Identifying robust strategies for assisted migration in a competitive stochastic metacommunity

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Abstract

Assisted migration is the translocation of species beyond their historical range to locations that are expected to be more suitable under future climate change. However, a relocated population might fail to establish within its donor community if there is high uncertainty in decision making, climate, and interactions with the recipient ecological community. To quantify the benefit to persistence and risk of establishment failure of assisted migration under different management scenarios, we built a stochastic metacommunity model to simulate several species reproducing, dispersing, and competing on a temperature gradient as temperature increases over time. Without assisted migration, the species in our model were vulnerable to climate change if they had low population sizes, short dispersal, and strong poleword competition. When relocating species that exemplified these traits, assisted migration increased the long-term persistence of the species most when relocating a fraction of the donor population, even if the remaining population was very small or rapidly declining. This suggests that leaving behind a fraction of the population could be a robust approach, allowing managers to repeat assisted migration in case they move the species at the wrong place and wrong time, especially when it is difficult to identify a species' optimal climate. We found that assisted migration was most beneficial to species with low dispersal ability and least beneficial to species with narrow thermal tolerances, for which assisted migration increased extinction risk on average. Lastly, while relocation did not affect the persistence of non-target species in our simple competitive model, researchers will need to consider a more complete set of community interactions to comprehensively understand invasion potential.

Keywords

managed relocation, community ecology, climate change, stochastic model, translocation, dispersal

Introduction

Global biodiversity is expected to decline with projected climate change (Urban 2015). Among the species at risk of extinction are those with limited dispersal, narrow ranges, narrow climate tolerance, and low population sizes (Pearson 2006; Tewksbury et al. 2008). Competition and other community interactions could increase extinction risk, as negative interactions can limit the dispersal of species that might be otherwise adequate dispersers (Davis et al. 1998; Gilman et al. 2010; Urban et al. 2012). Many of these climate-threatened species face a high likelihood of extinction without human intervention, prompting scientists and managers to consider a variety of novel approaches to conservation (Heller & Zavaleta 2009). Among these approaches is assisted migration (AM), in which managers relocate individuals from a threatened population to a location outside their historical range that is expected to be more suitable under future climates (McLachlan et al. 2007). By allowing these species to reach favorable climates in densities that they would not be able to reach on their own, AM could increase the likelihood of persistence for climate-threatened species or protect species with high ecological and socioeconomic value in ways that traditional conservation strategies might not (McLachlan et al. 2007; Heller & Zavaleta 2009; Lawler & Olden 2011; Schwartz et al. 2012, Lunt et al. 2013).

Even with potential conservation and socioeconomic benefits of AM, moving a species into a novel ecosystem could incur many risks (Ricciardi & Simberloff 2009; Hewitt et al. 2011). Ecological risks include the risk that a relocated species becomes invasive within its recipient community (Mueller & Hellmann 2008), the risk of spreading pathogens and parasites (Simler

et al. 2018), demographic costs of increased elevated stress on individuals when relocating individuals (Dickens et al. 2010), and the loss of genetic diversity when creating small founding populations and donor populations (Kekkonen & Brommer 2015). Demographic and genetic risks might contribute to the risk of a species failing to establish after relocation (Chauvenet et al. 2013; Plein et al. 2016) as seen with the low-to-intermediate success of previous conservation translocations across a wide range of taxa (Fischer & Lindenmayer 2000; Godefroid et al. 2011; Bellis et al. 2019). Establishment failure could accelerate the negative impacts on climate-threatened species by reducing the population size and genetic diversity while diverting the limited resources available to conservation (McDonald-Madden et al. 2008; Hewitt et al. 2011). This risk also depends, in part, on uncertainties that lead managers to relocate a species into the wrong place at the wrong time, especially if there are narrow conditions under which a species can persist. One source of uncertainty that leads to translocation failures is environmental stochasticity (Wolf et al. 1996), which will likely increase with climate change (Vasseur et al. 2014). Additional uncertainty stems from the difficulty in quantifying and differentiating between the abiotic and biotic drivers of species' ranges (Case et al. 2005), which could become increasingly uncertain with climate change (Boiffin et al. 2017). Given these uncertainties, a key management challenge is developing robust approaches over a range of conditions (McDonald-Madden et al. 2008) for the array of decisions involved in AM. This involves evaluating which species are vulnerable to climate-threatened extinction, which species will likely benefit from AM, when and where to move a species, and how many individuals to move (McDonald-Madden et al. 2011; Rout et al. 2013).

Despite a lack of consensus among the scientific community and the public about the benefits and risks of AM (Hewitt et al. 2011; Javeline et al. 2015; St-Laurent et al. 2018), several species are already being relocated (Seddon et al. 2015). Scientific guidance for AM endeavors is available from existing AM decision-making frameworks, which typically focus on optimizing a species' persistence under climate change using single-species models (McDonald-Madden et al. 2008; Armstrong and Reynolds 2012; Rout et al. 2013; Kling et al. 2016). Extending these to a multispecies framework is a crucial next step to account for the species interactions that give rise to the risks of invasiveness and uncertainty in the drivers of species range.

