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Research

Dispersal evolution in currents: spatial sorting promotes philopatry in upstream patches

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Substantial literature is devoted to understanding dispersal evolution, but we lack theory on how dispersal evolves when populations inhabit currents. Such theory is required for understanding connectivity in freshwater and marine environments; moreover, many animals, fungi and plants rely on wind-based dispersal, but the effects of currents on dispersal evolution in these organisms is unknown. We develop an individual-based model for evolution of dispersal probability along a linear environment with a unidirectional current. Even a slight current substantially reduces overall emigration probability compared to no current. Under stronger currents, emigration can be drastically reduced, especially in the upstream patches. When introducing rare long-distance dispersal that is not subject to the current, higher emigration probabilities evolve and the spatial variability in emigration propensity along the stream is reduced. Our results provide an alternative solution to the long debated 'drift paradox' concerning the loss of individuals from upstream populations due to advective forces. A combination of natural selection and spatial sorting generates and maintains downstream gradients in dispersal propensity, where individuals from upstream populations tend to be substantially more philopatric. This is likely to have major implications for ecological and genetic connectivity that will impact effective management strategies for populations inhabiting currents.

Keywords: biased dispersal, currents, dispersal, dispersal evolution, drift paradox, spatial sorting

Introduction

Understanding the role of currents, whether in air or water, is important in many ecological applications such as habitat restoration, predicting the spread of invasive species or species expanding their ranges into newly suitable climate space, and estimating connectivity loss due to anthropogenic impacts (Levine 2008). Many natural systems are characterised by currents, causing unidirectional or directionally-biased movement of organisms. Examples include wind- or waterborne seeds, freshwater organisms

inhabiting streams, rivers or estuaries (Pachepsky et al. 2005, Levine 2008, Jackiewicz et al. 2014, Zhou and Zhao 2018), marine plankton experiencing prevailing or residual currents (Gaines and Bertness 1992, Shanks and Eckert 2005, Gaylord and Gaines 2017), and marine fish moving in response to residual currents (Reid et al. 1997) or tides (Castonguay and Gilbert 1995). Often, these currents are used as the main vector for dispersal (Pollux et al. 2005), impacting abundance and distribution of species (Bertolo et al. 2012), including invasions (van Riel et al. 2011), genetic diversity and gene flow (Blasco-Costa et al. 2012, Paz-Vinas et al. 2015), levels of population spatial synchrony (Vindstad et al. 2019), and ecosystem-level processes such as community structure, connectivity and migration (Sedell et al. 1989, Castonguay and Gilbert 1995, Reid et al. 1997, Bilton et al. 2001, Levine 2008, Radinger and Wolter 2014, Tonkin et al. 2014).

The problems associated with dispersal in currents in terms of population persistence have been well-documented, focusing mainly on river and stream systems (Müller 1954, Waters 1972, Anholt 1995, Speirs and Gurney 2001, Pollux et al. 2005). Dispersal in these systems is considered to be more restricted than in marine or terrestrial systems as there are more well-defined corridors imposed by the landscape (Fagan 2002, Bohonak and Jenkins 2003, Pollux et al. 2005, Paz-Vinas et al. 2015), especially for fully aquatic species that do not have the option of aerial dispersal. This results in a long-standing ecological question dubbed the 'drift paradox' (Müller 1954) that asks how organisms faced with consistent downstream drift are able to persist even in the upper reaches of a stream. Several solutions to this paradox have been proposed over the decades, each attributing population persistence to a different aspect of population dynamics. These include equal upstream movement by reproducing adults ('colonisation cycle', Müller 1954, 1982, Hershey et al. 1993), excess production above carrying capacity ('production hypothesis', Dimond 1967, Waters 1972) and density dependence in reproduction eliminating the need for upstream movement (Anholt 1995). Humphries and Ruxton (2002) noted that, even with moderately high drift probabilities, large population sizes in combination with small upstream movements may slow extinction rates in upstream populations to millennia (Humphries and Ruxton 2002). One point of agreement is that without any mechanism to ensure even infrequent upstream movement of individuals, any slight advective forcing (i.e. involuntary downstream movement) would eventually move the population downstream like a moving wave and ultimately cause extinction of upstream patches. Speirs and Gurney (2001) speculated that a population could reduce individuals' advection probability by reducing the amount of time spent in the active current to the point that small amounts of random movement alone could be sufficient to retain upstream populations, but did not model this possibility explicitly (Speirs and Gurney 2001).

The evolution of dispersal strategies could provide a mechanism to enable species to survive in currents. However, to date we lack any spatially explicit evolutionary model to address the causes and consequences of dispersal evolution in currents. Here, we present theory on how one key component of dispersal, emigration propensity, evolves within a patchy population structured along a current. A substantial body of literature has provided an understanding of the different evolutionary drivers of emigration rate and the conditions under which we should expect selection for higher or lower emigration rates. In general, emigration is selected upwards when kin competition is higher, as a means to escape inbreeding and to bet hedge when environmental conditions vary in space and time (Hamilton and May 1977, Bengtsson 1978, Massol et al. 2011). Higher emigration rates also tend to evolve when population dynamics are less intrinsically stable, for example as can be generated by strongly over-compensatory density dependence (Holt and McPeek 1996, Duputié and Massol 2013). Acting against these selective pressures for higher emigration rates are costs of dispersal, including those paid physiologically if dispersive phenotypes are costlier than philopatric ones (e.g. additional or larger structures such as wings; Delattre et al. 2013), and costs paid during dispersal (e.g. mortality due to predation or desiccation) or on arrival (e.g. the destination is low quality habitat or is entirely unsuitable) (Bonte et al. 2012). Recently, spatial sorting has been recognised as another driver of spatial patterns in dispersal traits, relying on filtering of dispersal-enabling genotypes across space to promote evolution of new phenotypes at the expansion front (Shine et al. 2011, Phillips and Perkins 2019). However, while there is now a good understanding of what can lead to different emigration rates, the theory has not been extended to consider how predictions may change when the movement of emigrants is subject to a directional current.

