Spatial population structure drives extinction dynamics in climate-induced range shifts

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Abstract

Understanding the interplay between ecological and evolutionary factors is critical for predicting species' responses to anthropogenic climate change and for determining optimal conservation practices. Key parallels between range expansions (e.g. of invasive species) and range shifts in response to climate change allow us to draw upon current theory for range expansions to include initial spatial population structures and predict species' responses to climate change. Here, we use an individual-based model to explore the role of dispersal evolution, local adaptation, and a population's initial spatial structure in driving the dynamics of climate-induced range shifts. We show that populations with more pronounced initial spatial structure had substantially increased extinction probabilities and that evolution of dispersal ability was insufficient to rescue faltering populations. Rather, a population's fate during climate change was determined by the evolved composition of dispersal phenotypes within the initial range; only populations consisting of highly dispersive individuals prior to the onset of climate change survived. Our results demonstrate that dispersal evolution alone may be insufficient to save a range shifting population and that the initial spatial population structure plays a pivotal role in determining the outcome of climate-induced range shifts.

Key words: range shifts, eco-evolutionary dynamics, local adaptation, individual-based model

Introduction

Climate change is expected to dramatically reshape global biogeographic patterns as some species shift their ranges to track changing environmental conditions (Gonzalez et al., 2010). These range shifts are generally predicted to proceed upwards in latitude, elevation, or both as average global temperatures continue to rise (Loarie et al., 2009). Indeed, contemporary range shifts have already been observed in a wide variety of taxa, ranging from algae to mammals (Chen et al., 2011; Parmesan, 2006). Such range shifts present significant challenges to current and future conservation efforts as they can result in the extinction of populations failing to track a changing climate (Parmesan, 2006) as well as the creation of novel species assemblages as not all species are expected to respond to climate change or to shift their ranges at the same rate (Hobbs et al., 2009). Understanding the dynamics of such climate-induced range shifts could play a key role in informing current and future conservation work.

While the study of range shifts due to climate change is relatively new, important insights can be gained from the related but distinct process of range expansion, such as occurs when invasive species spread through a new environment. Decades of research on range expansions have led to a robust understanding of both the ecological (Hastings et al., 2005) and evolutionary (Shine et al., 2011; Excoffier et al., 2009) mechanisms responsible for shaping such expansions. For example, while the speed of a range expansion can be well approximated by a combination of the species' intrinsic growth rate and dispersal ability (Hastings et al., 2005), recent research demonstrates that evolution in both of these traits can increase both the mean and variance of expansion speed through time (Weiss-Lehman et al., 2017; Ochocki and Miller, 2017; Szűcs et al., 2017; Shaw and Kokko, 2015). As range shifts and expansions exhibit similar spatial dynamics, such as a leading edge of population advance with relatively low population density, they are likely to be affected by similar ecological and evolutionary mechanisms (Hargreaves and Eckert, 2014). However, while insights from range expansions are valuable for understanding and predicting dynamics of range

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shifts, it is important to recognize that these two processes have significant differences as well.

In particular, range expansions and shifts due to climate change involve fundamentally distinct initial population structure. Range expansions, especially for invasive and reintroduced species, typically begin from the successful establishment and subsequent spread of a small, founding population (Hastings et al., 2005). Such founding populations often represent samples from some larger source population and as such lack any initial spatial population structure. In contrast, range shifting populations initially have a more complex, but stable population structure that becomes disrupted with climate change or other environmental perturbations (Hargreaves and Eckert, 2014). A population's stable population structure incudes spatial variability in population size, adaptive traits, and range boundaries that manifests through a combination of local adaptation within the range and the severity of the gradient in population size from the range core to edge (Hargreaves and Eckert, 2014; Hargreaves et al., 2015; Henry et al., 2013).

