

# Geographic variation in dispersal distance facilitates range expansion of a lake shore plant in response to climate change

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## Abstract

**Aim:** Geographic variation in dispersal abilities is widespread and likely to affect species' range dynamics in response to climate change. However, distribution models that predict climate-induced range shifts do not account for spatial variation in dispersal. We developed an eco-genetic model to investigate how variation in dispersal distances across a species' range could interact with climate-induced selection and alter predicted range dynamics in a species with documented variation in dispersal traits.

**Location:** We investigated the range of an annual plant, *Cakile edentula* var. *lacustris*, which occupies beaches spanning a 555 km latitudinal gradient along the Laurentian Great Lakes.

**Methods:** We built a hybrid model that combines climatic niche modelling, based on decadal climate projections, with an individual-based model that allows for evolutionary processes to act upon a heritable dispersal kernel. We evaluated how spatial variation in dispersal distance and dispersal evolution influenced range dynamics, spatial and temporal variation in dispersal, and the distribution of neutral genetic variation. The model was parametrized with data on *C. edentula*'s distribution, life history and dispersal characteristics.

**Results:** Geographic variation in dispersal distance, adaptive dispersal evolution and dispersal distance increased the potential for local populations of *C. edentula* to keep pace with changing climatic conditions through range shifts. Dispersal distances always increased at the expanding and contracting range edges when dispersal was allowed to evolve. Furthermore, scenarios where dispersal distances were initially lower at the range edges resulted in the largest evolutionary changes over 105 years (>1.5 km increase in mean distance at northern edge). Adaptive dispersal evolution always reduced neutral genetic diversity across the species' range.

**Main conclusions:** Variation in dispersal abilities across *C. edentula*'s range and adaptive evolution led to different predicted outcomes in range dynamics during climate change illustrating the importance of including spatial variation in dispersal into species distribution models.

## KEYWORDS

*Cakile edentula*, climate change, dispersal evolution, expanding range limit, genetic diversity, geographic range

## 1 | INTRODUCTION

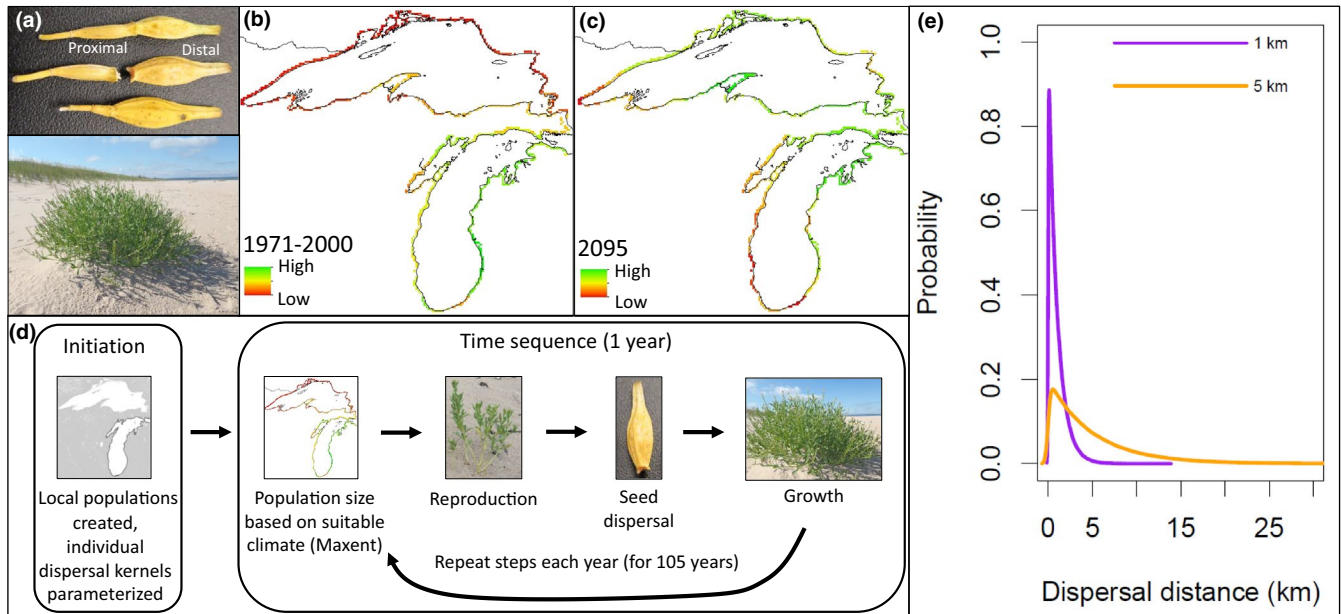
Recent empirical and theoretical work has demonstrated that diverse taxa may be able to rapidly adapt to environmental changes, such as those presented by habitat modification (Bosse et al., 2017) and climate change (Palkovacs, Kinnison, Correa, Dalton, & Hendry, 2012; Siepielski et al., 2017). Climate change is already acting as an important selective agent for many species, but it remains challenging to predict which species will be able to keep pace with changing conditions (Bateman, Murphy, Reside, Mokany, & VanDerWal, 2013; Siepielski et al., 2017). One way that populations may respond to climate change is through dispersal evolution—the heritable change in a dispersal kernel due to the selection on dispersal traits (Hargreaves & Eckert, 2014). Distribution models that are used to predict species' responses to climate change do not often include scenarios where dispersal can evolve as the geographic range changes (Bateman et al., 2013; but see Dytham, Travis, Mustin, & Benton, 2014; Hargreaves, Bailey, & Laird, 2015 for examples of general species models). However, recent empirical studies have shown that dispersal traits often exhibit heritable genetic variation and may be able to quickly respond to selection (Phillips, Brown, Webb, & Shine, 2006; Phillips, Anderson, & Schapire, 2006; Weiss-Lehman, Hufbauer, & Melbourne, 2017). Such rapid changes in dispersal could facilitate metapopulation persistence by influencing the rate at which new habitat can be colonized as it becomes available (Bell & Gonzalez, 2011; Boeye, Travis, Stoks, & Bonte, 2013; Hargreaves et al., 2015; Kubisch, Degen, Hovestadt, & Poethke, 2013).