We develop an individual-based model for dispersal evolution and start by asking how the strength of the current impacts the evolution of emigration rate along a homogeneous linear environment where dispersal is exclusively to nearest neighbour patches. We test the general prediction that lower emigration rates will evolve in the upstream patches under a process of spatial sorting, whereby only non-emigrating genotypes are retained there. We additionally predict that this effect will be strongest under the highest current strengths (i.e. lowest probability of upstream movement). We examine how this process depends upon key parameters including mutation rate and cost of dispersal, as well as boundary conditions. Subsequently, we add rare long-distance dispersal that may be by a different mechanism and thus not subject to the same current that affects most dispersers. For example, some juvenile invertebrates may be moved over long distances on the feet of ducks (Levine 2008) or some typically wind-dispersed seeds may be moved on people's shoes (Wichmann et al. 2009). We test the prediction that rare isotropic and longer distance dispersal will homogenise emigration rate throughout the stream by providing a source of higher-rate emigrants to upstream patches. We thus determine the degree to which rare isotropic and longer-distance dispersal is likely to impact the evolution of emigration rate in a current.

Methods and material

The model

We develop an individual-based model for the evolution of emigration probability. We adopt a discrete time, discrete space approach on a 1-dimensional lattice. We place populations of individuals into patches arranged in a linear string, and only allow dispersal movement left (upstream) or right (downstream) by one patch (i.e. nearest-neighbour dispersal; Fig. 1). We incorporate the possibility of asymmetric movement probabilities, governed by current strength ρ, which we parameterise as a proportion of emigrating individuals that move downstream. When no current is present, (ρ = 0.5) and movement in either direction occurs with equal probability. Increasing ρ simulates an increased current strength as a lower proportion of individuals can move upstream against the current. At ρ = 1, 100% of emigrating individuals will move downstream. Apart from affecting the probability with which dispersing individuals move up or down from their natal patch, current strength has no direct effect on emigration rate or dispersal distance, i.e. emigration rate is not automatically higher at high currents, and individuals never move further than one patch.

We model a species with asexual reproduction and non-overlapping generations. In each patch, we represent the local population dynamics using an individual-based formulation of Hassell and Comins (1978) (Hassell and Comins 1978, Travis and Dytham 1999, Hovestadt et al. 2001, Travis et al. 2009, Bocedi et al. 2012). Each individual, at time t, gives birth to a number of offspring drawn from a Poisson distribution with a mean M, given by the following expression:

$$M = \frac{\lambda}{\left(1 + aN\right)^b} \tag{1}$$

where a is a constant given by:

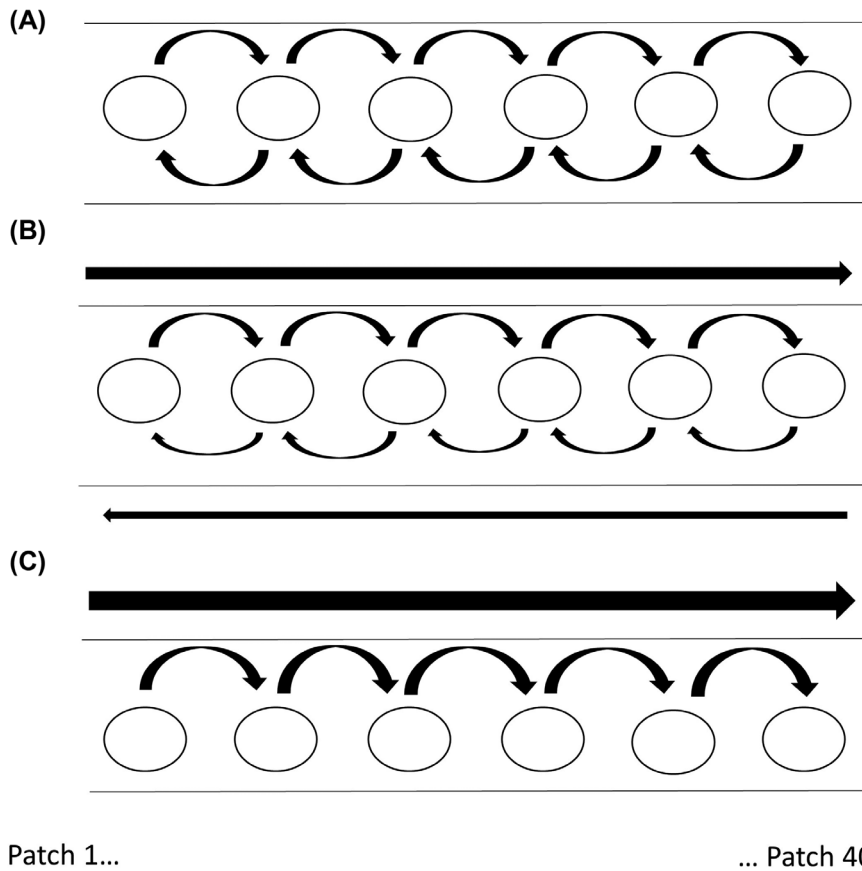$$a = \frac{\lambda^{\frac{1}{b}} - 1}{K} \tag{2}$$