In this paper, we quantify the benefit to persistence, risk of failed translocation, and risk of impeded non-target species response of AM given competitive interactions, multiple sources of uncertainty, and an array of management decisions. We built a stochastic metacommunity model to simulate competing species undergoing climate change to estimate which species were vulnerable to extinction, which species were likely to benefit from AM, and what fraction of the population to relocate. Though the dynamics of interacting communities that give rise to the risk of invasiveness are often complex as noted above, involving many direct and indirect trophic interactions (Holt 1984; Chesson & Kuang 2008), we focus on competitive interactions because of their role in driving species' range limits, rooted in long-standing ecological theory (Connell 1972) and established as the most extensively studied and best-supported species interaction for driving range limits (Sexton et al 2009). Due to this role in affecting species' ranges generally, competition has a significant potential to affect range shifts and persistence under climate change (Urban et al. 2012; Ettinger & HilleRisLambers 2013), the dynamic central to the AM decisions on which we focus. For abiotic drivers of the species' range, because

managers will have limited knowledge of a species' optimal climate (a reducible uncertainty), we simulated relocation with uncertainty in estimating of species' thermal optima. By repeating these simulations under different levels of environmental stochasticity (an irreducible uncertainty), we identified characteristics of successful AM approaches that were robust over a wide variety of uncertainty scenarios.

Methods

Model overview

To compare assisted migration (AM) strategies, we modeled metacommunity dynamics of multiple species competing on a one-dimensional linear temperature gradient subjected to climate change, analogous to a previous model by Urban et al. (2012) with environmental stochasticity. For simplicity, all species in this metacommunity are annuals competing over the same resources at the same trophic level. The model cycles through reproduction, dispersal, and competition, all with demographic stochasticity, in each time step (Fig. 1). Each species i has a unique dispersal distance (γ_i), thermal optimum (z_i), thermal tolerance breadth (σ_i), and a reproductive strength parameter (r_i) that scales the birth rate to create a specialist/generalist trade-off (Levins 1968). We simulate AM by selecting one target species and relocating a fraction of its total population toward the leading edge each time the population falls below a threshold population size. We compared outcomes when relocating different target species with different fractions of the population into different locations.

For our outcomes, we analyze the potential benefit of AM based on the target species' persistence likelihood throughout all locations. Persistence likelihood also indicates the risk of translocation failure due to uncertainty and stochasticity. We measure the risk of invasiveness from competitive interactions based on the persistence likelihood of non-target species as well as the overall gamma diversity (inverse Simpson's index). Though this metric only represents an extreme outcome on the continuum of possible invasive impacts on community structure and ecosystem function (Blackburn et al 2014), many other metrics would require investigation beyond competitive interactions within a trophic level.