A population's initial spatial structure has previously been shown to dramatically impact its response to climate change and its corresponding extinction probability. For example, the underlying mechanism responsible for the gradient in population size from the middle of the population (i.e. the more dense core) to the range edge can directly change the probability of extinction a species faces during a climate driven range shift (Henry et al., 2013). Extinction risk is also related to the degree of local adaptation within the range. Specifically, a broad environmental niche (i.e. little local adaptation) can decrease a population's ability to track a changing climate if dispersal occurs in a stepping stone manner, allowing some individuals to block dispersal of better adapted genotypes (Atkins and Travis, 2010). Local adaptation also has the potential to interact with dispersal evolution during climate change, driving increased dispersal probability in an asexual species as genotypes shift to keep pace with their environmental optimum (Hargreaves et al., 2015).

While the roles of dispersal evolution and local adaptation have been explored in isolation, using haploid, single locus models assuming asexual reproduction, it is unclear how these two processes might interact in a sexually reproducing species in which dispersal and local adaptation

are directly linked via gene flow. For example, evolution of increased dispersal could simultaneously reduce local adaptation within a population due to increased gene flow throughout the range. In fact, long-distance pollen dispersal in flowering plants has been shown to restrict local adaptation and, when pollen dispersal sufficiently outpaces seed dispersal, to lead to ecological niche shifts, rather than spatial range shifts, in response to simulated climate change (Aguilée et al., 2016). Additionally, the distribution of dispersal phenotypes within a population likely is influenced by the severity of the gradient at the range edge (Henry et al., 2013; Hargreaves and Eckert, 2014), further complicating the relationship between dispersal evolution and local adaptation during climate-induced range shifts.

Here, we develop a two-sex individual-based model with two genetically determined traits, one defining an individual's expected dispersal distance and the other determining an individual's environmental niche. In the model, we vary the degree of spatial population structure in the initial stable range to ascertain how the severity of the gradient at the range edge impacts a population's ability to track a changing climate. Further, we contrast the dynamics of extant and extinct populations to understand the joint impact of dispersal evolution and local adaptation on extinction risk during climate-induced range shifts.

Methods

A full description of the individual-based model using the Overview, Design concepts, and Details protocol (Grimm et al., 2010) is available in the online supplemental materials, while here we present a brief summary. Each simulated landscape consisted of a discrete lattice of habitat patches with a fixed width in the y dimension and unbounded length in the x dimension. Environmental conditions varied along the x dimension and remained constant across the y dimension (Fig. S1). To simulate climate change, environmental conditions shifted at a constant rate in the x dimension. In each generation, competition and reproduction occurred within each patch and local popula-

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tions were linked via dispersal, assuming wrapping boundaries in the y dimension to prevent edge effects.

Individuals were characterized by two traits (dispersal and an environmental niche), both defined by a set of 5 quantitative diploid loci, assuming no linkage. While the number of loci was arbitrary, 5 was chosen as a compromise between computational restrictions and the likely polygenic nature of such complex traits. The dispersal trait defined an individual's expected dispersal distance, assuming an exponential dispersal kernel. An individual's environmental niche trait allowed for local adaptation; the closer the niche value to the environmental optimum of the individual's patch, the higher the individual's realized fitness. The environmental optimum of individual patches could then be systematically altered across the range to allow for varying degrees of local adaptation (i.e. larger changes in environmental optima allowed for greater local adaptation of the population). In addition to the potential for local adaptation, simulated ranges were characterized by a decline in patch carrying capacity from the range center to the edge, the severity of which could be adjusted without altering the total carrying capacity of the landscape (see supplemental materials; Fig. S1). Reproduction within each patch occurred via a stochastic implementation of the classic Ricker model (Ricker, 1954; Melbourne and Hastings, 2008). We simulated non-overlapping generations consisting of discrete dispersal and reproduction phases (Fig. S2).

