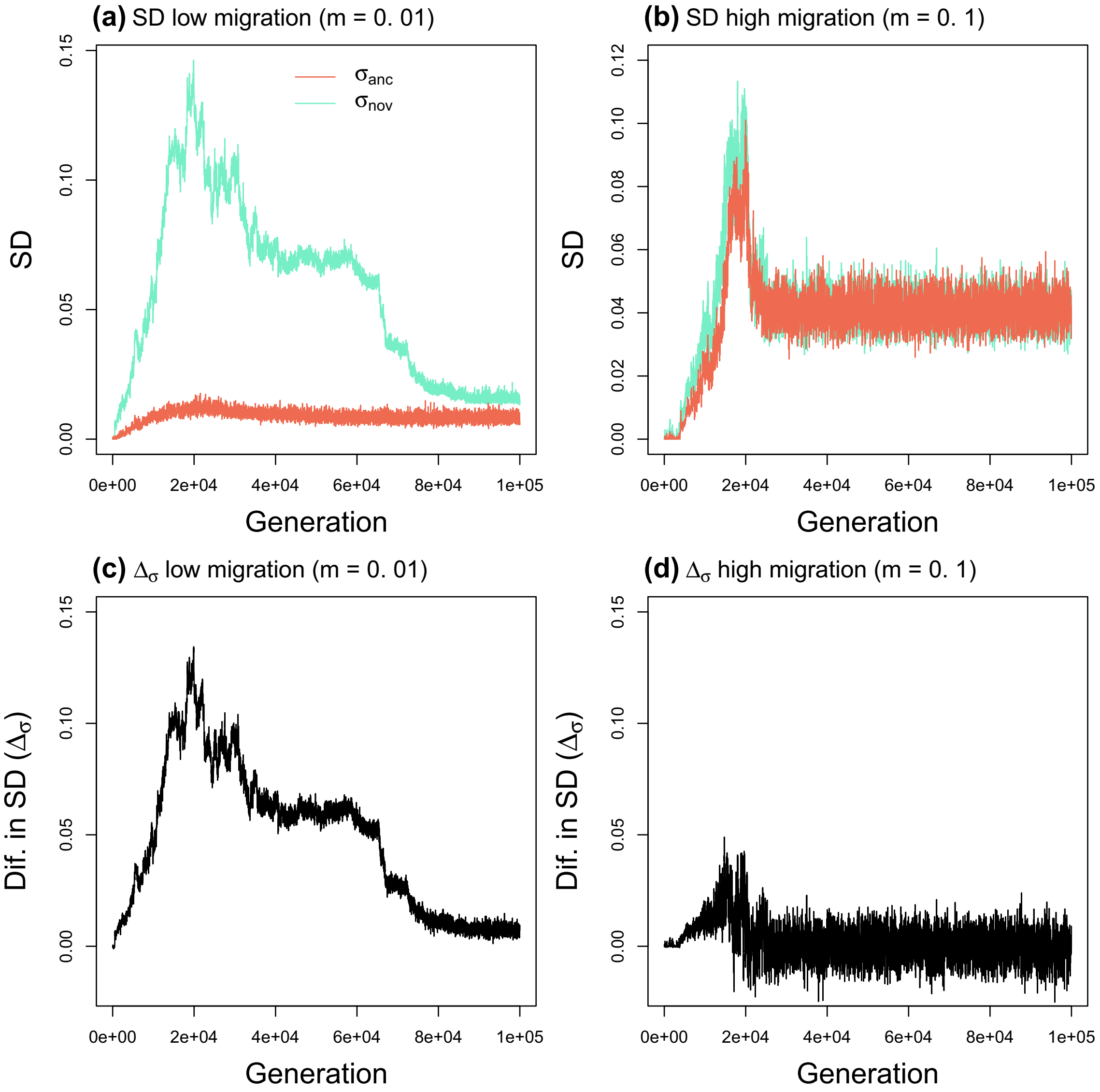


Fig. 5 These plots summarize patterns of adaptation from one pair of representative simulations with $s = 0.04$ and $L = 20$ for the patchwork patch configuration panel. Panels **a** and **b** show σ_{anc} (sd, ancestral), and σ_{nov} (sd, novel) over time for low **a** and high **b** migration. Panels **c** and **d** show the corresponding values of $\Delta\sigma = \sigma_{nov} - \sigma_{anc}$, for low **c** and high **d** migration