Figure 1. Schematic of the modelled environment incorporating a simple current. A linear landscape of patches, with only nearest-neighbour dispersal possible, under varying current strengths. The proportion of dispersing individuals moving downstream is (A) 0.5, that is equal to the proportion moving upstream (i.e. no current and random movement in both directions); (B) 0.7, 70% of dispersers move downstream and 30% upstream; (C) 1, all dispersing individuals move downstream. The relative thicknesses of the arrows indicate directional movement.

Patch 1...   ... Patch 40

Table 1. Parameter values for all experiments. The table specifies only those values that are varied within or between experiments. In all simulations, population growth rate λ = 2 and patch equilibrium density K = 50. LDD = long-distance dispersal.

Parameters	Baseline	Experiment 1: mutation probability	Experiment 2: dispersal cost	Experiment 3: LDD probability
Mutation probability, μ	0.01	0.001, 0.01, 0.02, 0.03	0.01	0.01
Dispersal cost, c	0.01	0.01	0.002–0.02	0.01
Long distance dispersal probability, ω	0	0	0	0.002–0.02 (interval 0.002)
Current strengths, ρ (proportion of individuals moving downstream)	0.5–1 (interval 0.1)	0.5–1	0.5–1	0.5–1

In Eq. 1 and 2, λ is the intrinsic rate of population increase, a relates to patch quality through K which represents the local equilibrium density. The parameter b represents the nature of density-dependent competition. $b = 1$ indicates contest competition (compensatory population dynamics); as b increases, it represents increasingly scramble competition (over-compensatory population dynamics). We assume $b = 1$. We tested different values of K and λ and observed an overall decrease in mean emigration probability with increasing K due to the reduced kin competition and demographic stochasticity (Travis and Dytham 1998, Cadet et al. 2003) (Supplementary material Appendix 1 Fig. A1). However, the general trends were unaffected and population sizes in general did not vary along the gradient (Supplementary material Appendix 1 Fig. A8). Therefore, all experiments presented here were run with λ = 2 and $K = 50$ (Table 1).

Individuals disperse after birth with a density independent emigration probability given by their genotype d. d is determined by a single haploid locus with continuous alleles bounded between 0.0 and 1.0. Individuals inherit d from their parent with a small probability, μ, of mutation. When a mutation occurs, a value drawn from a continuous uniform distribution between −0.2 and 0.2 is added to d. When an individual emigrates, current strength determines the probability for it to move downstream. For example, with ρ = 0.6, an emigrant will move downstream with probability 0.6 and upstream with probability 0.4.

An emigrant successfully recruits into a neighbouring patch with probability $1 − c$, where c represents the cost of dispersal, in terms of mortality probability. In the main results presented here, we assume a closed system with reflective boundaries, so individuals that are born in either the most upstream or most downstream patch and attempt to move upstream or downstream, respectively, simply recruit in their natal patch. However, for comparison, we also generate results for an open system (absorbing boundaries) in which those individuals emigrating beyond the system limits are lost, effectively suffering 100% mortality, and for a mixed system where the upstream boundary is reflective and downstream is absorbing (Speirs and Gurney 2001) (Supplementary material Appendix 1 Fig. A3).

In one set of simulations, we add rare long-distance dispersal events (LDD), a process that is likely to be important for some species living in a current. Parameter ω specifies the proportion of individuals that exhibit LDD, characterised by dispersing from their natal patch to any of the other patches within the landscape with equal likelihood. In these simulations we allow a small proportion (ω = 0.002–0.02, Table 1) of individuals to exhibit LDD. Long distance dispersal is equally likely to occur in individuals, regardless of whether they would otherwise have been philopatric or emigrated using the standard nearest-neighbour movement rule.

Simulation experiments

In our first experiment, we investigate how the current strength ρ influences the evolution of emigration probability d for a baseline set of parameter values (Table 1). We run simulations varying ρ from 0.5 to 1.0 in increments of 0.1. In further experiments, and in order to investigate the model's sensitivity to key parameters, we vary individual parameters, while keeping the rest at the baseline values (Table 1). We specifically ask how the evolution of emigration probability depends on mutation probability, dispersal cost and probability of long-distance dispersal. In all cases, we perform 100 replicates for each combination of parameter values. Simulations were run until mean emigration probability along the linear environment reached a quasi-equilibrium. This corresponded to 1000 generations in all but the simulations with μ = 0.001 which required 20 000 generations to reach quasi-equilibrium. Each simulation was initialised by placing 30 individuals in each patch. All individuals were initialised with the same genotype $d = 0.1$. Varying initial emigration propensity did not affect the results (Supplementary material Appendix 1 Fig. A2). We ran simulations with initial emigration propensity chosen at random from a variety of ranges (i.e. 0.1–0.5, 0.1–0.9, 0–1) and found that this had little effect on resulting trends beyond decreasing the difference between mean emigration rates of higher current strengths ever so slightly. The code for the model is available in a GitHub repository <https://github.com/rebekkaallgayer/Dispersal_Evolution_in_Currents>.