The dynamics of dispersal evolution are expected to be shaped by the distribution of genetic variation in dispersal traits across a species' range (Travis & Dytham, 1998), and prior studies have established that mean dispersal distances often vary geographically among populations within a species' range (Hargreaves & Eckert, 2014). For example, mean dispersal distances are sometimes shorter at the edges of a species' range compared to the interior (LaRue, Holland, & Emery, 2018; Talavera, Arista, & Ortiz, 2012). Furthermore, the evolutionary responses of dispersal traits may vary at different positions within the species' range, such as the range edges versus the interior, due to the genetic composition of individual populations (Bridle & Vines, 2007). For example, edge populations may have low additive genetic variation in dispersal traits due to founder effects (Eckert, Samis, & Loughheed, 2008; Razgour et al., 2013), which in turn may limit the potential for dispersal-related traits to quickly respond to selection. Nevertheless, the strength of selection imposed by climate change may be stronger in marginal populations that are near rapidly changing habitat (Hargreaves & Eckert, 2014), and the failure for dispersal traits to adaptively evolve may hinder metapopulation persistence. Furthermore, evolutionary processes

may influence a species' ability to respond to changing patterns of selection by shaping the amount and distribution of genetic variation in traits that influence organismal performance within habitat patches (Edmonds, Lillie, & Cavalli-Sforza, 2004; Klopstein, Currat, & Excoffier, 2006). Genetic bottlenecks during colonization events can cause reduced variation in populations that are expanding into new habitat patches (e.g., neutral genetic variation), which in turn may limit the evolutionary potential of those populations during and after establishment (Bridle & Vines, 2007; Gaston, 2009). Currently, we lack models that evaluate how pre-existing geographic variation and evolutionary change in dispersal strategies directly influence species' range dynamics and neutral genetic variation in response to climate change (Johnson et al., 2019).

The global diversity of species' dispersal mechanisms results in orders of magnitude of differences in their dispersal distances, making it critical that models of range shifts in response to climate change are grounded in taxa-specific dispersal properties. For example, plants and animals can be widely different in the extent of their maternal control on their offspring's dispersal (Starrfelt & Kokko, 2010). Maternal plant traits directly influence dispersal of their offspring by determining how they are released into the environment (e.g., the height at which wind-dispersed seeds are released) and their external characteristics (e.g., seed morphology) (Donohue, 1999); in contrast, the dispersal kernel of mammals tends to be dominated by the phenotype of the offspring (Starrfelt & Kokko, 2010). These differences can have implications for range dynamics: for example, dispersal kernels determined by offspring can result in more rapid range expansion than those determined by the maternal phenotype (Starrfelt & Kokko, 2010). Similarly, in organisms that engage in passive dispersal, geographic variation in the dispersal vectors that they rely upon can lead to drastically different range dynamics. Seeds that disperse by water, such as floating seeds, lead to more rapid colonization and range expansion than seeds that fall directly to the ground and are pulled down by gravity as they fall (Nathan, 2006). Collectively, the diversity of dispersal mechanisms in nature raises the need to fine-tune distribution models that incorporate dispersal variation to represent the dispersal properties of the studied organism.

Here, we present a spatially explicit, individual-based model that evaluates the interplay between geographic variation in dispersal and subsequent evolution in response to climate change. Given that model outcomes would be highly dependent on the dispersal kernels, we chose to base model parameters on the biology of *Cakile edentula* subsp. *edentula* var. *lacustris* (Brassicaceae; Figure 1a), because extensive information about its dispersal strategy (Donohue, 1998; Donohue, 1999), geographic variation in dispersal traits (LaRue et al., 2018), and its geographic range was readily available (LaRue et



**FIGURE 1** The dispersal strategy of *Cakile edentula*, example maps of predicted habitat suitability across its geographic range in the Great Lakes, model steps and range of dispersal kernel shapes. (a) The home-site (proximal) and water-dispersing (distal) fruits of *C. edentula* (top) and the typical growth form of the plant on a Great Lakes beach (bottom). (b) The predicted distribution of habitat suitability under present day climate (1971–2000) and (c) under projected high emissions climate change in year 2095, where green represents high habitat suitability, yellow represents intermediate habitat suitability and red represents low habitat suitability. (d) General overview of steps in our hybrid species distribution model that combined climatic niche modelling with an individual-based model. First, the population genetic and demographic characteristics of populations across the range are initiated at the beginning of the simulation (year 2000). The remaining steps occur each year (until year 2105) in order including: the determination of the metapopulation and local carrying capacities based on climatic habitat suitability values, asexual reproduction, dispersal of the offspring based on the maternal dispersal kernel, seed establishment, death of parental plants and plant growth for seed production in the next year

al., 2018; Rodman, 1973). This annual herb occupies beach habitats that outline the shores of the Great Lakes, with a geographic range that spans 555 km from 41 to 46 degrees of latitude north (Rodman, 1973) (Figure 1b, c). *Cakile edentula* reproduces predominantly via self-pollination, so seed dispersal likely accounts for most of the gene flow within and among populations (Rodman, 1973). Individual plants produce dimorphic fruits that disperse locally by wind or longer distances by water (Rodman, 1973). Previous work has documented heritable variation in wind and water dispersal traits across the species' range, including reduced potential for water dispersal at the range edges (LaRue et al., 2018). While our analyses were based on the biology of *C. edentula*, we expect that our results may be relevant to organisms that exhibit passive, long-distance dispersal (e.g., many plant, insect and marine organisms). In our analysis, we first evaluated how existing patterns of dispersal distance and geographic variation in dispersal properties can influence our predictions for how a species' range will shift in response to climate change. Next, we evaluated how the adaptive evolution of dispersal traits over time altered these predictions. We also tracked variation at neutral loci to monitor how dispersal variation and evolution alters the distribution of genetic diversity as a species' range adjusts with climate change. To do this, we used neutral markers as a proxy for genetic variation that does not influence dispersal genotypes, but instead is shaped by the patterns of colonization and gene flow that

result from the dispersal patterns that drive range expansion and contraction under climate change. Our results revealed that the initial dispersal distance and spatial distribution of dispersal distances across the range of *C. edentula* had large effects on species' range dynamics and that dispersal trait evolution facilitated metapopulation persistence. More generally, these results demonstrate that incorporating variation in dispersal traits, both across a species' range and through time, can substantially alter the predictions of species' distribution models as climate change proceeds.