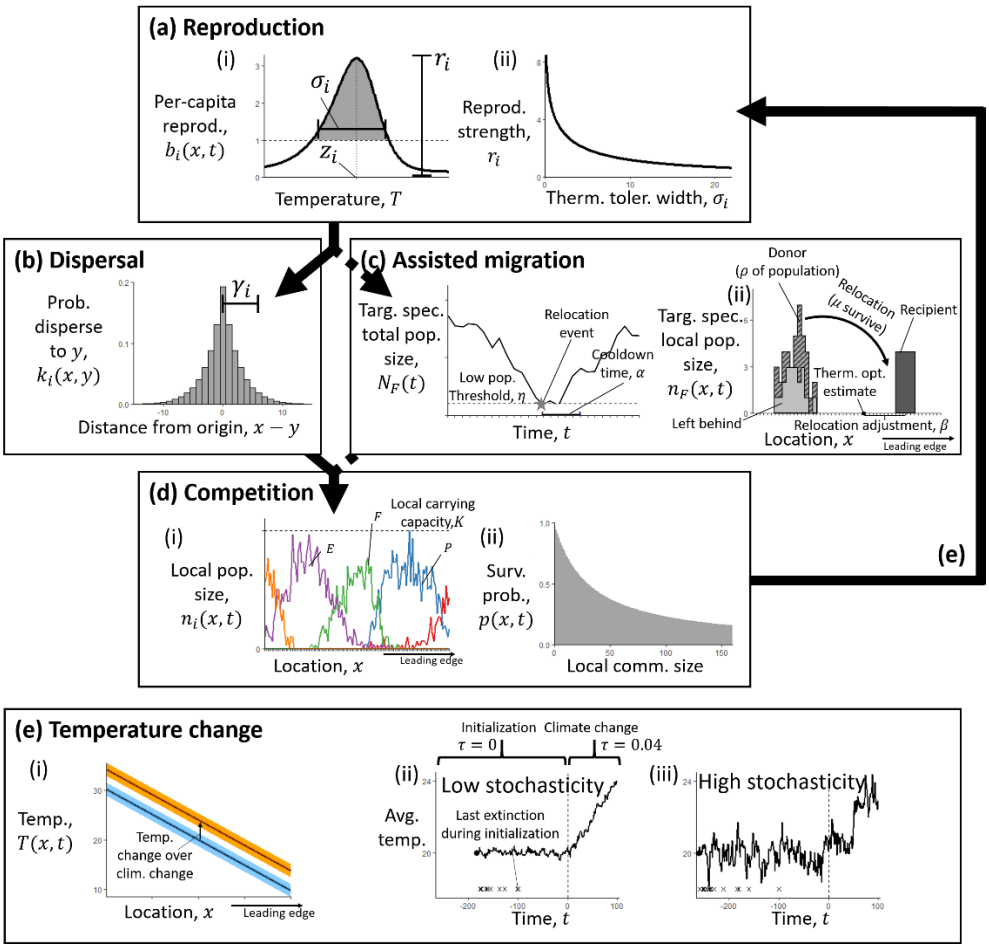

Figure 1: During each time step of the model, all extant species cycle through (a) reproduction, (b) dispersal, and (d) competition before (e) the temperature changes and the next time step continues. The target species also experiences (c) assisted migration during certain time steps. (a.i) Per capita reproductive output $b_i(T(x,t))$ is skew-normal, dependent on temperature $T(x,t)$. This function is shaped by species' thermal optimum z_i and thermal tolerance breadth σ_i. (a.ii) Reproductive strength r_i scales the total reproductive output so that species with narrow σ_i (specialists) have higher reproduction and species with broad σ_i (generalists) have lower reproduction. (b) The dispersal kernel is a long-tailed "double geometic" distribution with a mean dispersal distance γ_i. (c.i) Relocation occurs once the total population of target species F falls below a threshold η. To avoid repetition while F recovers, no relocations occur during a cool-down period following relocation α. (c.ii) A fraction ρ of population F is removed from its original distribution and moved to a new location (only μ survive) β patches beyond the leading edge. Remaining individuals disperse naturally. (d.i) All species compete over limited space, where each patch has a carrying capacity K. Here each line represents a different species. (d.ii) In each patch, individual survival probability $p(x,t)$ decreases as the total community size increases. (e) Temperature changes stochastically over time. (e.i) Mean temperature decreases linearly with space. Over time, between $t = 0$ (lower line) and $t = 100$ (upper line), the temperature increases by 4°C. (e.ii-iii) Temperature variation over time depends on level of environmental stochasticity. Both examples have the same autocorrelation (κ), but (ii) has a higher standard deviation (ψ). The vertical dashed line designates when the model changes from the initialization phase (average temperature change ($\tau = 0$)) to the climate change phase ($\tau = 0.04$). Climate change only occurs after a relatively stable metacommunity has been assembled, after 100 time steps have passed with no extinctions.

Population dynamics

Each species i has a local population size of $n_i(x,t)$ individuals in discrete patch x and a total metapopulation size over all space X of $N_i(t) = \sum_{x \in X} n_i(x,t)$ at discrete time t. First, all individuals reproduce (Fig. 1a) with a reproductive output $b_i(T(x,t))$ that depends on local temperature $T(x,t)$. Temperature-dependence is skew-normal, given skewness constant λ, where highest values around the thermal optimum z_i and a sharp decrease above z_i (Norberg 2004). Thermal tolerance breadth σ_i and reproductive strength r_i determine the breadth and height of the temperature-dependence. Altogether, $b_i(T(x,t))$ is

$$b_i\big(T(x,t)\big) = \exp\left(r_i\left\{\exp\left[-\left(\frac{T(x,t)-z_i}{\sigma_i}\right)^2\right]\cdot\left[1+erf\left(\lambda\frac{T(x,t)-z_i}{\sigma_i}\right)\right]-1\right\}\right) \quad (1)$$

(following Urban et al. 2012). To incorporate demographic stochasticity, the number of propagules produced by species i in patch x is a Poisson random variable with mean equal to the reproductive output, $n_i^*(x,t) \sim \mathrm{Poisson}(n_i(x,t)b_i(T(x,t))$ (Melbourne & Hastings 2008).

Next, each propagule disperses from its origin (Fig. 1b). We adapted the Laplace dispersal kernel to a discrete-space analog (Appendix S1). We define γ_i as the mean absolute distance (in patches) that species i moves from its origin and let kernel parameter $q_i = \frac{\gamma_i+1-\sqrt{\gamma_i^2+1}}{\gamma_i}$. Thus, the probability of a propagule from patch x moving to patch y is

$$k_i(x,y) = \left(\frac{q_i}{2-q_i}\right)(1-q_i)^{|x-y|}. \quad (2)$$

All propagules of species i disperse from patch x throughout all space X with the random vector $M_i(n_i^*(x,t), x, X, t) \sim \text{Multinomial}\big(n_i^*(x,t), k_i(x,X)\big)$, and the vector of local populations after dispersal is $n_i^{**}(X,t) = \sum_{y \in X} M_i(n_i^*(y,t), y, X, t)$.