Results

When dispersal evolves within a current, emigration is substantially reduced compared to when movements occur symmetrically (Fig. 2). Under no current (ρ = 0.5), mean emigration probability evolved to 0.44 at equilibrium. The introduction of a current (ρ > 0.5), however, increasingly reduces the mean emigration probability as current strength
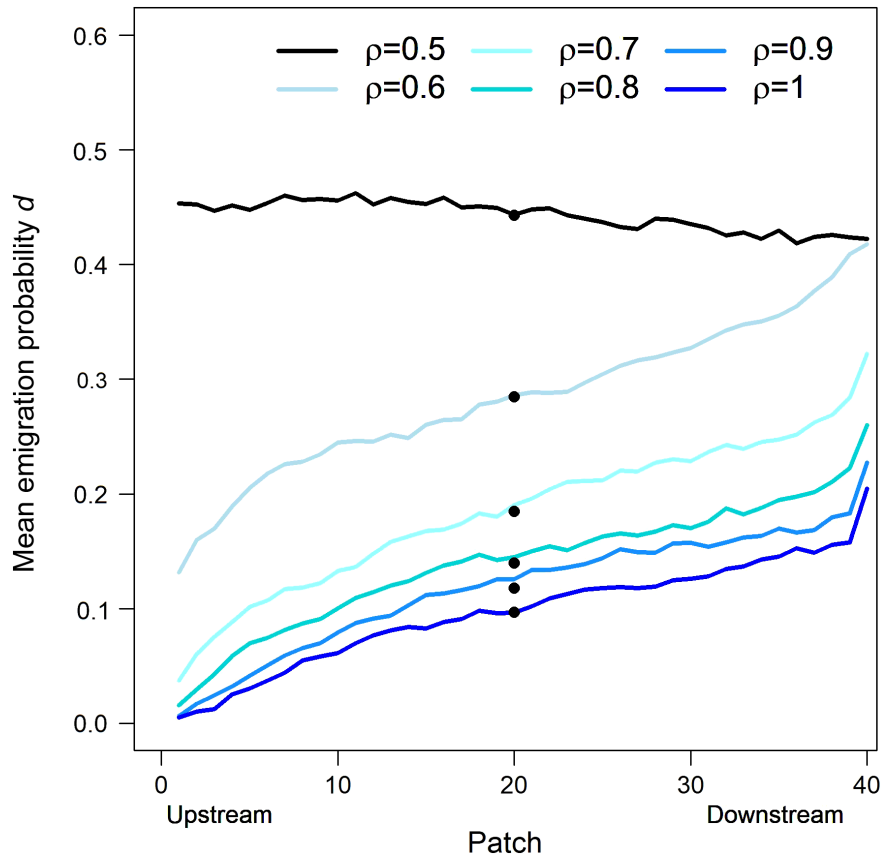
Figure 2. Substantially reduced emigration probabilities evolve when there is a current. Emigration probabilities are structured along the upstream–downstream gradient with much lower values upstream. Mean emigration probability (*d*) averaged through the whole stream under each current strength (ρ) is illustrated by solid black points. Results are reported at the end of 1000 generations. Parameters: dispersal cost $c=0.01$, long distance dispersal probability $\omega=0$, mutation probability $\mu=0.01$, reflecting boundaries. Results are presented as the mean from 100 replications; standard errors (SE) of the mean never exceeded 0.02 (apart from when $\rho=0.5$ where $SE=0.041$) and are thus not plotted. The steep increase in mean emigration probability in patch 40 results from reflective boundary conditions causing more dispersive genotypes to accumulate in the last patch.

increases. The steepest changes in emigration probabilities occur at intermediate currents strengths ($\rho=0.6$–0.7).

Furthermore, in the presence of a current strong spatial structure emerges in the distribution of emigration probabilities along the stream. Upstream patches are consistently populated by individuals with lower emigration probability than downstream patches, with near-zero mean values for emigration found in upstream patches when $\rho > 0.8$. Mean emigration probability increases along the linear environment, creating a positive downstream gradient under all current strengths. These results do not depend on boundary conditions (Supplementary material Appendix 1 Fig. A3).

The resulting population genotypic variance in emigration probability depends on the location of a patch within the stream and on the current strength. In the presence of a current, upstream patches always exhibit low genetic variance with mean genotype close to 0 (Fig. 3). Moving downstream, the genetic variance increases alongside the increase in mean emigration probability and the decrease in the proportion of individuals with zero emigration probability. Stronger currents lead to less population genotypic variance

being maintained, especially in the most upstream patch. Regardless of location in the stream, there is always a notable proportion of philopatric individuals, showing that despite downstream patches continuously receiving more dispersive genotypes, there is selection for maintaining philopatric genotypes across the stream. Further, the proportion of fully philopatric individuals in the upstream patches increases with increasing current strength, being almost 1 when $\rho > 0.8$ (Fig. 3 and Supplementary material Appendix 1 Fig. A5). Patterns of downstream patches vary slightly with boundary conditions (Supplementary material Appendix 1 Fig. A4), with absorbing boundaries leading to a higher proportion of philopatric individuals downstream, as the more dispersive genotypes progressively move out of the system.