values of σ_{nov} and σ_{anc} were 0.13 (range 0.090–0.17) and 0.12 (range 0.069–0.28), respectively. And similarly with the patchwork habitat configuration, the mean maximum values were $\sigma_{nov} = 0.12$ (range 0.11–0.13) and $\sigma_{anc} = 0.10$ (range 0.099–0.11). In the case of high migration, μ_{nov} and μ_{anc} initially increased together. That is, the derived alleles increased in frequency in both the ancestral (where they were deleterious) and novel (where they were beneficial) patch types; maximum values of μ_{anc} across replicates ranged from 0.27 to 0.30 for the patchwork configuration (generations 12,970–30,140) and from 0.097 to 0.23 for the random configuration (generations 3210–7670). This moderately high frequency of derived alleles persisted until a threshold was reached, where the standard deviation parameters decreased and μ_{anc} dropped quickly, as derived alleles became rarer in the ancestral habitat patches (e.g., by generation 40,000, and even by generation 20,000 in most simulations, μ_{anc} was approximately 0.099 and 0.044 for the patchwork and random configurations, respectively). The initial concurrent spread of derived alleles across habitat patch types and similar values of σ_{nov} and σ_{anc} resulted in near-zero values of $\Delta\sigma$, suggesting system-wide adaptation (Figs. 3, 4, 5d and 6d). Qualitatively similar results were obtained for weaker selection (s 0.02; Figs. S2, S3, S4d and S5d). Thus, among-deme variation in adaptation was greater—i.e., adaptation occurred in a more ‘deme-by-deme’ than system-wide fashion—when migration was low than when it was high.