Lastly, dispersed propagules compete within each patch x given community-wide carrying capacity K (Fig. 1d). We assumed a variation on lottery competition (Sale 1978; Chesson & Warner 1981), where each individual has an equal probability of surviving,

$$p(x,y) = \left(1 + \frac{\sum_{j=1}^{S} n_j^{**}(x,t)}{K}\right)^{-1}. \tag{3}$$

The total number of propagules of species i in patch x that survive after competition is a binomial random variable $n_i(x, t+1) \sim \text{Binomial}(n_i^{**}(x,t), p(x,t))$ (Melbourne & Hastings 2008). Therefore, the overall quality of a location, in terms of how it drives production and survival, depends on the constant carrying capacity K and match between the local environment and species thermal tolerance.

Spatial structure

Metacommunity dynamics occur across a one-dimensional, linear temperature gradient of L patches (Fig. 1e), representing gradual latitudinal or sharp elevational change (Urban et al. 2012). We remove propagules that disperse outside of the spatial gradient. Because these absorbing boundary conditions could bias our analyses, we disregard the first $\frac{L}{8}$ patches on the poleward edge and the last $\frac{3L}{8}$ patches on the equatorward edge when measuring species and community metrics.

Temperature changes each time step by mean τ with autocorrelation κ and standard deviation ψ around white noise $\omega(t)$. The stochastic component of yearly temperature change is $\epsilon(t+1) = \kappa\epsilon(t) + \omega(t)\sqrt{1+\kappa^2}$, with the square root term to remove the effect of autocorrelation on the variance (Wichmann et al. 2005). Altogether, the temperature in patch x changes over time as

$$T(x, t+1) = T(x, t) + \tau + \psi\epsilon(t). \tag{4}$$

Assisted migration

AM focuses on a single target species (Fig. 1c), species F. We relocate species F if its total metapopulation size $N_F(x, t)$ is below a threshold η at the beginning of a time step. Though population size would need to be estimated in real-world applications, we assume perfect knowledge of population size in our focus on uncertainty in the drivers of a species' range. To avoid repeating AM before species F recovers, we only relocate if we did not previously relocate within the last α time steps. After reproduction, we select a fraction of propagules ρ for AM, randomly chosen from throughout the species' range, while the remaining propagules are left behind to disperse naturally (the donor population). From the propagules chosen for AM, only a proportion μ survive relocation, and those are relocated uniformly among five connected patches around a patch β spaces poleward of the patch that most closely matches the species' estimated thermal optimum (the recipient population).

We considered three methods of estimating the thermal optimum of species F. The perfect knowledge estimate is the exact value of the true thermal optimum z_F. The realized

175 niche estimate is the temperature in the median patch of the target species' distribution at $t =$
176 0. The fundamental niche estimate measures species' limits without competition by simulating
177 100 time steps with $\tau = 0$°C/year and only species F. This estimate is the temperature in the
178 median patch of the resulting distribution.

179 *Parameterization and implementation*

180 Simulations occurred on a temperature gradient with $L = 512$ patches, where initial
181 temperatures linearly varied over space from 9.78°C to 30.22°C. We considered two types of
182 environments, defined by the degree of stochasticity. Low-stochasticity environments had an
183 annual temporal standard deviation of $\psi = 0.1639$°C, equal to the standard deviation of mean
184 combined global land-surface air and sea-surface water temperature anomalies from 1880 to
185 1979 (GISTEMP Team 2019; Lenssen et al. 2019), and high-stochasticity environments had four
186 times that amount. Both had an annual temporal autocorrelation of $\kappa = 0.767$, also from
187 temperature anomalies from 1880 to 1979. We used skewness constant $\lambda = -2.7$ (Urban et al.
188 2012) and carrying capacity $K = 30$ individuals. We chose this parameter space, including low
189 values for *K*, so that extinctions do occur for some species and AM is a relevant management
190 consideration (Appendix S2).

191 Before simulating climate change, we performed an initialization to assemble a
192 metacommunity with multidecadal coexistence under background environmental stochasticity.
193 First, we generated a pool of $S = 32$ randomized species, each with unique dispersal distances
194 γ_i, thermal optima z_i, and thermal tolerance breadths σ_i, all randomly generated from default
195 values in Urban et al. (2012) (Table 1). We numerically derived the reproductive strength r_i

from σ_i, such that each species had the same overall reproductive potential $B = 5$ when integrating over temperature. This emulates a jack-of-all-trades-master-of-none trade-off (Levins 1968), so that species ranged from generalists (wide σ_i, low r_i) to specialists (narrow σ_i, high r_i). We placed 25 individuals from each species into five adjacent patches that most closely matched each species' thermal optimum and iterated through the model with mean temperature change $\tau = 0$ °C/year until 100 time steps passed without any extinctions. The remaining communities set initial conditions for subsequent climate change simulations (Appendix S3).