## 2 | METHODS

We evaluated how geographic variation in dispersal and dispersal trait evolution can alter predictions for range dynamics under climate change by combining the projected habitat suitability from a *C. edentula*-specific species distribution model with an eco-genetic, individual-based model (Figure 1d). Future climate change projections of air temperature were obtained monthly for the decades 2020–2090 and used as climate change projections for input into MAXENT. To obtain these projections, we used the NorESM1-M model from the CMIP5 multi-model ensemble (Coupled Model Intercomparison Project; Taylor, Stouffer, & Meehl, 2012) with the Intergovernmental Panel on Climate Change (IPCC) representative concentration pathways of

RCP 2.6 (low emission) and RCP 8.5 (high emission) (IPCC, 2014). We chose to use the NorESM1-M as our climate change framework because it represents a medium amount of future projected change in temperature for the Great Lakes region. We relied on a simple delta method to produce future temperature values (Prudhomme, Reynard, & Crooks, 2002) by calculating changes between the projected future decade and modelled historical period (1971–2000) on a monthly basis and then adding those changes to an observed data set of historical temperature. By applying the delta method, we did not have to correct for global circulation model biases, because we compensated for differences between the historical and projected future temperatures at specific locations. It is important to note that our method does not eliminate model bias, but it does allow us to initialize our climate data from a realistic starting point based on historical temperature observations. The historical data consisted of the University of Delaware Air Temperature and Precipitation observations (Willmott & Matsuura, 2001) obtained from the NOAA/OAR/ESRL PSD website (Boulder, Colorado, USA; <http://www.esrl.noaa.gov/psd/>).

We used the program MAXENT to predict future habitat suitability under present and future climate change scenarios (Elith et al., 2011; Phillips, Brown, et al., 2006; Phillips, Anderson, et al., 2006; Phillips, Dudik, & Schapire, 2004; Figure 1b,c). MAXENT estimates the potential distribution of a species' habitat suitability based on maximum entropy distribution, which requires species presence data and treats the remaining spatial points as background data as opposed to absences. Documented occurrences of *C. edentula* were obtained from the published literature (Gormally, Hamrick, & Donovan, 2011; LaRue et al., 2018) and the GBIF database (Lane, 2008). We used the SDMToolbox in ARCMAP 10.2 (Brown, 2014) to inspect a matrix of pairwise Spearman correlation coefficients between twelve-monthly average temperature variables because extreme collinearity between predictor variables in MAXENT can lead to unreliable results (Brown, 2014). We then removed redundant climate variables with correlation coefficients  $>0.80$ , while retaining those that were not highly correlated. The final variables used were temperature in the months of January and July. The default settings for the cross-validate method in MAXENT were used, except we increased the number of independent models runs from 1 to 20, starting with a random seed, and increased the number of iterations from 500 to 5,000.

We constrained analyses to the coastal habitat of the Great Lakes, where *C. edentula* is restricted due to its obligate association with sandy beaches. We created a raster of habitat suitability across the range of *C. edentula* from MAXENT output, which contained the probability of species presence from 0 to 1 for each cell (Elith et al., 2011; Phillips, Brown, et al., 2006; Phillips, Anderson, et al., 2006; Phillips et al., 2004). We incorporated the entire 555 km extent of the species' latitudinal range; however, we restricted the longitudinal extent of the range to Lakes Michigan and Superior (approximately one half of the species' entire longitudinal range) due to computational constraints of using large geographic areas (Figure 1d). This process resulted in a total of 876 patches (i.e., raster cells) along the coast where the final size

of each individual patch was 36 km<sup>2</sup>. Like all distribution models using MAXENT (Elith et al., 2011), this approach assumes that the climatic niche of *C. edentula* can be estimated from its current distribution. We consider this assumption reasonable given that *C. edentula*'s range limits have remained relatively stable in recent history (LaRue et al., 2018; Rodman, 1973) despite its potential for long-distance dispersal by water (Rodman, 1973), and thus, it is likely that the species' distribution limits reflect the bounds of its climatic tolerances (Hargreaves, Samis, & Eckert, 2014).

Habitat suitability values were recalculated each year for 25 years of present-day climate and 80 years of projected climate change. Control scenarios assumed present-day habitat suitability values in all patches ranged from 0 to 1 for the entire 105 years. For climate change scenarios, we changed the habitat suitability values across the species' range at nine time points. The values for the first 25 years (2000–2025) were based on the present-day climate map. Over the next 80 years (2025–2095), we generated a new habitat suitability map every 10 years using projected climate change estimates.

Habitat suitability values were used to determine the simulated dynamics of the population sizes of local patches and the global population size each year. We chose an average patch population size of 50 individuals, because it is well within the range of observed natural populations in field surveys (LaRue et al., 2018). We constrained the maximum number of individuals living in the range each year to be less than or equal to the product of the average patch population size (50) and the total number of patches with suitability values  $>0$ . This allowed for a possible maximum global population size of 43,800 individuals if all 867 patches had habitat suitability values greater than zero, but the actual size varied each year due to variation in the number of suitable patches available. The maximum number of individuals that could live within each local habitat patch was calculated each year as the product of the habitat suitability value for a given habitat patch and 50 individuals. As seen in our study, the machine learning algorithm of MAXENT does not always produce a maximum predicted habitat suitability of 1 (e.g., the highest habitat suitability across the entire range equalled 0.6), which could lead to an actual local population size of less than the average of 50 across the range. This would result in a smaller global population size than expected; therefore, when this occurred, we scaled the local carrying capacities to reach the expected value of the global population size, but never more than the size of the carrying capacity of the global population each year. This scaling process resulted in local population sizes that ranged from 1 to 120 individuals (Figure S1.1) and a mean of 50 individuals. We also incorporated density-independent demographic processes in the population size of patches by randomly sampling a new value of population size for each occupied habitat patch from a normal distribution with a mean equal to the population size within each patch and a standard deviation equal to two.