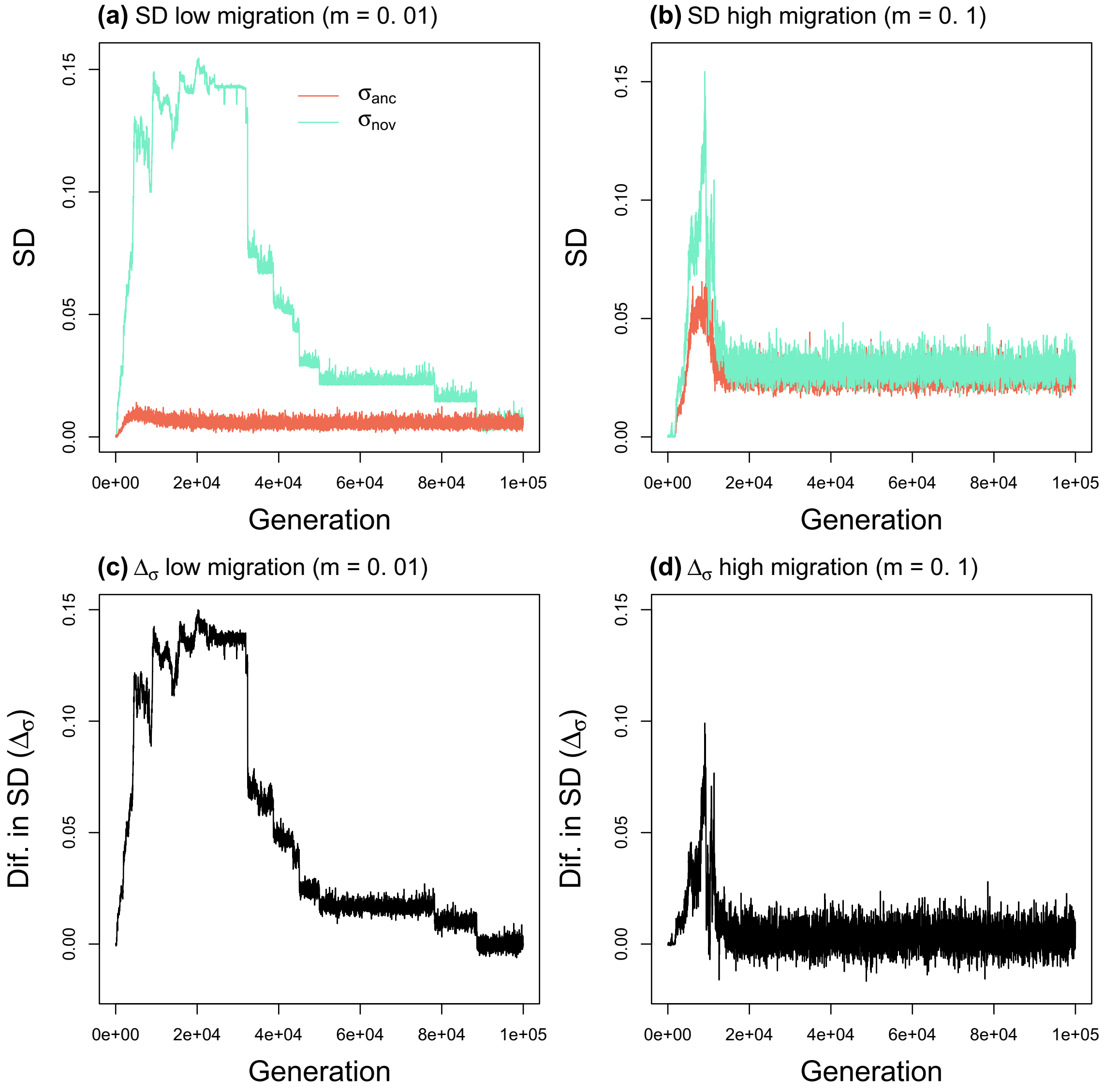


Fig. 6 These plots summarize patterns of adaptation from one pair of representative simulations with $s = 0.04$ and $L = 20$ for the random patch configuration panel. Panels **a** and **b** show σ_{anc} (sd, ancestral), and σ_{nov} (sd, novel) over time for low **a** and high **b** migration. Panels **c** and **d** show the corresponding values of $\Delta\sigma = \sigma_{nov} - \sigma_{anc}$, for low **c** and high **d** migration

Differences between patchwork (less connected) and random (more connected) simulations were also seen, but were less pronounced than those for migration rate variation. With high migration the initial spike in μ_{anc} was more pronounced in meta-populations with the patchwork configuration than the random configuration (Figs. S7b versus S8b; mean maximum values were 0.29 versus 0.15 for patchwork versus random). Likewise, the patchwork configuration caused a slightly greater increase in σ_{nov} in the low migration simulations than was seen with a random configuration of patch types (Figs. S7c versus S8c; mean maximum values were 0.18 versus 0.14 for patchwork versus random). In short, among-deme variation in adaptation for a given migration rate was greater in the random than in the patchwork configuration, but these differences were slight compared to differences caused by migration rate variation.

To more fully quantify the association between migration rate and the ‘deme-by-deme’ nature of adaptation, we next considered a gradient of migration rates where m = (0.001, 0.005, 0.01, 0.02, 0.03, 0.04, 0.05, 0.06, 0.07, 0.08, 0.09, 0.10). Consistent with the analyses with $m = 0.01$ or 0.1, we found that adaptation and differentiation occurred in a more ‘deme-by-deme’ manner when migration was low (particularly for $m \leq 0.01$), and did so to a greater extent for the random configuration (Fig. 7). Thus, our metric of ‘deme-by-deme’ differentiation (Δσ) declined with increasing migration rate.