Table 1: Definitions of the symbols used in the model.

Parameter	Symbol	Values	Units
Total species	S	32	species
Dispersal distance of species i	γ_i	Lognormal; mean=2.5, st. dev.=2.5	patches
Thermal optimum of species i	z_i	Uniform; 9.78 to 30.22	°C
Thermal tolerance breadth of species i	σ_i	Lognormal; mean=5, st. dev.=5	°C
Reproductive strength of species i	r_i	Derived from σ_i	-
Skewness constant	λ	-2.7	-
Fraction of population relocated	ρ	0, 0.05, 0.1, …, 1	-
Assisted migration survival probability	μ	0.8	-
Low population threshold	η	42	individuals
Cooldown time between relocations	α	5	years
Relocation adjustment (relative to optimum)	β	10	patches
Total patches	L	512	patches
Patch carrying capacity	K	30	Individuals
Mean annual temperature change	τ	0.04	°C/year
Annual temporal autocorrelation	κ	0.767	-
Annual temporal standard deviation	ψ	low=0.1639, high=0.6556	°C
Initial total population size of species i	$N_i(0)$	-	individuals
Difference in thermal optimum with species i	$z_{\mathrm{diff},i}$	-	°C
Inverse Simpson's index of region W	D_W	-	-
Measured temperature change	c_T	-	°C
Measured SD in temperature	s_T	-	°C
Deviation in thermal optimum estimate	$z_{\mathrm{est,dev}}$	-	°C

Next, we modeled metacommunity dynamics under climate change without AM to determine which characteristics related to species, communities, and environments could predict species' vulnerability when unmanaged. After generating 2^{16} initialized communities under both low and high stochasticity, we iterated through 100 time steps with mean annual temperature change $\tau = 0.04$°C/year to reflect projected temperature changes under RCP8.5 (Urban et al. 2012, IPCC 2014). From these no-AM simulations, we chose the low-population threshold for AM $\eta = 42$, high enough that relocation could occur before extinction but low enough to avoid relocating species that would have persisted even without AM (Appendix S1).

Finally, we modeled metacommunity dynamics under climate change with AM to test the success of a suite of potential relocation decisions. We initialized 10000 metacommunities under both low and high stochasticity and chose several target species that could be considered vulnerable to climate change, including: the species with the shortest dispersal, the species with the narrowest thermal tolerance breadth, the species with the closest poleward neighbor, the species with the lowest initial population size, and a randomly selected species. All target species were initially extant within an interior region of the temperature gradient, $W \in [65,320]$, ensuring that their thermal optimum would likely exist after climate change and that there was competitive pressure on both the trailing and leading edges. We simulated each combination of target species type, fraction relocated ρ from 0 to 1 (by 0.05), and thermal optimum estimate while keeping consistent values for AM survival probability $\mu = 0.8$, cooldown time $\alpha = 5$, and relocation adjustment $\beta = 10$.

To determine which ecological characteristics could best predict species' vulnerability to climate change, we ran random forest classifications (`randomForest` 4.6-14 package, R Version 3.5.1) on all simulations without AM (separately for low and high stochasticity). The dependent variable was the fate of a single random species after climate change: global extinction or persistence throughout all locations, disregarding the fate in the original range. The independent variables were target species' thermal optimum (z_F), difference in thermal optimum between target species and neighbors ($z_{\mathrm{diff},P}$, $z_{\mathrm{diff},E}$), target and neighbor species' dispersal (γ_F, γ_P, γ_E), target and neighbor species' thermal tolerance breadths (σ_F, σ_P, σ_E); target and neighbor species' initial population sizes ($N_F(0)$, $N_P(0)$, $N_E(0)$), inverse Simpson's diversity index of the initial community (D_W), measured temperature change (c_T), and

measured standard deviation in temperature (s_T). Because persistence was more common than extinction, we down-sampled for equal sample sizes. The unscaled permutation variable importance of each independent variable estimated how well these characteristics predicted vulnerability and partial dependence quantified the marginal effect of the characteristics on vulnerability.

To determine what types of species and communities are conducive to AM success (increased persistence likelihood with AM), we ran another set of random forest classifications. The dependent variable was the fate of the target species and the independent variables were the same as above in addition to the deviation between the estimated and true thermal optimum ($z_{\mathrm{est,dev}}$). To focus on cases where target species specifically benefited from AM, we only included simulations in which the target species went extinct without AM. To simplify analysis, we focused on simulations with fraction-moved $\rho = 0.5$, shortest dispersers, and realized niche estimates.