To allow dispersal to evolve, each individual in the model was assigned a unique dispersal kernel and genetic variation within populations in the dispersal distance parameter. To allow for a spatial resolution that spanned the latitudinal extent of the Great

Lakes, we combined the wind and water dispersal traits into a single dispersal kernel. This procedure allows for some seeds to successfully disperse long-distances via water dispersal pathways, while allowing for more seeds to successfully disperse shorter distances via wind dispersal pathways, which is in accordance with studies on reproductive success and fitness (Donohue, 1997). Based on this rationale, we used a Weibull distribution to model the fat-tailed dispersal kernel (Nathan et al., 2012) of *C. edentula* seeds that can disperse locally as well as long distances by water. The Weibull distribution was fitted with two parameters: a fixed shape parameter of 1.0 so that some offspring could be philopatric (i.e., many seeds do not reach the lake, where they would disperse via water), and a scale parameter that varied in units of kilometres to set the dispersal kernel width. For simplicity, we refer to this scale parameter as the dispersal distance, where a larger value indicates a broader dispersal kernel and greater expected dispersal distances than smaller values (Figure 1e). We incorporated genetic variation in dispersal distance among individuals in the first generation by randomly sampling the predetermined mean dispersal distance (varied between parameter sets, Table S1) from a normal distribution with a standard deviation of 0.5 km. Reproduction occurred through asexual reproduction of adults each year; while *C. edentula* reproduces sexually, it does so primarily through self-pollination (Donohue, 1997); thus, we simplified reproduction to be asexual for computational tractability (Dytham, 2009). Each offspring inherited a slightly modified dispersal distance parameter from their parent, which was created with a random deviate drawn from a normal distribution (mean = parental dispersal distance, standard deviation = 0.1 km) to incorporate genetic and non-genetic sources of phenotypic variation (i.e., mutation and/or environmental variation of a maternally determined dispersal kernel). Dispersal was simulated as the movement of seeds away from the parent plant (Figure 1d). First, we calculated the Euclidian distance between the parent plants' home habitat patch and all other suitable patches. Next, we used the parental dispersal kernel (assuming that parental traits contribute more to the dispersal kernel than seed traits; Donohue, 1999) to calculate the probabilities that each seed could disperse from its home patch to every other habitat patch in the metapopulation. A longer parental dispersal distance value results in a higher probability for a seed to recruit into other suitable patches (and patches need not be immediately adjacent) versus remaining in the parental patch. Each parent produced 50 seeds, a number consistent with field observations (Donohue, 1998; LaRue et al., 2018). We then proportionately distributed up to 50 offspring per parent across suitable patches based on the dispersal probability values from the parent's dispersal kernel. If the total number of offspring from all parents that dispersed into a habitat patch exceeded the local population size (based on the habitat suitability score), we randomly removed offspring from each patch until the population size in the patch was met. All parents were removed after the dispersal of offspring was completed, consistent with the annual life cycle of *C. edentula* (Rodman, 1973).

The effects of geographic variation in dispersal and dispersal distance were evaluated by comparing model outcomes for four different initial patterns of dispersal distance across the species' range: (a) uniform-1 km, (b) uniform-5 km, (c) shorter at the range edges than interior (short range-edge dispersal) or (d) longer at the range edges than interior (long range-edge dispersal). The two uniform scenarios had no initial variation in dispersal among populations representing the assumptions of a traditional species' distribution model. The long range-edge scenario represents systems where range-edge populations have higher mean dispersal distances compared to those in the interior (e.g., *Abronia umbellata*; Darling, Samis, & Eckert, 2008), while the short range-edge dispersal scenario represents systems where the mean dispersal distance is shorter at the range edges than interior (e.g., *C. edentula*; LaRue et al., 2018). These spatial patterns were implemented using a quadratic equation ( $x$  = latitude,  $y$  = dispersal distance; Table S1.1), assuming that the centre of the range was halfway between the southern and northern limits at 45.5°N. In these four scenarios, genetic variation in dispersal distance existed within populations to allow for the opportunity of an adaptive evolutionary response to selection to be able to occur. However, we also ran a neutral model for each of the four dispersal scenarios, in which there was no genetic variation in dispersal within populations. Under these conditions, adaptive evolution in dispersal was impossible in the two uniform scenarios, and only occurred in the short and long range-edge scenarios when dispersing offspring successfully colonized any new habitat patch for which that dispersal phenotype did not exist before (e.g., colonization could result in genetic variation being introduced into a population which was previously fixed in its dispersal distance). Finally, we conducted a separate set of analyses that used the same range mean dispersal distance from the short range-edge and long range-edge scenarios, but assumed a uniform distribution across the species range, to ensure that any differences we observed between the uniform and non-uniform dispersal scenarios was due to geographic variation in dispersal distances and not the differences in the grand means. These results confirmed our predictions and are presented in Figure S1.3.

To test how adaptive dispersal evolution and geographic variation of dispersal influence neutral genetic diversity as climate change proceeded, we assigned each individual 50 polymorphic microsatellite loci to measure neutral genetic diversity of populations across the range. At the beginning of each model run during initiation (Figure 1d), each locus had 50 alleles where allele frequencies were specified by the equation:

$$A_i = \frac{i}{(Na + 1 - i)} \cdot \sum_{i=1}^{Na} \frac{i}{(Na + 1) - i} \quad (1)$$

where  $Na$  equalled the total number of alleles and  $i$  equalled allele  $i$  in the set 1:Na. This equation provides allele frequencies that are typical of neutral allele frequency distributions (adapted from

Bernatchez & Duchesne, 2000). Genotypes were created in Hardy-Weinberg equilibrium for each locus, and individuals were assigned multi-locus genotypes by randomly sampling genotypes at each locus with replacement. At the end of the simulated 105 years, we measured the expected heterozygosity and average number of alleles per locus.

We ran the model under the different scenarios for projected climate change, dispersal and evolutionary potential in dispersal (Table S1.2) and recorded the distribution, abundances and dispersal distances of all individuals at decadal time points during each simulation. Results of preliminary analyses were not sensitive to variation in the average local population size or the number of offspring per parent (Figure S1.2), and therefore, we maintained values of 50 for each of these parameters across all subsequent analyses. We recorded the mean dispersal distance, expected heterozygosity of microsatellite loci and the proportion of the landscape occupied every ten years between year 2000 (year zero) and 2105. The results for each variable were calculated as the average value over 40 replicate iterations. The model and all data analyses were implemented with R version 3.2.4 (R Core Team, 2018).