To determine the effect of spatial population structure on the eco-evolutionary dynamics of range shifts, we varied parameter combinations to explore the interacting roles of local adaptation and the severity of the gradient in environmentally suitable habitat at the range edge (Table S1 and S2). Specifically, we considered a factorial combination of three experimental factors: (1) no, low, and high potential for local adaptation, (2) shallow, moderate, and stark gradients in suitable habitat at the range edge, and (3) slow, moderate, and fast speeds of climate change. This yielded a total of 27 different scenarios, each explored with 200 simulations. Each simulation ran for 2150 generations with stable climate conditions for the first 2000, followed by 100 generations of climate change and a final 50 generations of stable conditions. Figure 1 shows an example

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of a single simulation undergoing climate change. For each scenario, we evaluated the role of dispersal evolution and initial spatial population structure in driving the dynamics of the range shifting populations.

We calculated dispersal evolution in each patch throughout the landscape as the change in mean dispersal phenotype from the beginning of the period of climate change to the end. For this analysis, we defined individual patches by their relative location within the range rather than with their fixed spatial coordinates (e.g. leading edge vs. core populations). Due to local extinctions, not all patches were occupied at the end of the period of climate change. To quantify dispersal evolution in these patches, we used data from the last generation in which the population had at least 10 individuals. Changes in mean dispersal phenotype were calculated by subtracting the initial mean dispersal phenotype from the value at the end of climate change (or at the last generation of at least 10 individuals occupying the patch in the case of population extinctions); positive values indicate an increase in the mean dispersal phenotype. All simulations and data processing were performed in R version 3.4.4 (Team, 2000) and the code is available at `https://github.com/tpweiss06/ShiftingSlopes`.

Results

In all scenarios, populations shifted their range in response to climate change, however the proportion of populations that successfully tracked the changing climate for the full 100 generations depended on the initial spatial population structure. Successful populations shifted their spatial distributions at essentially the same rate as climate change (e.g. Fig. 1), while populations that failed to keep pace and lagged behind the shifting climate went extinct. Populations defined by a higher potential for local adaptation and by stark habitat gradients at the range edge experienced the greatest probability of extinction due to climate change (quantified by the proportion of simulated populations to go extinct through time; Fig. 2). While both aspects of a population's range

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influenced extinction probabilities, the potential for local adaptation drove more dramatic changes to extinction dynamics, with greater changes in environmental optima across the landscape causing severe increases in the probability of extinction during climate change. Here, we widely varied both parameters (the potential for local adaptation doubled from the low to high scenario and the parameter defining the severity of the environmental gradient was increased by a factor of 100 from shallow to stark gradients; Table S2), suggesting that potential for local adaptation may be the stronger driver of extinction risk during climate-induced range shifts across a wide region of parameter space, and corresponding biological scenarios. Additionally, as expected, the pace of climate change also influenced extinction probabilities with faster climate change corresponding to greater extinction risk (Fig. S3 & S4). However, this effect was independent of the roles of local adaptation and the habitat gradient at the range edge in determining the extinction probability during a range shift.

Dispersal evolution is predicted to play a key role in aiding populations as they shift to track a changing climate. While some, individual simulations confirmed these expectations with average dispersal phenotypes increasing through time (e.g. Fig. 1), examining all simulations from each experimental scenario revealed no differences in the magnitude or direction of dispersal evolution between successful and extinct populations (Fig. 3a&b). Populations in all parameter combinations experienced both increases and decreases in average dispersal phenotypes, with all distributions of observed changes to dispersal phenotypes centered on 0 (Fig. S5-S7). The similarity in evolved changes to dispersal between surviving and extinct populations suggests that dispersal evolution alone cannot explain which populations successfully tracked moving conditions and which became extinct.