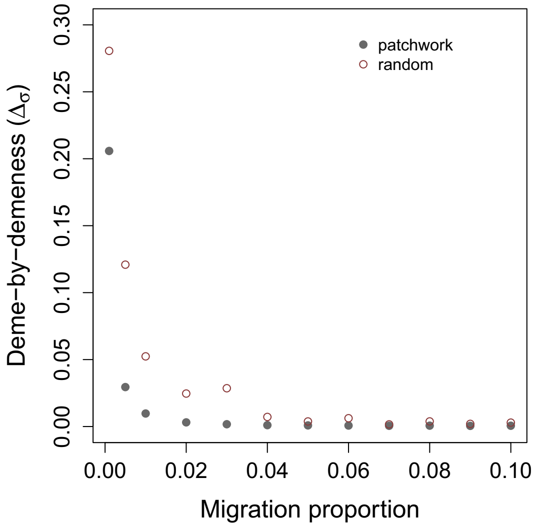


Fig. 7 A metric of how 'deme-by-deme' (versus system-wide) adaptation is ($\Delta\sigma$, y-axis) is shown as a function as the migration proportion (m, x-axis). Points denote median results across ten replicate simulations, with 500,000 (patchwork) or 100,000 (random) generations, $L=20$, and $s=0.04$

Discussion

We used computer simulations to study the dynamics of adaptation for sub-populations (i.e., demes) connected by migration. We found that among-deme variation in adaptation was greater—i.e., adaptation occurred in a more 'deme-by-deme' than system-wide fashion—when migration was low than when it was high. Thus, increased connectivity was associated with more sudden and system-wide changes and decreased connectivity associated with more gradual and localized differentiation. These results are necessarily based on a limited set of conditions and parameter combinations, and thus it is unclear whether or to what extent they can be generalized. With that said, our results are consistent with those from a range of other complex systems, such as ecosystems and financial systems (Scheffer et al. 2001, 2009, 2012, 2015; Scheffer 2009, 2010). We below discuss the role of migration in evolution, the implications of our results for conservation biology, and some key directions for future work.

The role of migration in evolution

Our results highlight variable roles for gene flow in evolution. Migration (i.e., gene flow) is often considered a homogenizing force that constrains adaptation (Hendry et al. 2001; Lenormand 2002, 2012; Hendry and Taylor 2004; Nosil and Crespi 2004; Hendry 2017). Indeed, we observed higher overall levels of local adaptation when migration rates were low (i.e., μ_{anc} close to 0 and μ_{nov} close to 1). However, we also found that migration can play a creative role in facilitating rapid system-wide transitions through a set of sub-populations. This creative role involves two inter-related processes.

First, with migration, new adaptive mutations do not have to be of local demic origin. They can occur anywhere across the landscape, including demes of the alternate habitat type where they are initially maladaptive, and be transported to a different deme by migration, where they become adaptive. Thus, local demes are not restricted to acquire new adaptive genetic variation from scratch in the same way they would be if there were small in size and isolated (in some sense, migration increases the effective population size). Consistent with this result, there is now substantial empirical evidence that gene flow among populations or species can serve as a source of adaptive mutations (e.g., Whitney et al. 2006; Song et al. 2011; Hufford et al. 2013; Huerta-Sanchez et al. 2014; Suarez-Gonzalez et al. 2018).

Second, migration means that the build up of standing variation can occur across the landscape as demes move together in unison to a threshold that allows rapid adaptation. Thus, the system as a whole rapidly goes through a transition, rather than seeing individual demes adapt independently. In the shifting-balance model, a combination of selection and drift play a role in adaptation, with a phase of disconnection between the two (adaptation arises locally but then spreads globally) (Wright 1982; Wade and Goodnight 1998; Coyne et al. 1997; Mallet 2010). Our model has some similarities, in terms of the role of migration in spreading adaptive gene combinations, but differs in many details such as (i) the lack of epistasis for fitness, (ii) it being primarily driven by selection, not drift, and (iii) gene flow, rather than its absence, being important in early phases of the process.

Implications for conservation biology

Our results have implications for conservation biology because the conservation of species is often planned in the context of habitat loss and fragmentation. Indeed, species on the planet increasingly live in patchy or fragmented habitats, due to deforestation and other human-induced changes (Butchart et al. 2010). Habitat fragmentation can have numerous ecological and evolutionary effects, such as reduced population size (and thus increased extinction risk) and local adaptation, respectively. These issues are reviewed in detail elsewhere (Hanski et al. 2013; Rybicki and Hanski 2013), and thus we focus here on two issues most pertinent to our results.