### 3 | RESULTS

#### 3.1 | Geographic variation in dispersal without adaptive evolution

When dispersal could not evolve, the distribution of individual dispersal distances remained relatively constant across the range over time, regardless of the initial pattern of dispersal variation or the climate change scenario imposed (Figure 2). We found no evidence for range expansion or contraction under either present-day or low-emission climate change scenarios when the initial patterns of dispersal variation were either uniform-1 km (Figure 2a,b) or shorter at the range edges than the interior (Figure 2g,h). When the initial dispersal distances were uniform-5 km or when edge populations started with longer dispersal distances than interior populations (i.e., long range-edge), range limits remained stable under present-day climate scenarios (Figure 2d,j), while the northern range limit expanded under both low- and high-emission climate change scenarios (Figure 2e,f,k,l). The southern range limit, by contrast, contracted only under the high-emission climate change scenarios, regardless of the initial pattern of dispersal variation (Figure 2c,f,i,l).

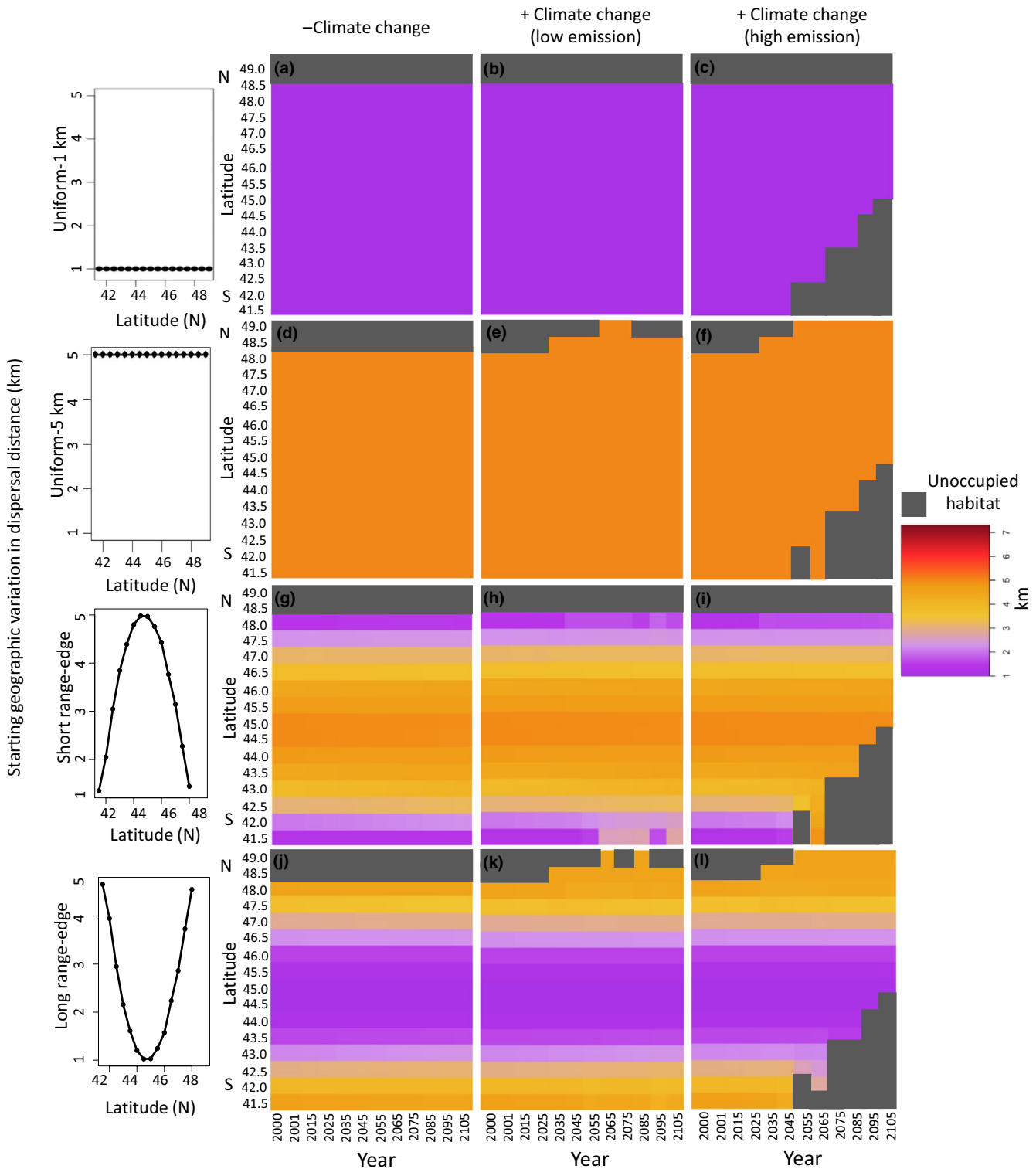
#### 3.2 | Geographic variation in dispersal with adaptive evolution

Adaptive evolution interacted with initial geographic patterns in dispersal and dispersal distance to shape dispersal and range dynamics as climate change proceeded. When dispersal was allowed to evolve, the northern range limit remained stable under present-day climatic conditions (Figure 3a,d,g,j) and expanded