Instead, the stable distribution of dispersal phenotypes prior to the onset of climate change played a key role in determining the ultimate fate of simulated populations. Simulated populations evolved a range of dispersal phenotypes over the 2000 generations of stable climatic conditions in response to the potential for local adaptation and the severity of the habitat gradient at the

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range edge (Fig. S8-S10). The populations that survived climate change were those with higher initial dispersal phenotypes, occupying the right-tail of the distribution of observed dispersal phenotypes (Fig. 3c&d). Comparing the dispersal phenotypes of individuals in successful populations across different parameter combinations revealed a common threshold separating individuals from successful and extinct populations at each speed of climate change (Fig. S8-S10). In fact, this threshold corresponded to the dispersal phenotype necessary to produce an expansion wave traveling at exactly the speed of climate change. To prove this, we used the well-known approximation for the speed of an expanding population, $2\sqrt{rD}$ (Hastings et al., 2005), where r is the intrinsic growth rate of the population and D is the diffusion coefficient. The 2 dimensional diffusion coefficient can be calculated directly from the dispersal phenotypes as $D = \frac{1}{4}d^2$ since d^2 represents the mean squared displacement of an individual with phenotype d during a dispersal period (see the model description in the supplemental materials). Using these relationships and solving for the dispersal phenotype producing each of the speeds of climate change used in our simulations yields the threshold value distinguishing those populations that ultimately survived climate change from those that went extinct (Figures S8-S10, vertical dashed line).

Intriguingly, the populations that survived climate change tended to be characterized by reduced fitness at the range margins compared to populations that went extinct (Fig. S11-S13). This pattern was most evident in the simulations with either (1) a gradual environmental gradient at the range edge or (2) a high potential for local adaptation. Intuitively, there was no spatial pattern in fitness for populations with no potential for local adaptation. As the populations that survived climate change were also characterized by heightened dispersal (Fig. 3), the observed reduction in average patch fitness at the margins is likely due to increased gene flow from the range core hampering the abilities of these edge populations to adapt to local conditions.

Discussion

Range shifts due to climate change represent a global threat to biodiversity and much recent research has focused on exploring the underlying ecological and evolutionary dynamics of such range shifts to inform conservation efforts. Here we developed an individual-based model to explore the eco-evolutionary dynamics of climate-induced range shifts in sexually reproducing, diploid populations with both dispersal and environmental niche traits defined by multiple loci. In contrast, previous models have focused on a subset of these factors: ecological dynamics (e.g. (Brooker et al., 2007)), evolution in a single trait only (e.g. (Atkins and Travis, 2010; Henry et al., 2013)), and relatively simple genetic scenarios (e.g. single-locus haploid genetics in asexual populations (Boeye et al., 2013; Hargreaves et al., 2015)). Here, we tested the generality of previous results and the interplay of eco-evolutionary dynamics under realistic levels of biological complexity. Specifically, we demonstrated the role of spatial population structure, in the form of local adaptation and the environmental gradient defining the range edge, in determining extinction risk for range shifting populations via impacts on the initial distribution of dispersal phenotypes and environmental niche values.

Our results suggest that populations most likely to keep pace with climate change will be those with little to no local adaptation within the pre-expansion, stable range and in locations with shallow environmental gradients defining the range edge (Fig. 2). A survey of the scientific literature found evidence for local adaption in approximately 71% of studies, suggesting a high prevalence of local adaptation in natural populations (Hereford, 2009). Further, a recent meta-analysis of 1400 bird, mammal, fish, and tree species found no evidence for consistent declines in abundance towards range edges (Dallas et al., 2017), suggesting many species exhibit similar abundances at the edge and center of their ranges similar to the stark environmental gradients imposed in our study. While some of these patterns could represent a publication bias, for example against negative results in studies of local adaptation, combined with our results they suggest many species will face

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elevated extinction risks in climate-induced range shifts due to the spatial population structure of their initial ranges.