First, the negative ecological effects of habitat fragmentation may be more severe for species with limited dispersal ability, because they have greater difficulties dispersing between patches of remaining suitable habitats (Stamps et al. 2005; Fountain et al. 2016). A flip side of this issue is that species with low dispersal ability in fragmented habitats may evolve local adaptation, because homogenizing gene flow between habitat types is low (Blanquart et al. 2012). However, as discussed above, fragmentation can have negative effects on the geographic spread of adaptive mutations throughout a species range, and thus constrain adaptation. Our results, coupled with past work, thus show how there are several layers to the effects of fragmentation on ecological and evolutionary dynamics (e.g., Cushman 2006; Legrand et al. 2017). Adding local extinction and re-colonization events, which we did not consider here, would add even further complexity, and is a clear avenue for future research (see below for more detailed consideration).

Second, in addition to dispersal ability and migration rates, the spatial clustering of habitat types within a system (e.g., meta-population) can affect ecological and evolutionary dynamics. For example, the negative effects of fragmentation can sometimes be countered by aggregating habitat fragments into clusters rather than to place them randomly across the landscape (Rybicki and Hanski 2013), as this reduces gene flow between habitat types and can promote local adaptation. In turn, local adaptation might have positive demographic effects, increasing population size and thus reducing the risk of local extinction (Ronce and Kirkpatrick 2001; Lenormand 2002; Hanski et al. 2011; Farkas et al. 2013, 2016). Our results add a layer to this issue, by showing how the clustering of habitat types promotes more sudden and system-wide dynamics of local adaptation. Although these effects were modest compared to those of variation in migration rate, we note that we only examined a weak degree of clustering (that caused by a random rather than patchwork distribution). Thus, the effects of higher levels of clustering warrant further examination.

Extensions and future directions

We emphasize that our current results pertain to evolutionary dynamics, not ecological/demographic ones. In other words, local adaptation in our models did not affect population sizes/carrying capacities and our models thus differ from those with meta-population dynamics sensu stricto (i.e., hard selection), where adaptation affects population sizes and thus extinction-recolonization dynamics (Ronce and Kirkpatrick 2001; Lenormand 2002, 2012; Hanski and Saccheri 2006; Hanski and Mononen 2011; Hanski et al. 2011; Hanski 2011). A clear avenue for future work is to add ecological and demographic dynamics to the types of scenarios considered here.

Another consideration is habitat choice, which was random in our model. Although habitat choice can speed up local adaptation and speciation-with-gene flow (Bush 1969a, b, 1975), its effects on ecological and evolutionary dynamics can be nuanced and difficult to predict. For example, strong habitat fidelity might actually constrain the evolution of mate choice via reinforcement-like processes (Yukilevich and True 2006; Nosil and Yukilevich 2008). Additionally, phenotype-dependent habitat matching might have stronger effects on adaptation and speciation than habitat choice that is random with respect to phenotype (Bolnick et al. 2009; Edelaar and Bolnick 2012; Izen et al. 2016; Edelaar et al. 2017). Finally, the genetic basis of habitat choice, such as the numbers of loci involved (Gavrilets and Losos 2009) and whether based on a one- or two-allele mechanism (Felsenstein 1981; Kirkpatrick and Ravigné 2002; Ortíz-Barrientos and Noor 2005), might affect the dynamics observed. Thus, further work is required to clearly understand how habitat choice would affect the ‘deme-by-deme’ versus system-wide dynamics of adaptation observed here.

A final issue is the effects that various aspects of genetic architecture, such as epistasis, that were not part of our model, have on systems dynamics. In addition to epistasis, recombination rate variation warrants consideration in future work. There is accumulating evidence that structural features that reduce recombination, such as chromosomal inversions, can promote local adaptation and speciation (Noor et al. 2001; Rieseberg 2001; Feder et al. 2003, 2011; Kirkpatrick and Barton 2006; Hoffmann and Rieseberg 2008; Faria and Navarro 2010). How such features would influence the dynamics reported here warrants exploration.

Despite the need for such future work, we suspect that our core qualitative conclusions concerning connectivity are robust, given they are consistent with those observed for a wide range of complex systems. Increased connectivity among sets of sub-populations can promote sudden and system-wide adaptation (i.e., across an entire landscape or ‘set’ of demes) over more localized changes (i.e., within individual demes), with implications for conservation biology, adaptation, and evolution. The falling costs of genome sequencing should facilitate the empirical study of the population biological and genomic issues considered here.