Effect of varying mutation probability and dispersal cost

As the mutation probability μ increases, mean emigration probability increases throughout the stream (Fig. 4). However, changing the mutation probability does not change
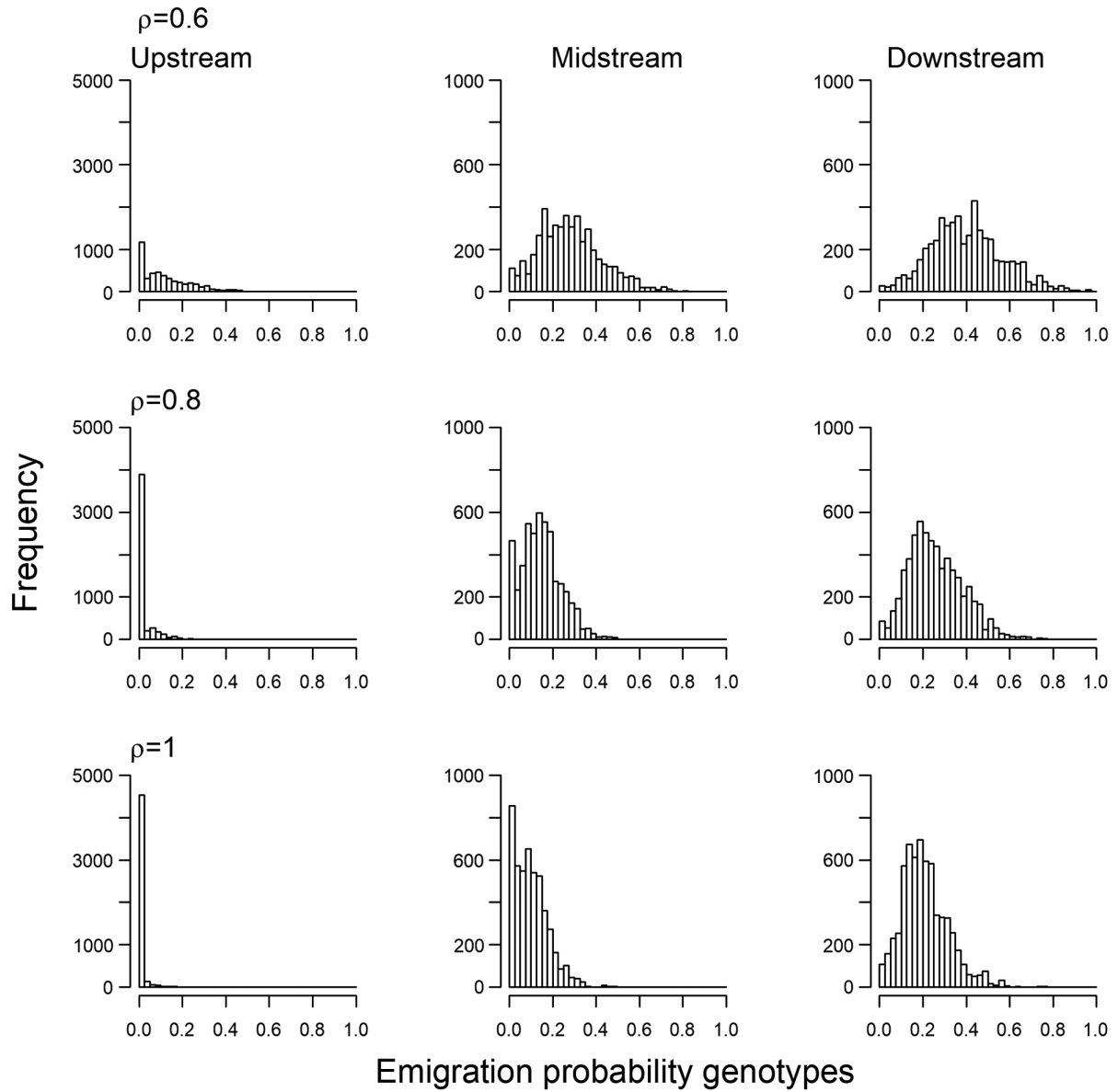
Figure 3. Increasing current strength (ρ) reduces the range of genotypic variation in all patches, while still maintaining the positive downstream gradient in emigration probability. Upstream patches increasingly lose genotypic variation, with most genotypes being 0 under all current strengths. Results presented are for populations after 1000 generations using baseline parameter values, pooled across 100 replicates.

the positive downstream gradient in emigration probabilities resulting under the baseline parameterisation ($\mu = 0.01$). Though overall mean emigration probability is greatly reduced at $\mu = 0.001$, downstream patches still have higher emigration propensities than upstream patches, even if the steepness of this gradient is shallower. The greatest effects of varying the mutation probability are seen downstream, while upstream patches – especially patch 0 – evolve to very similar low emigration probabilities when a current is present regardless of the rate of supply of novel mutations. We also tested the effect of mutation rate when initial emigration rate was chosen at random, allowing for individual variability

in starting conditions, but found that it had no significant effect under most circumstances. The only exception was when mutation rate was 0.001, where varying the initial conditions did alleviate the negative effect of the low mutation rate slightly, though as current strength increased, this effect reduced.