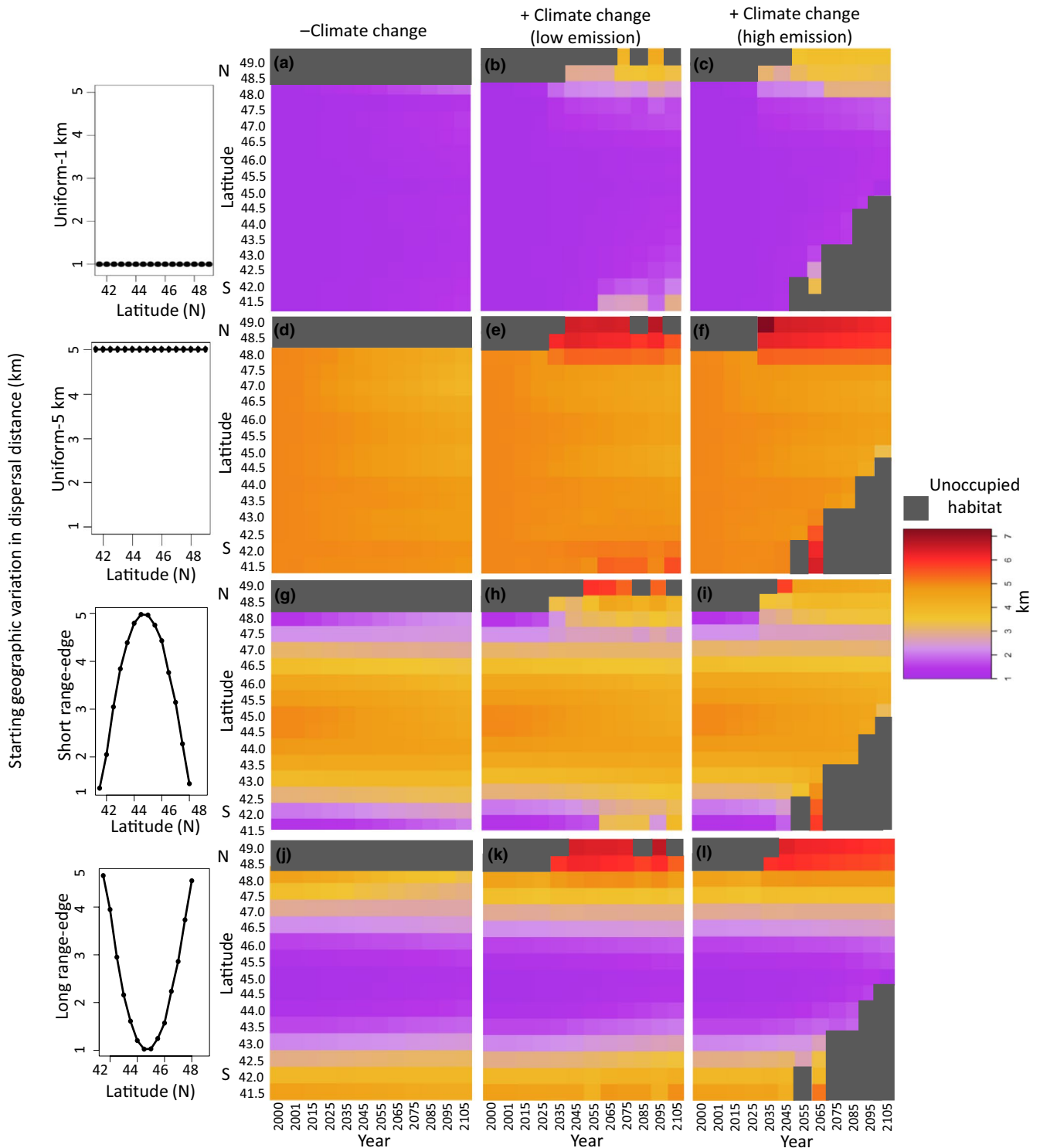
under low- and high-emission scenarios (Figure 3b,c,e,f,h,i,k,l), regardless of the initial patterns of dispersal variation across *C. edentula's* range. Under high emission climate change, the uniform-5 km dispersal scenario colonized new habitat in the north (Figure 3f) one decade faster than the short range-edge (Figure 3i) and long range-edge dispersal scenarios (Figure 3l), and two decades faster than the uniform-1 km dispersal scenario (Figure 3c). Increased dispersal distances evolved at the northern range limit under all climate change scenarios (Figure 3; Figure S1.3), and the magnitude of this change increased with growing levels of climate change, the presence of starting geographic variation in dispersal and initial dispersal distance (Figure 3). The greatest response to selection at the northern limit (i.e., the difference between the initial and final average dispersal distance) occurred in the short range-edge scenario under high-emission climate change (Figure 3h,i), with mean dispersal distance at the expanding northern limit evolving from 1 km to 6 km within two decades of the onset of climate change. A relatively weaker response to selection on dispersal was observed in the uniform-1 km scenario (Figure 3b,c), where the mean dispersal distance at the northern limit evolved from 1 km to only 3 km within three decades of the onset of climate change (Figure 3c). Increased dispersal distances also evolved at the expanding northern edge in the long-edge (Figure 3k,l) and uniform-5 km scenarios (Figure 3e,f), with an initial mean dispersal distance of 5 km growing to 6.5 km and 7 km, respectively, in the northernmost populations within two decades of the onset of high-emission climate change (Figure 3f). Like the northern limit, the southern limit remained stable under low-emission and present-day climates (Figure 3a,b,d,e,g,h,j,k) and expanded northward (contracting) under the high-emission climate scenario (Figure 3c,h,i,l). Selection drove the evolution of increased dispersal distance in southern populations under both climate change scenarios, regardless of the initial dispersal parameters applied (Figure 3c,f,i,l).

#### 3.3 | Impact of adaptive evolution and dispersal variation on neutral genetic diversity

Geographic variation in dispersal and adaptive evolution influenced the distribution of neutral genetic diversity across the range. Expected heterozygosity was always lower across the range when dispersal was allowed to evolve (cf., Figure S1.4; Figure 4). We found that expected heterozygosity was lower at the range edges compared to the interior under the low- and high-emission climate change scenarios (Figure 4). We also found that expected heterozygosity was by far the lowest in the northern range-edge populations than elsewhere in *C. edentula's* range under all climate scenarios and was most pronounced when climate change occurred (Figure 4; Figure S1.4). Range-wide genetic diversity measured as the average number of alleles per locus was slightly greater in the absence of climate change (NA = 45.1) and low-emission climate scenarios (NA = 45.2) in comparison with the high-emission climate change scenarios (NA = 41.7) (Figure 4).