Acknowledgements The work was funded by a grant from the H2020 European Research Council (NatHisGen R/129639) to PN, a Royal Society University Research Fellowship to PN, a Leverhulme Trust Early Career Fellowship to VSC, a National Science Foundation grant to JFL, a United States Department of Agriculture NIFA grant to JLF, a National Science Foundation Grant to SMF (DEB 1627483), and a National Science Foundation Grant to ZG (DEB 1638768). The support and resources from the Center for High Performance Computing at the University of Utah are gratefully acknowledged. We thank Rus A. R. Hoelzel and the organizers of the workshop on Conservation of Adaptive Potential and Functional Diversity that took place the 14–15th September in Durham, UK, as well as this special issue.

References

Barr KR, Kus BE, Preston KL, Howell S, Perkins E, Vandergast AG (2015) Habitat fragmentation in coastal southern California disrupts genetic connectivity in the cactus wren (*Campylorhynchus brunneicapillus*). Mol Ecol 24:2349–2363

Barton NH (1983) Multilocus clines. Evolution 37:454–471

Barton NH, de Cara MAR (2009) The evolution of strong reproductive isolation. Evolution 63:1171–1190

Barton NH, Hewitt GM (1985) Analysis of hybrid zones. Annu Rev Ecol Syst 16:113–148

Bierne N, Welch J, Loire E, Bonhomme F, David P (2011) The coupling hypothesis: why genome scans may fail to map local adaptation genes. Mol Ecol 20:2044–2072

Blanquart F, Gandon S, Nuismer SL (2012) The effects of migration and drift on local adaptation to a heterogeneous environment. J Evol Biol 25:1351–1363

Blanquart F, Kaltz O, Nuismer SL, Gandon S (2013) A practical guide to measuring local adaptation. Ecol Lett 16:1195–1205

Bolnick DI, Snowberg LK, Patenia C, Stutz WE, Ingram T, Lau OL (2009) Phenotypic-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. Evolution 63:2004–2016

Bush GL (1969a) Mating behavior, host specificity, and ecological significance of sibling species in frugivorous flies of genus Rhagoletis (Diptera-Tephritidae). Am Nat 103:669-&

Bush GL (1969b) Sympatric host race formation and speciation in frugivorous flies of genus Rhagoletis (Diptera, Tephritidae). Evolution 23:237–251

Bush GL (1975) Modes of animal speciation. Annu Rev Ecol Syst 6:339–364

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Morcillo MH, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vie JC, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Coulon A, Cosson JF, Angibault JM, Cargnelutti B, Galan M, Morellet N, Petit E, Aulagnier S, Hewison AJM (2004) Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual–based approach. Mol Ecol 13:2841–2850

Coyne JA, Barton NH, Turelli M (1997) Perspective: a critique of Sewall Wright's shifting balance theory of evolution. Evolution 51:643–671

Crespi BJ (2004) Vicious circles: positive feedback in major evolutionary and ecological transitions. Trends Ecol Evol 19:627–633

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biol Cons 128:231–240

Dixo M, Metzger JP, Morgante JS, Zamudio KR (2009) Habitat fragmentation reduces genetic diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest. Biol Cons 142:1560–1569

Edelaar P, Bolnick DI (2012) Non-random gene flow: an underappreciated force in evolution and ecology. Trends Ecol Evol 27:659–665

Edelaar P, Jovani R, Gomez-Mestre I (2017) Should I change or should I go? Phenotypic plasticity and matching habitat choice in the adaptation to environmental heterogeneity. Am Nat 190:506–520

Faria R, Navarro A (2010) Chromosomal speciation revisited: rearranging theory with pieces of evidence. Trends Ecol Evol 25:660–669

Farkas TE, Mononen T, Comeault AA, Hanski I, Nosil P (2013) Evolution of camouflage drives rapid ecological change in an insect community. Curr Biol 23:1835–1843

Farkas TE, Mononen T, Comeault AA, Nosil P (2016) Observational evidence that maladaptive gene flow reduces patch occupancy in a wild insect metapopulation. Evolution 70:2879–2888