In the absence of a current ($\rho = 0.5$), increasing the dispersal cost substantially reduces the evolved mean emigration probability. However, the effect of dispersal cost gradually disappears with increasing current strength, until there is almost no effect to be observed when $\rho = 0.9$ or 1 (Fig. 4). With all levels of dispersal cost and current strength above
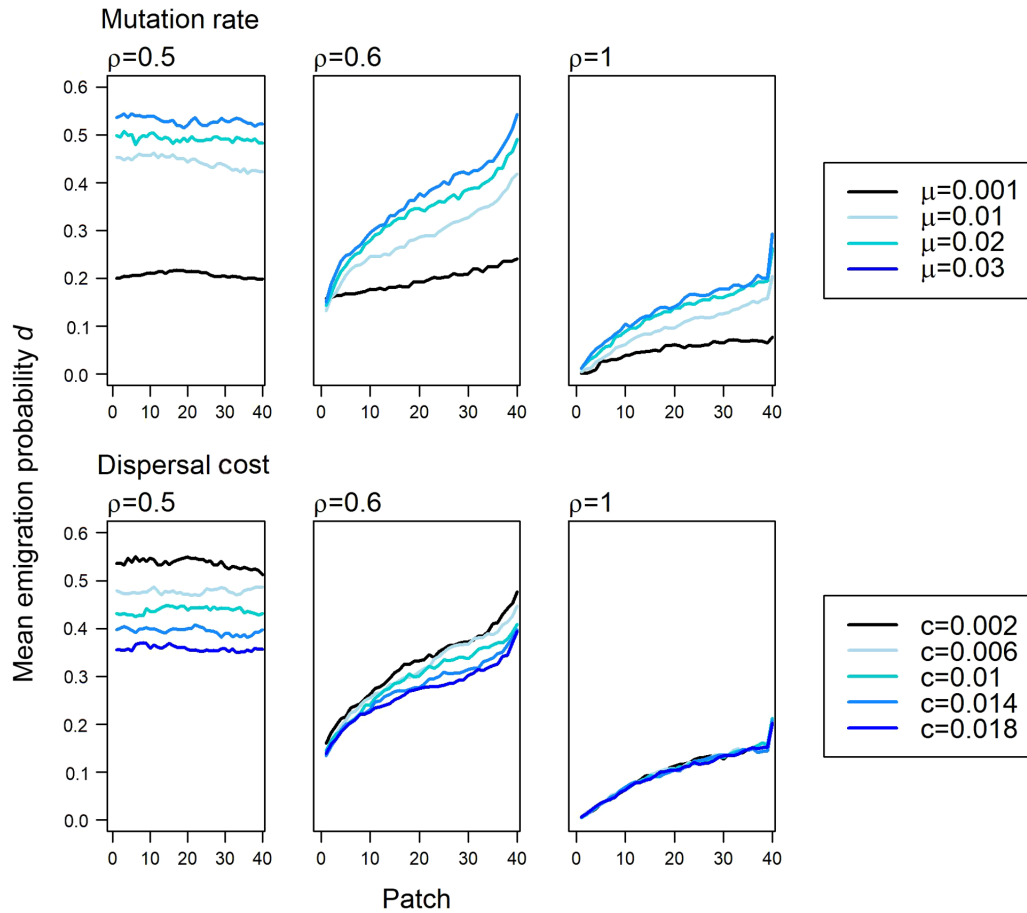
Figure 4. Mean emigration probability (*d*) evolved along the linear environment under different mutation probabilities (μ) and dispersal costs (*c*). Higher mutation probabilities lead to similar emigration probabilities evolving upstream, but higher probabilities evolving downstream. The difference in emigration probability between mutation probabilities decreases as current strength increases. At high current values (ρ), dispersal costs have little to no effect on mean emigration probabilities anywhere along the landscape. Results are reported at the end of 1000 generations (except in the case of μ = 0.001, where 20 000 generations were needed) and are means of 100 replicates. Initial emigration probability *d* = 0.1, long distance dispersal probability ω = 0. The steep increase in mean emigration probability in patch 40 results from reflective boundary conditions causing more dispersive genotypes to accumulate in the last patch.

ρ = 0.5, the downstream gradient in emigration probability observed in the baseline experiment remains.

The effect of rare long-distance dispersal

Introducing rare LDD increases the overall level of emigration probability throughout the stream system, and especially in midstream patches (Fig. 5). Moreover, increasing the LDD probability ω increases the spatial gradient in emigration probability in upstream patches (~patches 0–10), and reduced the spatial gradient in downstream patches (~patches 10–40). For more detail on the patch-by-patch response to increased LDD probabilities that produce these spatial patterns, see Supplementary material Appendix 1 Fig. A6.

Incorporation of any long-distance dispersal increases the genotypic variation in upstream patches under all current strengths, ρ > 0.5 (Supplementary material Appendix 1 Fig. A7). Otherwise, the spatial pattern of increasing genotypic variance when moving downstream (Fig. 3) is maintained.