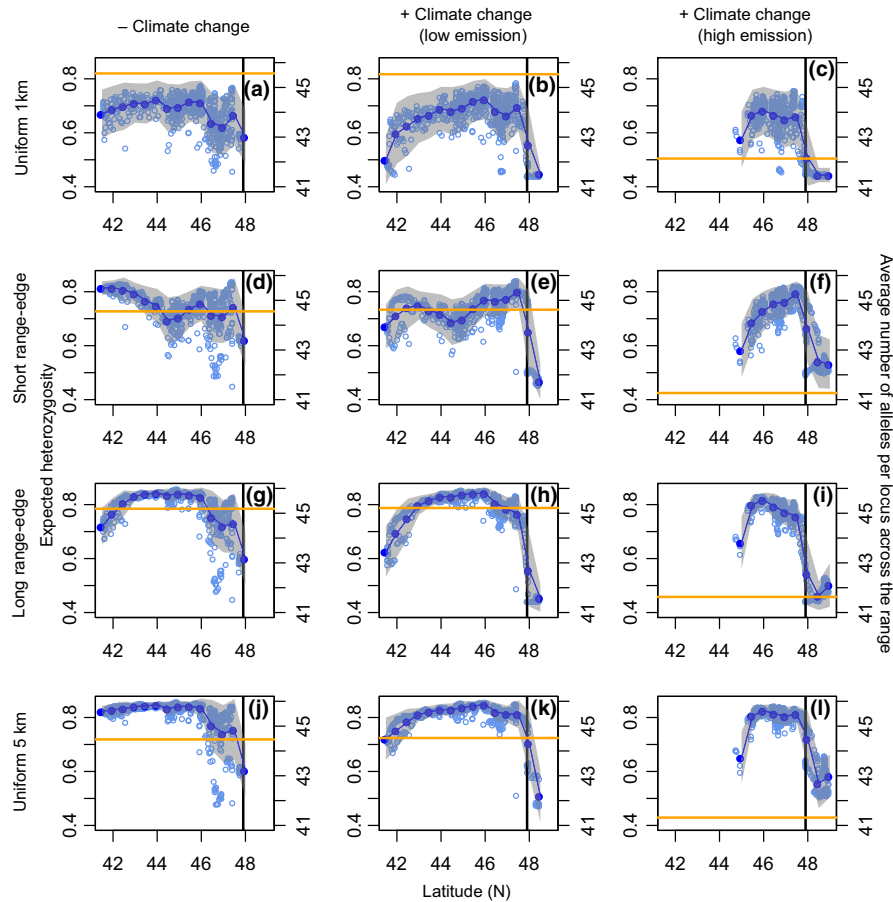


**FIGURE 2** Changes in the dispersal kernel over 105 generations for dispersal scenarios with no adaptive evolution. (a) present-day climate and uniform-1 km dispersal, (b) low-emission and uniform-1 km dispersal, (c) high-emission and uniform-1 km dispersal, (d) present-day climate and uniform-5 km dispersal, (e) low-emission and uniform-5 km dispersal, (f) high-emission and uniform-5 km dispersal, (g) present-day climate and short range-edge dispersal, (h) low-emission and short range-edge dispersal, (i) high-emission and short range-edge dispersal, (j) present-day climate and long range-edge dispersal, (k) low-emission and long range-edge dispersal and (l) high-emission and long range-edge dispersal. Insets (far left) illustrate the dispersal distance across the latitudinal range at the beginning of the simulation and colour scale (far right) illustrate the average dispersal distance ranging from short (purple) to long (red). Grey squares indicate a 0.5 degree area of latitude in the range that contained no individuals



**FIGURE 3** Changes in the dispersal kernel over 105 generations for scenarios when dispersal kernels were allowed to evolve in response to climate-induced changes to habitat quality over the course of the simulation. (a) present-day climate and uniform-1 km dispersal, (b) low-emission and uniform-1 km dispersal, (c) high-emission and uniform-1 km dispersal, (d) present-day climate and uniform-5 km dispersal, (e) low-emission and uniform-5 km dispersal, (f) high-emission and uniform-5 km dispersal, (g) present-day climate and short range-edge dispersal, (h) low-emission and short range-edge dispersal, (i) high-emission and short range-edge dispersal, (j) present-day climate and long range-edge dispersal, (k) low-emission and long range-edge dispersal and (l) high-emission and long range-edge dispersal. Insets (far left) illustrate the dispersal distance across the latitudinal range at the beginning of the simulation and colour scale (far right) illustrate the average dispersal distance ranging from short (purple) to long (red). Grey squares indicate a 0.5 degree area of latitude in the range that contained no individuals





**FIGURE 4** Effects of geographic variation in dispersal distance and adaptive evolution of dispersal distance on the spatial distribution of expected heterozygosity (left y-axis) and average number of alleles per locus for 50 microsatellites across the species' range (right y-axis). Panels are as follows: (a) present-day climate and uniform-1 km dispersal, (b) low-emission and uniform-1 km dispersal, (c) high-emission and uniform-1 km dispersal, (d) present-day climate and short range-edge dispersal, (e) low-emission and short range-edge dispersal, (f) high-emission and short range-edge dispersal, (g) no climate change and long range-edge dispersal, (h) low-emission and long range-edge dispersal and (i) high-emission and long range-edge dispersal, (j) present-day climate and uniform-5 km dispersal, (k) low emission and uniform-5 km dispersal and (l) high emission and uniform-5 km dispersal. Expected heterozygosity was calculated for each locus and then averaged across loci within a patch. The filled blue circles represent the mean expected heterozygosity over 0.5 degrees of latitude at year 2105 (left y-axis), the grey shading is the standard deviation of the mean, and the light blue open circles are the estimates for individual populations. The orange horizontal line represents the average number of alleles per locus across the range in year 105 (right y-axis). The black vertical line at latitude = 47.9 marks the northern range limit from year 0 to 25 during present-day climate

## 4 | DISCUSSION

Even in the absence of dispersal evolution, geographic variation in dispersal distances can play an important role in determining range-wide outcomes for species' responses to climate change. In our analysis of *C. edentula*'s geographic range, individuals that had longer (5 km) dispersal distances, either uniformly across the species' range or only in edge patches, could colonize novel habitats more quickly, enabling the species' northern range edge to keep pace with changing environmental conditions (Figure 2). When individuals had uniformly short dispersal distances across the species' range, or when range-edge populations had relatively short dispersal distances, the northern limit could not keep pace with changing climatic conditions because patches that became suitable north of the range limit were not colonized. To date, remarkably few studies have rigorously

quantified the extent and distribution of intraspecific variation in dispersal (Johnson et al., 2019; Saastamoinen et al., 2018). Our results highlight that the incorporation of empirical estimates of key dispersal parameters could substantially alter predictions of species' range dynamics in response to climate change.