Feder JL, Roethele FB, Filchak K, Niedbalski J, Romero-Severson J (2003) Evidence for inversion polymorphism related to sympatric host race formation in the apple maggot fly, *Rhagoletis pomonella*. Genetics 163:939–953

Feder JL, Geji R, Powell THQ, Nosil P (2011) Adaptive chromosomal divergence driven by mixed geographic mode of evolution. Evolution 65:2157–2170

Felsenstein J (1981) Skepticism towards Santa Rosalia, or why are there so few kinds of animals? Evolution 35:124–138

Flaxman SM, Wacholder AC, Feder JL, Nosil P (2014) Theoretical models of the influence of genomic architecture on the dynamics of speciation. Mol Ecol 23:4074–4088

Fountain T, Nieminen M, Sirén J, Wong SC, Lehtonen R, Hanski I (2016) Predictable allele frequency changes due to habitat fragmentation in the *Glanville fritillary* butterfly. Proc Natl Acad Sci 113:2678–2683

Gavrilets S, Losos JB (2009) Adaptive radiation: contrasting theory with data. Science 323:732–737

Hanski IA (2011) Eco-evolutionary spatial dynamics in the *Glanville fritillary* butterfly. Proc Natl Acad Sci USA 108:14397–14404

Hanski I, Mononen T (2011) Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. Ecol Lett 14:1025–1034

Hanski I, Saccheri I (2006) Molecular-level variation affects population growth in a butterfly metapopulation. PLoS Biol 4:719–726

Hanski I, Mononen T, Ovaskainen O (2011) Eco-evolutionary metapopulation dynamics and the spatial scale of adaptation. Am Nat 177:29–43

Hanski I, Zurita GA, Bellocq MI, Rybicki J (2013) Species-fragmented area relationship. Proc Natl Acad Sci USA 110:12715–12720

He HS, DeZonia BE, Mladenoff DJ (2000) An aggregation index (AI) to quantify spatial patterns of landscapes. Landscape Ecol 15:591–601

Hendry AP (2017) Eco-evolutionary dynamics. Princeton University Press, Princeton

Hendry AP, Taylor EB (2004) How much of the variation in adaptive divergence can be explained by gene flow? An evaluation using lake-stream stickleback pairs. Evolution 58:2319–2331

Hendry AP, Day T, Taylor EB (2001) Population mixing and the adaptive divergence of quantitative traits in discrete populations: a theoretical framework for empirical tests. Evolution 55:459–466

Hoffmann AA, Rieseberg LH (2008) Revisiting the impact of inversions in evolution: from population genetic markers to drivers of adaptive shifts and speciation? Annu Rev Ecol Evol Syst 39:21–42

Holyoak M (2000) Habitat patch arrangement and metapopulation persistence of predators and prey. Am Nat 156:378–389

Huerta-Sánchez E, Jin X, Bianba Z, Peter BM, Vinckenbosch N, Liang Y, Yi X, He M, Somel M, Ni P, Wang B (2014) Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. Nature 512:194

Hufford MB, Lubinksy P, Pyhäjärvi T, Devengenzo MT, Ellstrand NC, Ross-Ibarra J (2013) The genomic signature of crop-wild introgression in maize. PLoS Genet 9:e1003477

Izen R, Stuart YE, Jiang YX, Bolnick DI (2016) Coarse- and fine-grained phenotypic divergence among threespine stickleback from alternating lake and stream habitats. Evol Ecol Res 17:437–457

Kirkpatrick M, Barton N (2006) Chromosome inversions, local adaptation and speciation. Genetics 173:419–434

Kirkpatrick M, Ravigné V (2002) Speciation by natural and sexual selection: models and experiments. Am Nat 159:S22–S35

Legrand D, Cote J, Fronhofer EA, Holt RD, Ronce O, Schtickzelle N, Travis J, Clobert J (2017) Eco-evolutionary dynamics in fragmented landscapes. Ecography 40:9–25

Lehtonen J, Kokko H (2012) Positive feedback and alternative stable states in inbreeding, cooperation, sex roles and other evolutionary processes. Philos Trans R Soc B Biol Sci 367:211–221