Discussion

While the effects of currents on dispersal have been investigated for decades (Müller 1954, Waters 1972, Anholt 1995, Speirs and Gurney 2001, Levine 2008), the topic remains largely unexplored from an evolutionary perspective. Although there have been several empirical studies demonstrating that organisms disperse more readily when exposed to stronger currents (Müller 1982, Henry et al. 2016) and to changes in benthic density (Elliott 2002, Kennedy et al. 2014), these have typically not investigated genetic effects. We have investigated how a key component of dispersal, emigration rate, evolves within a 1-dimensional array of homogenous patches subject to various strengths of currents. River systems, although they can be highly dendritic and complex, can be well approximated in their essential structure as a linear model (Speirs and Gurney 2001, Pollux et al. 2005, Levine 2008, Blasco-Costa et al. 2012) with patches representing 'stepping stones'. Our results show a striking effect of
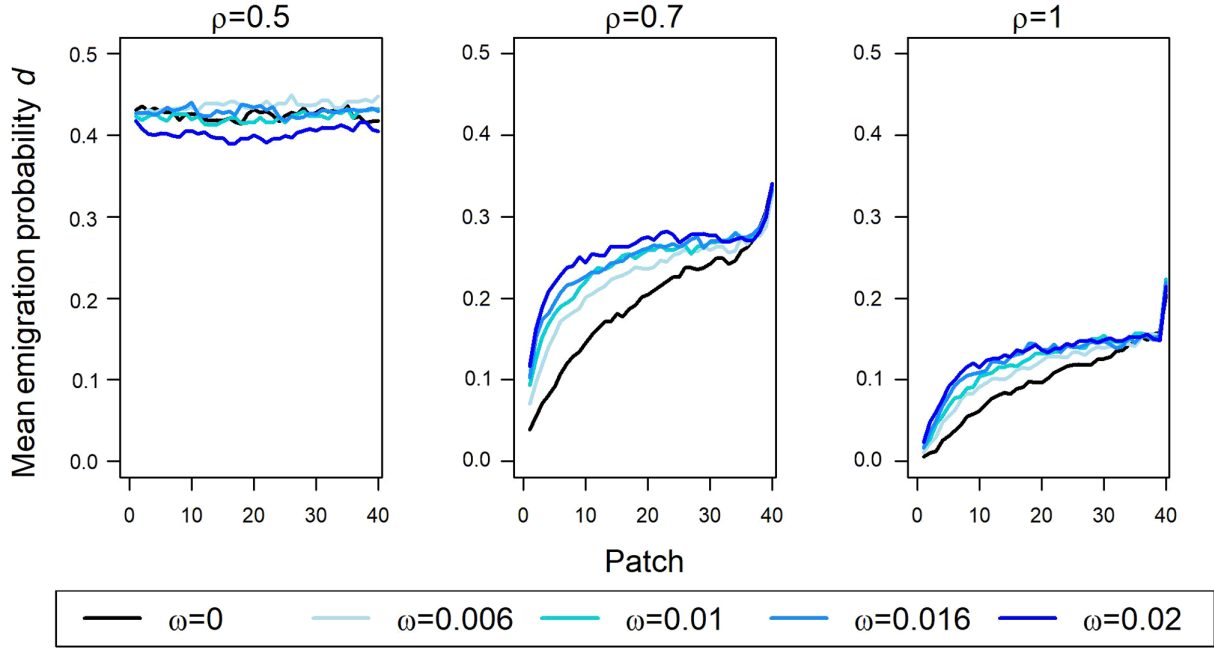
Figure 5. Increased rare long-distance dispersal (LDD) probability ω substantially modifies the spatial patterns of mean emigration probability along the linear environment under varying current strengths ρ. Values are mean emigration probabilities of 100 replicates, measured after 1000 generations. Mutation rate μ = 0.01, dispersal costs c = 0.01. The steep increase in mean emigration probability in patch 40 results from reflective boundary conditions causing more dispersive genotypes to accumulate in the last patch.

currents on dispersal evolution that can be strong relative to several key drivers of dispersal.

It is helpful to consider the following thought experiment. Imagine a passively dispersing organism subject to current strength ρ = 1, such that all dispersing individuals move downstream. One would expect a domino-effect of patches evolving complete philopatry (emigration probability = 0), as advective forcing would select against dispersal. This is expected because 1) more dispersive genotypes are progressively removed from the patch, and 2) there is no further influx of dispersive genotypes due to the strength of the current. However, while we observe a substantial decrease in mean emigration rate in the system, regardless of current strength (Fig. 2), this cascade effect does not occur. Instead, our model shows the emergence of a positive downstream gradient in emigration probability, where even the most upstream patch maintains a small degree of genetic variation for dispersal due to recurrent mutations. The persistence of upstream populations and maintenance of genetic variation in the whole linear landscape, even under external advective forces selecting against dispersal, indicates the importance of including evolution in explanations of the drift paradox (Hastings 1983, Lam et al. 2015, Zhou and Zhao 2018).

The positive downstream gradient in emigration probability is mirrored by a positive downstream gradient in genotypic variation (Fig. 3). This is consistent with previous studies showing that asymmetric movement in linear systems suppress the maintenance of genetic variation of upstream populations in comparison to more complex, dendritic systems (Morrissey and De Kerckhove 2009, Blasco-Costa et al.

2012, Paz-Vinas et al. 2015). Additionally, the higher the genotypic value for dispersal and the strength of the current, the further downstream the genotype is transported. The combination of mutational input and current increases the proportion of genotypes for higher emigration probabilities in downstream populations, diluting the effect of local selection favouring philopatric genotypes. This is supported by two observations. First, the stronger the current (i.e. the higher the proportion of dispersers moving downstream) the lower the overall emigration probability along the system, as mutations that progressively increase emigration probability do not have the time to accumulate. Second, the lower the mutation probability, the lower the overall emigration probability, as selection against dispersal is more effective with lower mutational input. This process of progressively increasing emigration probability downstream can be seen as spatial sorting (Shine et al. 2011, Phillips and Perkins 2019) for more philopatric individuals: in upstream patches, there is sorting for the more philopatric phenotypes, as the more dispersive phenotypes are effectively washed downstream. The strength of this spatial sorting increases with stronger currents as a higher proportion of emigrants are swept downstream.