Results

Without AM

Without assisted migration (AM), 91.3% of species persisted under climate change in low-stochasticity environments compared with 84.7% persistence under high stochasticity (Fig. 2a-b). In both cases, persistence depended most strongly on a small number of characteristics (random forest classifications; out-of-bag error: 8.09% low stochasticity, 11.27% high stochasticity) (Fig. 2c-d, Appendix S4). Persistence was lowest when a species had low initial

population sizes $N_F(0)$, short dispersal distances γ_F, and close poleward neighbors $z_{\mathrm{diff},P}$. Comparatively, competition largely determined persistence under low stochasticity, whereas dispersal largely determined persistence under high stochasticity (Appendix S5).

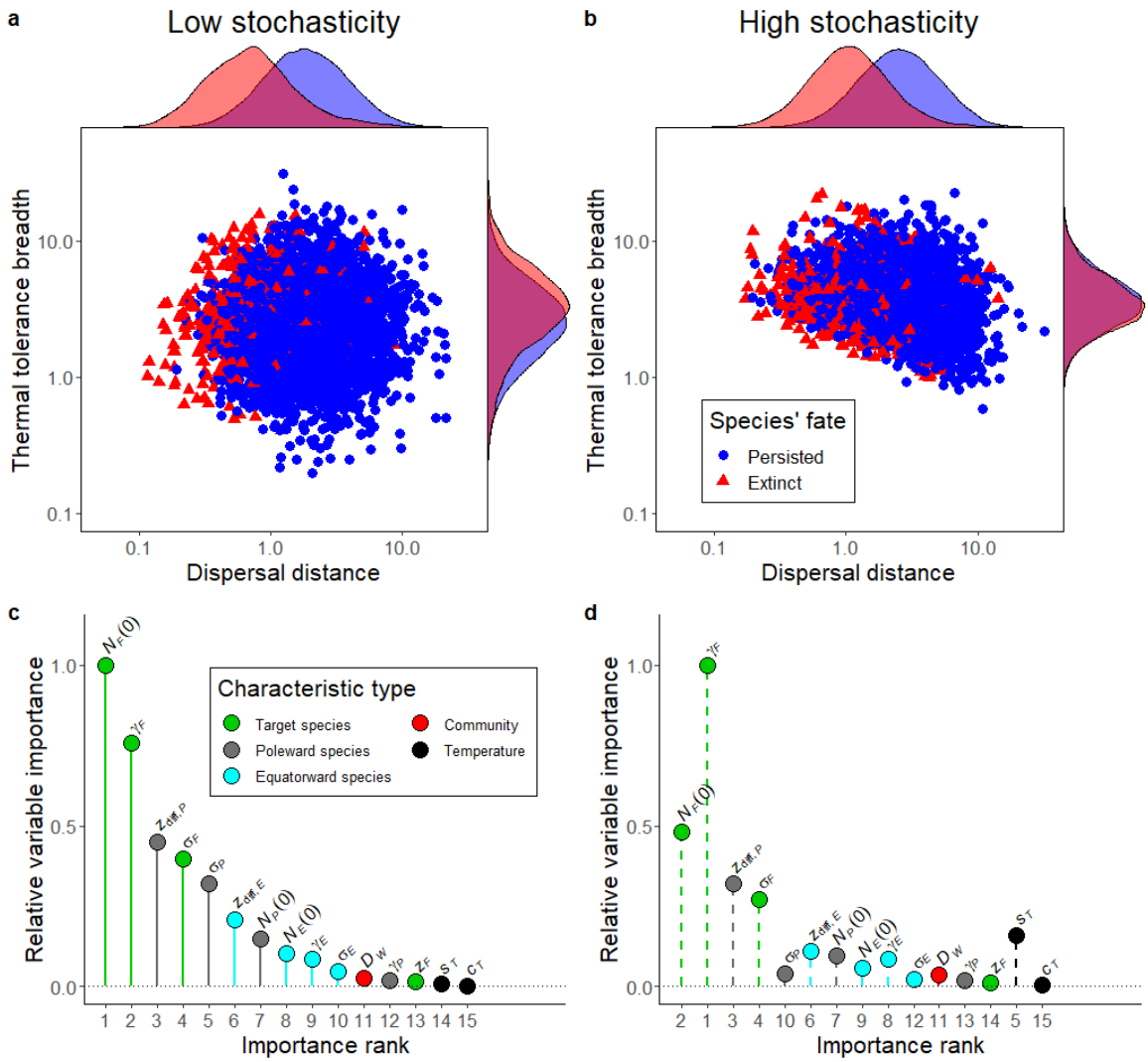

Figure 2: Species' persistence and the characteristics that predicted persistence varied with environmental stochasticity. (a,b) Each point shows the fate of a single species (triangle: extinction; circle: persistence) following climate change from a subset of unique simulations plotted over dispersal distance (horizontal axis) and thermal tolerance breadth (vertical axis). On the top and right of these plots are the marginal distributions of these parameters, separated by species' fate. Each axis is on a logarithmic scale. (c,d) Relative unscaled permutation importance of independent variables on species' persistence. Each characteristic is colored depending on whether it is a characteristic of the species, its neighbors, the full community, or the environment. The horizontal axis shows the rank of the variable importance compared to other variables (1 being the most important), arranged in the same order for both plots. See Table 1 for definitions of symbols.