Our results emphasize the importance of the initial distribution of dispersal phenotypes composing the stable range in determining a population's extinction risk during climate change (Fig. 3c&d). Survival in the face of climate change was primarily determined by the dispersal phenotypes making up the population, specifically whether the population included individuals with dispersal phenotypes at or above a given threshold value. Importantly, the threshold necessary to survive climate change itself was constant across all parameter combinations for a given speed of climate change (Fig. S8-S10). Scenarios with no potential for local adaptation and gradual environmental gradients had larger proportions of high dispersal phenotypes under stable climate conditions, and therefore a lower probability of extinction during climate change. A high potential for local adaptation, in contrast, selected against such high dispersal phenotypes due to dispersal's homogenizing effect on population genetic structure (Lenormand, 2002). Similarly, a more severe habitat gradient at the range edge increased the risk of dispersing beyond the boundary of suitable habitat, resulting in selection against heightened dispersal (Shaw et al., 2014). Thus, attributes defining the spatial structure of the range altered the distribution of dispersal phenotypes under stable climate conditions, subsequently determining the extinction risk of populations during climate change. Importantly, dispersal evolution during climate change was unable to counter the influence of spatial population structure in the stable range on extinction dynamics.

While high dispersal phenotypes prior to climate change increased the probability that populations tracked changing conditions, it had the additional effect of reducing average fitness at the range margins when populations had a moderate to high potential for local adaptation (Fig. S11-S13). In the model, populations at the range margins tended to have lower abundance than populations in the range core, thus increasing their susceptibility to gene flow from the core (Lenormand, 2002). Thus, in populations with high dispersal phenotypes prior to climate change, increased gene flow from the core reduced fitness at the range edge by preventing adaptation to local conditions.

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As a result, the populations most likely to survive climate change were, counterintuitively, also those characterized by lower fitness prior to the onset of climate change. While not all populations are characterized by small populations at the range edges (Dallas et al., 2017), our results suggest that populations exhibiting high levels of local adaptation within their stable range are likely to be at greater risk of extinction during periods of climate change.

Previous research has suggested that evolution of increased dispersal ability during climate change may be a key mechanism in rescuing populations that would otherwise be unable to keep pace with shifting environmental conditions (Boeye et al., 2013). Our results suggest this is not always the case, and in fact may only be possible under certain, relatively narrow conditions. Previous models showing that dispersal evolution may rescue populations during climate change have typically used relatively simple genetic frameworks to model dispersal, including haploid and single-locus models (Boeye et al., 2013; Hargreaves et al., 2015). As dispersal evolution during range expansions and shifts occurs via the formation of strong spatial structure from the core to the range edge (Shine et al., 2011), such simplified genetic frameworks may allow more efficient sorting of highly dispersive alleles compared to our more complex model multiple diploid loci contributing to dispersal. Additionally, many previous models of climate-induced range shifts assume asexual reproduction which can result in more rapid rates of evolutionary change under certain conditions (Crow and Kimura, 1965; Smith, 1968). The negligible role played by dispersal evolution in our model (Fig. 3a&b) suggests that when such simplifying assumptions are relaxed, the potential for population rescue via evolution of heightened dispersal is greatly reduced, thus increasing the role of the initial spatial population structure within the range in determining a population's fate under climate change.

Conclusion

Understanding the various ecological and evolutionary drivers of climate-induced range shifts is crucial to current and future conservation efforts. In particular, a deeper, process-based understand-

ing of how various mechanisms combine to shape extinction probabilities of populations under-going range shifts, will, in turn, allow more focused interventions. Our results suggest that initial spatial population structure, as determined by local adaptation and the environmental gradient at the range edge, has the potential to dramatically alter the extinction probability faced by species responding to climate change. Further, in contrast to other studies assuming more simplified breeding and genetic structure, we find very little role for the evolution of heightened dispersal abilities to rescue a population composed of low-dispersing individuals. Future work should continue to examine the interplay between initial conditions in range shifts and the potential for evolutionary rescue. As climate change continues to accelerate (Chen et al., 2017), it is imperative to not only identify those factors leading to increased extinction risk in range shifting populations, but also to develop meaningful conservation strategies to mitigate such increased risk.