The introduction of rare long-distance dispersal (LDD) provides a mechanism to redistribute genetic variation along the linear system and has significant effects on the distribution of dispersal genotypes in the upstream patches. This is highly relevant to an extraordinary range of stream-dwelling species with life-stages that can be dispersed by more mobile species (Bilton et al. 2001). Previous work has shown that the addition of rare long-distance dispersal events affects

community structure and diversity through connectivity of isolated patches (Muñoz et al. 2004). We implemented LDD in our model as a probability of being randomly transported to any patch in the system, regardless of location. This simulates, for example, transportation by an animal vector such as waterfowl (Levine 2008) or exceptional storm surges (Goodrich et al. 1989) and flooding events (Epifanio et al. 1988). LDD increased mean emigration probabilities overall, and mitigated the effect of current, especially in midstream patches, making the positive downstream gradient shallower (Fig. 5). Mid- and downstream patches experienced a cumulative effect of LDD and advection, receiving genotypes both from upstream patches as well as rare LDD from anywhere in the stream, which overall flattened the downstream gradient in emigration probabilities. Genetic variation clearly increased in upstream patches compared to no LDD, because of the greater input of genotypic values (Supplementary material Appendix 1 Fig. A7). We found that even a 1% chance of long-distance dispersal that is not subject to the prevailing current can dramatically change the genetic structure and connectivity of communities in a system characterised by currents.

Interestingly, the importance of the cost of dispersal (Bonte et al. 2012) in driving evolution of lower emigration probability depended on the strength of the current. A relatively high dispersal cost would reduce emigration probability in the absence of currents. However, this effect is completely swamped by increasing current strengths, where spatial sorting processes are more important drivers of dispersal evolution than is the survival cost. Ultimately, the balance between mutational inputs, current strengths and selective pressures such as the cost of dispersal, determines the evolved strategy along a linear system affected by advective forces.

We have investigated the effects of currents on the evolution of emigration propensity under the simplest of circumstances. Many further extensions of this work are possible, each adding a layer of complexity and realism. Application of our model on more complex landscapes, or more highly dimensional habitats such as are experienced by terrestrial, wind-dispersed organisms (2D) or marine species (3D), would provide valuable insight into the interaction of the effects of currents and system complexity on dispersal strategies, genetic variability (Morrissey and De Kerckhove 2009, Paz-Vinas et al. 2015) and community structure (Fagan 2002, Tonkin et al. 2014). Running dispersal evolution models within suites of simulated artificial river networks (Carraro et al. 2020) would provide an effective means for generating predictions on how different river characteristics are likely to exert different selective forces. Introducing temporal variability in current strength would allow us to investigate the resilience of populations to occasional disturbances (Bonte et al. 2012, Travis et al. 2012) such as storm surges, flooding events or local patch extinction due to pollution events. Environmental heterogeneity and resource gradients are very common in habitats under the influence of currents, and it would be important to understand the effect that current strength has on the ability of an individual to track these co-occurring gradients (Hershey et al. 1993, Lou and Lutscher 2013, Lam et al. 2015, Zhou and Zhao 2018). This would include differences in velocity, both along the stream as well as in different depth strata (Speirs and Gurney 2001), temperature, resource availability and habitat quality (Bonte et al. 2012, Travis et al. 2012).

Additionally, even though dispersal is composed of three stages – emigration, transfer and settlement (Travis et al. 2012) – in this study we have only allowed emigration probability to evolve. The evolution of the other stages of dispersal in the presence of currents is currently completely unexplored. For example, for active dispersers, the propensity to swim against a current could be under strong selective pressure in an environment characterised by advective forces.

This work has revealed a novel process, namely rapid and spatially varying patterns of dispersal evolution, that can generate substantial variation in dispersal propensity in systems characterised by currents. Importantly, our model provides an additional possible solution for the much-debated 'drift paradox', showing that the interplay between spatial sorting and natural selection along a system characterised by currents can result in upstream patches being occupied by almost entirely philopatric individuals, thus preventing loss of individuals from upstream patches due to currents. This model has produced some key testable predictions that would benefit from the support of empirical studies. The prediction that a current generates a positive downstream gradient in emigration propensity is extremely interesting and could readily be empirically tested in natural systems. Furthermore, taking an experimental microcosm approach (Altermatt et al. 2015) could allow for testing the prediction that the effect of a current overwhelms dispersal cost as major driver of emigration. Following additional empirical validation, our model could have significant application potential. Recent work has shown that when designing river restoration actions, it is important to take dispersal abilities of colonisers into account when choosing areas to restore, in order to ensure success (Tonkin et al. 2014). Similarly, assisted relocation schemes should take certain dispersal traits into account when trying to predict knock-on ecological effects, so as to avoid unwanted invasions and to increase the probability of successful translocation (Parkyn and Smith 2011). Our insights into dispersal evolution are therefore relevant the context of managing habitats characterised by the presence of currents.

Data availability statement

The code for the model is available in a GitHub repository: <https://github.com/rebekkaallgayer/Dispersal_Evolution_in_Currents>.

Author contributions

Rebekka Allgayer: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal).
Alice Scarpa: Software (supporting); Validation (supporting); Writing – review and editing (supporting). **Paul Fernandes**: Writing – original draft (supporting); Writing – review and editing (supporting). **Peter J. Wright**: Writing – original draft (supporting); Writing – review and editing (supporting).
Lesley Lancaster: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Greta Bocedi**: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Justin Travis**: Conceptualization (equal); Funding acquisition (lead); Methodology (supporting); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

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