The interaction between geographic variation in dispersal and dispersal evolution results in complex outcomes that are not always intuitive. For example, a *C. edentula* range characterized by short range-edge dispersal ultimately evolved longer dispersal distances and colonized habitat more quickly at range limits than a range with a uniform initial dispersal distance of 1 km (cf., Figure 3i,b). This result occurred because gene flow from the interior portion of the range increased the genetic variation in dispersal distances at the range edge more quickly than mutation, allowing a faster response to selection. In all four dispersal scenarios, longer dispersal distances

evolved than were present in any habitat patch at the start of the simulations, which is consistent with other individual-based models that investigated how dispersal evolves in response to climate change (Boeye et al., 2013; Dytham et al., 2014; Hargreaves et al., 2015; Henry, Bocedi, Dytham, & Travis, 2014; Hillaert, Boeye, Stoks, & Bonte, 2015). This result suggests that even if metapopulations are at equilibrium with respect to dispersal distances prior to the onset of climate change, they are unlikely to remain at equilibrium as climate change progresses. Spatial sorting has the potential to substantially increase dispersal distance at an expanding range front without dispersal evolving (Shine et al., 2011). However, we found the distribution of dispersal distances across the species' range through time remained relatively constant when dispersal was not allowed to evolve (Figure 2), suggesting that spatial sorting alone does not explain the increases in dispersal distances that developed at expanding northern limits when dispersal evolved (Figure 2c; Figure 3c), at least at the spatial scale evaluated in our model. Finally, our model suggests that, when dispersal is heritable, longer dispersal distances will evolve at southern range limits in response to climate change. Previous studies have shown that there can be both selection for (Hillaert et al., 2015) or against long-distance dispersal at contracting range edges (Boeye et al., 2013; Henry et al., 2014); our result can be explained by the short-term increases in individual fitness that are gained by dispersing away from the contracting southern range limit where habitat quality is declining. However, because our model only included the evolution of dispersal distance and not direction (as expected for many passively dispersing organisms, but not necessarily active dispersers), consistent with spatial sorting (Hastings, 1983), the descendants of highly dispersing parents continued to occupy the southern-most habitat patches. This phenomenon was observed in both the low- and high-emission scenarios but was more commonly observed with an initial short range-edge than with the long range-edge dispersal pattern.

The overall ability for a species to colonize new habitat over short time-scales (e.g., years to decades) may depend upon both the initial dispersal potential of the species and the pattern of geographic variation in dispersal. When the initial mean dispersal distance in northern edge populations are relatively small, as in the uniform-1 km and short range-edge scenarios, dispersal evolution was required for range expansion to occur under climate change (Figure 2b,c,h,i; Figure 3b,c,h,i). However, dispersal evolution was not required for range expansion when northern populations had relatively high dispersal potential prior to the onset of climate change, as in the uniform-5 km and long range-edge scenarios (Figure 2e,f,k,l). Collectively, these results indicate that even though dispersal is likely to evolve under all climate change scenarios, successful range expansion is highly dependent on dispersal evolution when the populations at the expanding edge have limited dispersal potential. Furthermore, geographic variation in dispersal influenced range expansion even in the presence of long dispersal distances; the long and short range-edge dispersal scenarios could not colonize habitat as quickly (one decade slower) as the scenario with the longest uniform dispersal distance.

In this model, we assumed that the dispersal patterns of the offspring were determined by the parental plant, as is the case for *C. edentula* (Donohue, 1999), such that the parental plants not only dictate the dispersal characteristics of the seeds, but also contribute directly to dispersal via characteristics such as plant height. Maternal dispersal traits are particularly likely to influence the dispersal kernel of offspring in plants compared to that in animals (Starrfelt & Kokko, 2010). These differences highlight the importance of creating species' distribution models that include taxa-specific dispersal characteristics, such as the parental contribution to the dispersal kernel. When the phenotypic characteristics that determine the dispersal kernel for a species are known, data on variation in those traits can be paired with models that evaluate how variation in these traits influence predicted range shifts under environmental change (Dytham et al., 2014). To incorporate evolutionary changes in traits, it is also useful to know their underlying genetic architecture (e.g., numbers of loci, dominance, epistasis) and heritability under varying environmental conditions (Saastamoinen et al., 2018).

Neutral genetic diversity within populations across a species' range is an important consideration in conservation and should be incorporated into species' distribution models that strive to predict the response of species to climate change (i.e., Edmonds et al., 2004; Klopstein et al., 2006). While the interactive effects of geographic variation in dispersal and dispersal evolution may ultimately dictate if new patches are colonized, the neutral effects associated with colonization, such as population bottlenecks, can have large effects on remaining genetic diversity. In our analysis, adaptive evolution always reduced neutral genetic diversity across the species' range (Figure 4; Figure S1.4); furthermore, dispersal evolution allowed for increased colonization of new habitat, further reducing the amount of neutral genetic diversity in all newly colonized populations due founder effects (Edmonds et al., 2004; Klopstein et al., 2006). These effects unfolded irrespective of climate change regime or the initial pattern of geographic variation in dispersal. The genome-wide reduction in genetic diversity associated with increased colonization may be substantial, as loci that are putatively neutral with respect to climate change may be required for future adaptive responses to other environmental changes (e.g., infectious disease, habitat alterations) (Bridle & Vines, 2007; Eckert et al., 2008; Gaston, 2009).

Even though the interaction between geographic variation and adaptive evolution in dispersal is complex, accounting for these multifaceted interactions can substantially improve our potential to design conservation strategies that successfully manage populations, species and communities threatened by climate change. Here, we found that incorporating dispersal variation and adaptive evolution into species distributions models had large effects on the range dynamics that are predicted for one species, and we hypothesize that predictions for other species would change as well. According to our study, dispersal measured at one point in a species' range will potentially lead to significant errors in predicted range shifts with climate change if dispersal distances vary across the species' range. Overall, our results emphasize that more detailed experimental and observational studies of dispersal variation for individual taxa are required to better predict

the eco-evolutionary responses of different species to ongoing and future environmental change.

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## DATA ACCESSIBILITY

The habitat suitability maps and code for the individual-based model used to generate all data in the manuscript are available from the Dryad Digital Repository: DOI: <https://doi.org/10.5061/dryad.64d2h47>.

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## BIOSKETCH

The goal of this research team is to further the understanding of how rapid evolution influences range dynamics under environmental change through the combination of modelling and empirical approaches. The team focuses on critical drivers underlying species distributions such as dispersal, habitat specialization and the evolution of domestication or invasion. This study was the product of a doctoral dissertation project conducted at Purdue University by E.A.L.

Author contributions: E.A.L., N.C.E and M.R.C. conceived the study idea; L.B. created the climate data; E.A.L. and M.R.C. developed the individual-based model; E.A.L. collected the data, analysed the data and led the writing; all authors edited the manuscript.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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