Acknowledgements

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Figure legends

Figure 1. A single example of a simulation with a high potential for local adaptation and a moderate habitat gradient defining the range edge. Information on the (a) abundance, (b) dispersal, and (c) fitness of individuals in each patch is shown for time periods beginning with the last generation of stable climate conditions ($t = 0$) to 40 generations after the start of climate change. Log transformed mean dispersal phenotypes (b) are shown for each patch. Average patch fitness (c) was calculated based on the mean local environmental niche phenotype and the optimal niche value for that location.

Figure 2. The cumulative probability of extinction due to climate change in different experimental scenarios. Graphs show the proportion of simulated populations that went extinct through time for scenarios with (a) no, (b) low, and (c) high potential for local adaptation, and in environments characterized by a shallow (solid line), moderate (dashed line), or stark (dotted line) gradient at the range edge.

Figure 3. Patterns in the evolution and the initial distribution of the dispersal trait, highlighting extant simulations. Evolution in dispersal (a and b) is shown as the change in the mean dispersal phenotype of each patch from the beginning of the period of climate change to the end. Positive values indicate an increase in average dispersal ability in the patch. Initial distributions of the dispersal trait (c and d) are shown as log transformed dispersal phenotypes of individuals in populations after 2000 generations of stable climate conditions. In all panels, values associated with extant populations are shown in dark blue. Results are shown for populations with no potential for local adaptation and a gradual environmental gradient at the range boundary (a and c; $n = 155$ extant populations) and for populations with a high potential for local adaptation and a stark gradient at the range boundary (b and d; $n = 14$ extant populations). Full results for all parameter combinations are provided in the online supplement.
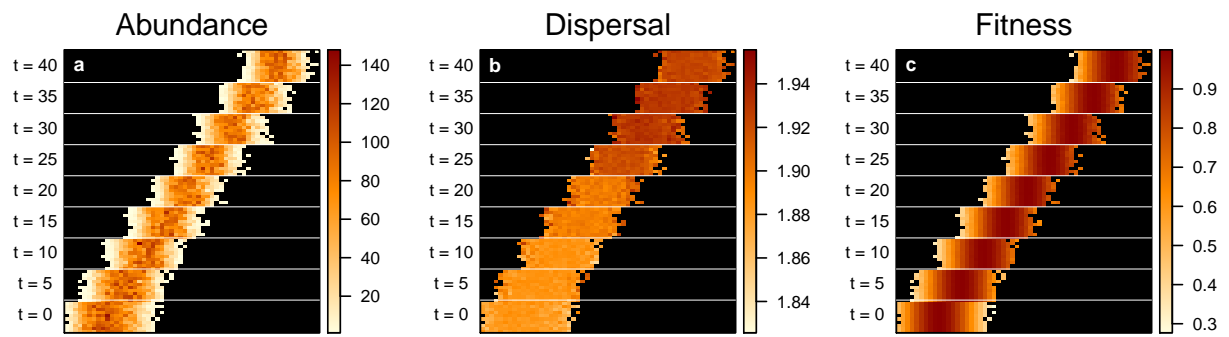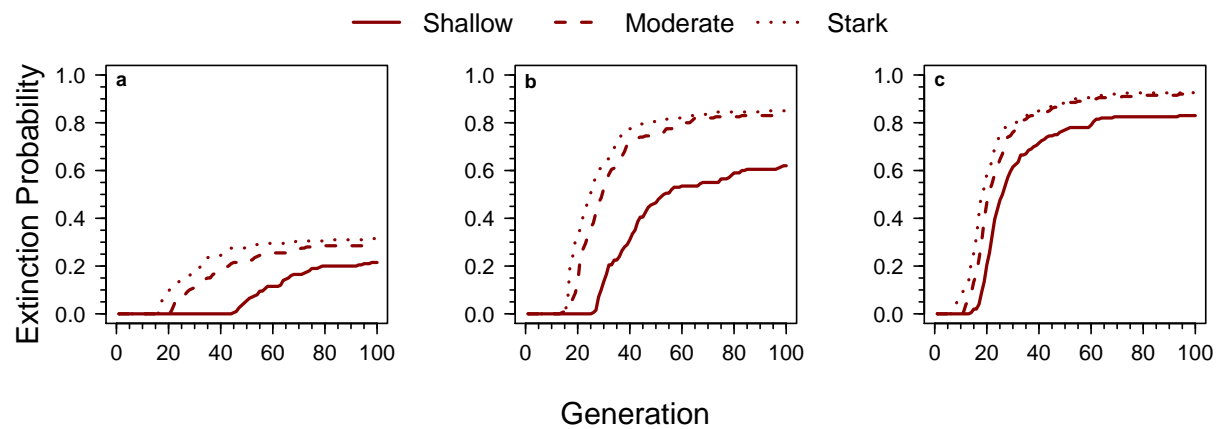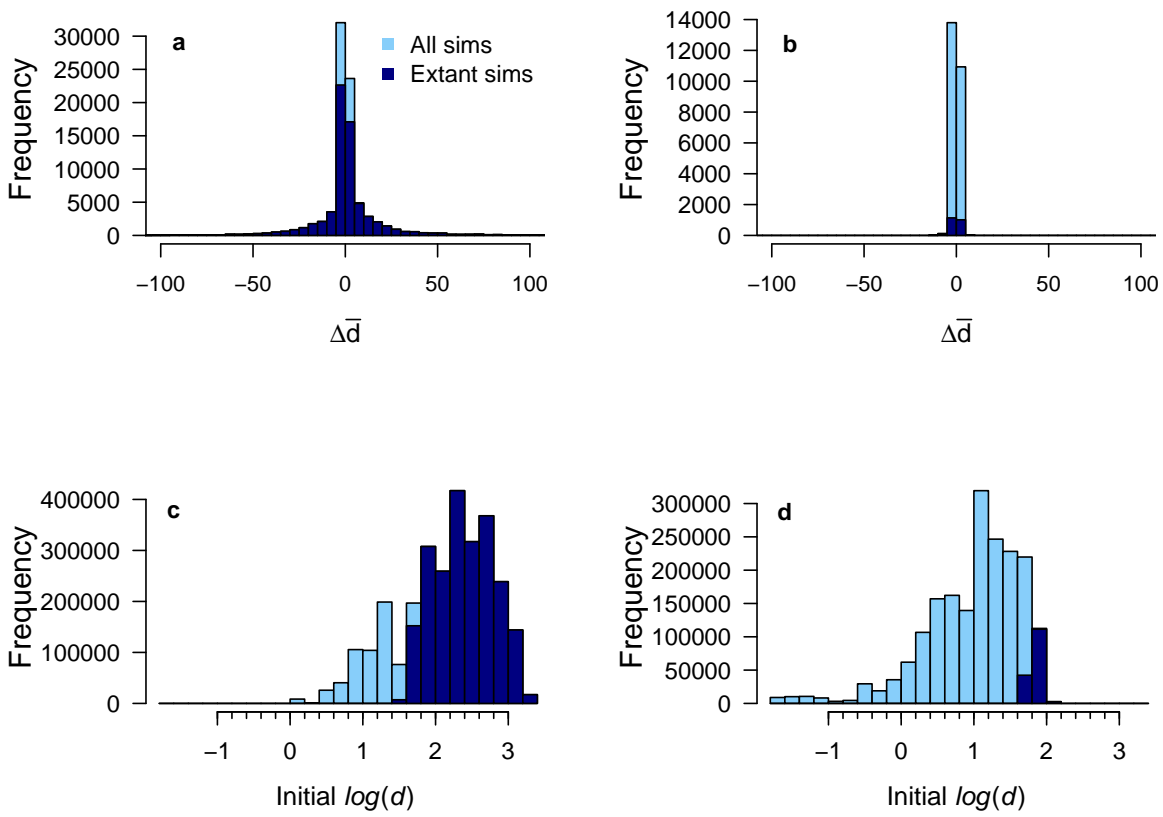
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Figure 3