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613

Lenormand T (2002) Gene flow and the limits to natural selection. Trends Ecol Evol 17:183–189

Lenormand T (2012) From local adaptation to speciation: specialization and reinforcement. Int J Ecol. https://doi.org/10.1155/2012/508458

Mallet J (2010) Shift happens! Shifting balance and the evolution of diversity in warning colour and mimicry. Ecol Entomol 35:90–104

Noor MAF, Grams KL, Bertucci LA, Reiland J (2001) Chromosomal inversions and the reproductive isolation of species. Proc Natl Acad Sci USA 98:12084–12088

Nosil P, Crespi BJ (2004) Does gene flow constrain adaptive divergence or vice versa? A test using ecomorphology and sexual isolation in *Timema cristinae* walking-sticks. Evolution 58:102–112

Nosil P, Yukilevich R (2008) Mechanisms of reinforcement in natural and simulated polymorphic populations. Biol J Lin Soc 95:305–319

Nosil P, Feder JL, Flaxman SM, Gompert Z (2017) Tipping points in the dynamics of speciation. Nat Ecol Evol 1:0001

Ortíz-Barrientos D, Noor MAF (2005) Evidence for a one-allele assortative mating locus. Science 310:1467–1467

Rasanen K, Hendry AP (2008) Disentangling interactions between adaptive divergence and gene flow when ecology drives diversification. Ecol Lett 11:624–636

Rieseberg LH (2001) Chromosomal rearrangements and speciation. Trends Ecol Evol 16:351–358

Ronce O, Kirkpatrick M (2001) When sources become sinks: migrational meltdown in heterogeneous habitats. Evolution 55:1520–1531

Rybicki J, Hanski I (2013) Speciesarea relationships and extinctions caused by habitat loss and fragmentation. Ecol Lett 16:27–38

Scheffer M (2009) Critical transitions in nature and society. Princeton University Press, Princeton

Scheffer M (2010) COMPLEX SYSTEMS foreseeing tipping points. Nature 467:411–412

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413:591–596

Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. Nature 461:53–59

Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, Dakos V, van de Koppel J, van de Leemput IA, Levin SA, van Nes EH, Pascual M, Vandermeer J (2012) Anticipating critical transitions. Science 338:344–348

Scheffer M, Carpenter SR, Dakos V, van Nes EH (2015) Generic indicators of ecological resilience: inferring the chance of a critical transition. Ann Rev Ecol Evol Syst 46:145–167

Schwander T, Vuilleumier S, Dubman J, Crespi BJ (2010) Positive feedback in the transition from sexual reproduction to parthenogenesis. Proc R Soc B Biol Sci 277:1435–1442

Servedio MR, Saetre GP (2003) Speciation as a positive feedback loop between postzygotic and prezygotic barriers to gene flow. Proc R Soc B Biol Sci 270:1473–1479

Song Y, Endepols S, Klemann N, Richter D, Matuschka FR, Shih CH, Nachman MW, Kohn MH (2011) Adaptive introgression of anticoagulant rodent poison resistance by hybridization between old world mice. Curr Biol 21:1296–1301

Stamps JA, Krishnan VV, Reid ML (2005) Search costs and habitat selection by dispersers. Ecology 86:510–518

Suarez-Gonzalez A, Hefer CA, Lexer C, Cronk QC, Douglas CJ (2018) Scale and direction of adaptive introgression between black cottonwood (*Populus trichocarpa*) and balsam poplar (*P. balsamifera*). Mol Ecol 27:1667–1680

Wade MJ, Goodnight CJ (1998) The theories of Fisher and Wright in the context of metapopulations: when nature does many small experiments. Evolution 52:1537–1553

Whitney KD, Randell RA, Rieseberg LH (2006) Adaptive introgression of herbivore resistance traits in the weedy sunflower *Helianthus annuus*. Am Nat 167:794–807

Wright S (1982) The shifting balance theory and macroevolution. Annu Rev Genet 16:1–19

Yukilevich R, True JR (2006) Divergent outcomes of reinforcement speciation: the relative importance of assortative mating and migration modification. Am Nat 167:638–654