With AM

Under all scenarios, target species had a higher chance of persisting when relocating an intermediate fraction of the total population during AM (Fig. 3, 4a-b). Moreover, target species

261 persistence was typically lower when relocating 100% of the total population than under no
262 relocation (except when the target species was the shortest disperser). Relocating an
263 intermediate fraction of the total population typically allowed the target species to exist in
264 higher densities relative to interacting species in both the donor and recipient communities
265 (Fig. 4c-d). On average, this increased the likelihood of long-term persistence of both the donor
266 and recipient populations (Fig. 4e-f) and overall persistence compared to no management
267 action (Fig. 3, solid vs. dotted lines). Often, AM involved multiple relocations (Fig. 5a-b), and the
268 higher AM success when relocating intermediate fractions came with more individual relocation
269 events (Fig. 5c-d). Assisted migration had little effect on the persistence of non-target species
270 and final community diversity (Appendix S6), so the remaining results focus on persistence
271 instead of invasion risk arising from the competitive interactions modeled here.

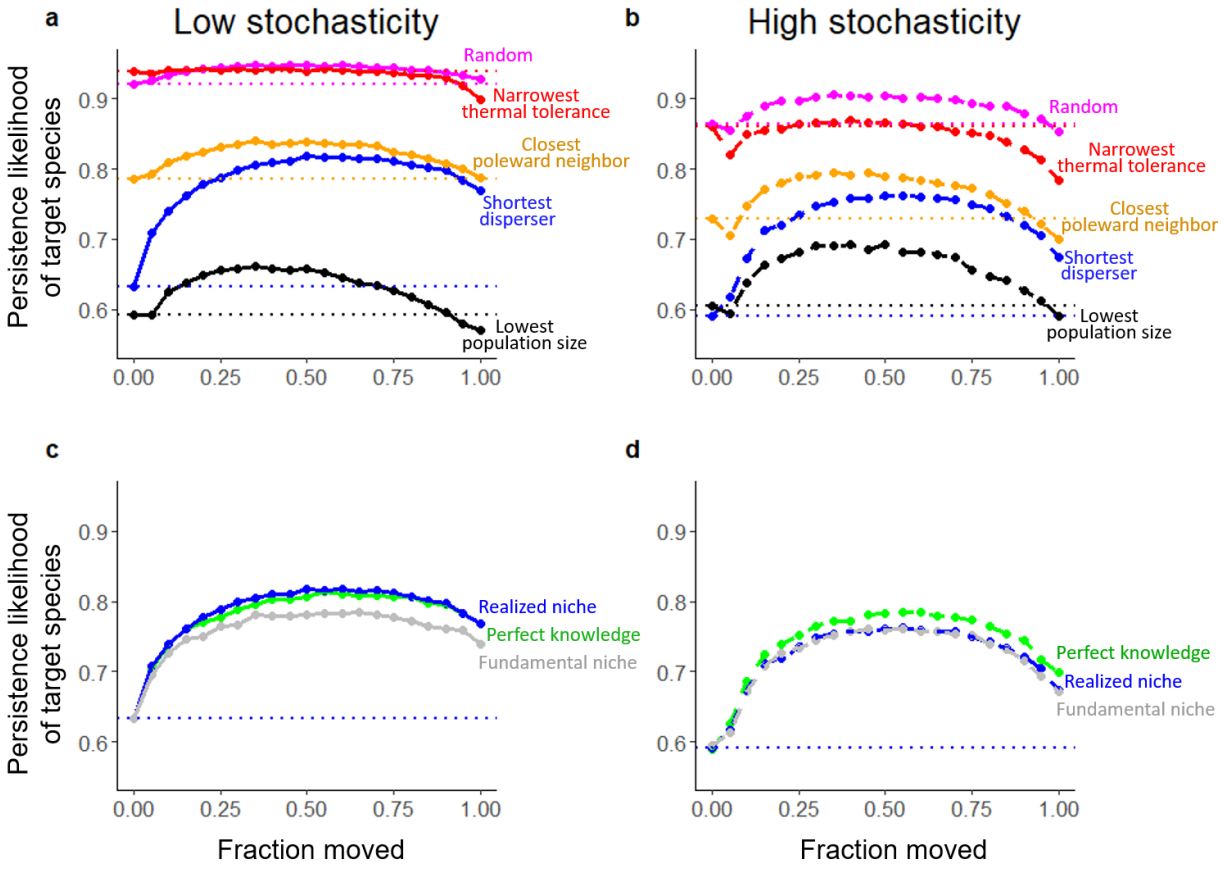

Figure 3: During climate change simulations, the persistence likelihood of a target species chosen for assisted migration (vertical axis) depended on the fraction of that population that was relocated (horizontal axis), and the level of environmental stochasticity (a,c: low, b,d: high). The dotted horizontal lines correspond to persistence likelihood without AM (zero moved, or no management action) and are colored to match each comparison. (a,b) The effect of assisted migration on target species' persistence with different types of target species chosen for relocation: random, narrow thermal tolerance, closest poleward neighbor, shortest dispersal, or lowest population size. The thermal optimum estimate used in each of these was the realized niche estimates (based on the species initial distribution). (c,d) The effect of assisted migration on target species' persistence with different types of thermal optimum estimates for relocation decisions: realized niche, fundamental niche, or perfect knowledge. The target species in each of these simulations was the species with the shortest dispersal. Note that the persistence likelihood for non-target species is unaffected (Fig. S5.1).

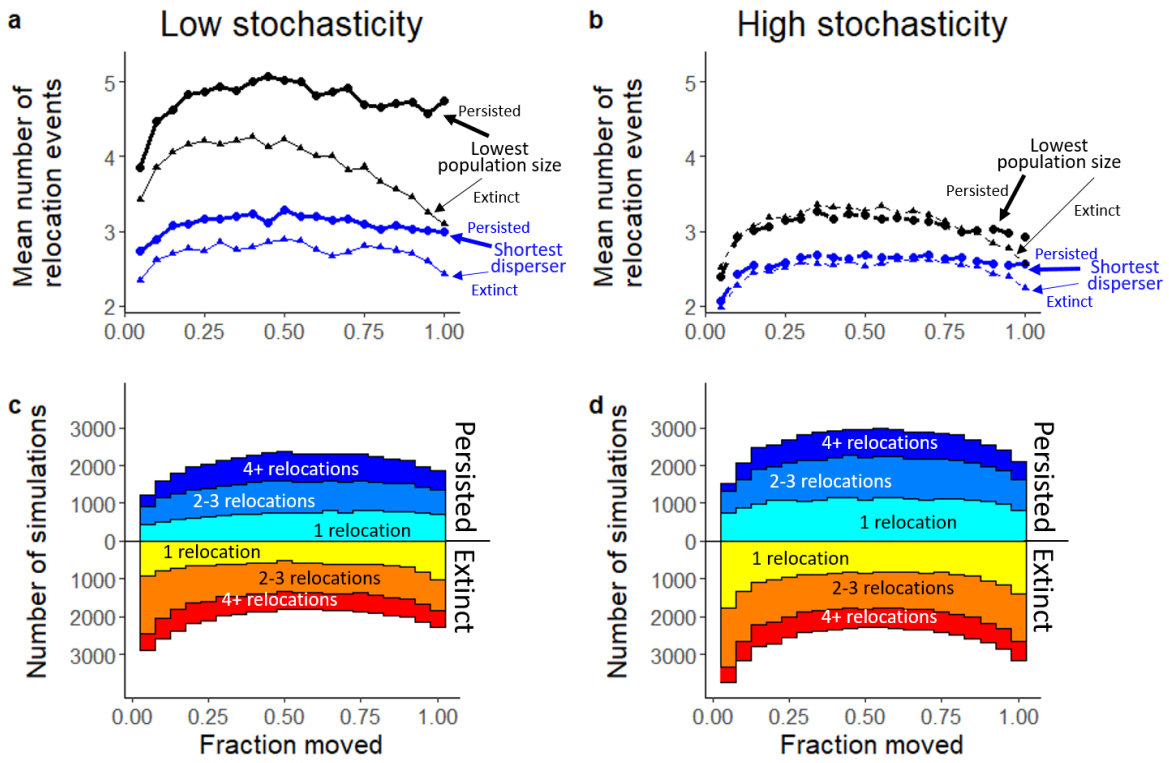

Figure 4: The number of independent relocation events that occurred during assisted migration simulations for low stochasticity (a,c) and high stochasticity (b,d) environments. (a,b) Among species that were relocated at least one time, the mean number of independent relocation events (vertical axis) that occurred under a range of values for the fraction of the population that was relocated each time (horizontal axis). Simulations are separated by target species (color) and whether or not the species went extinct (thick: persisted, thin: extinct). The simulations shown here use the initial distribution (realized niche) estimate of the species' thermal optimum. (c,d) We categorized assisted migration simulations by fate of the species (persistence/extinction) and the number of independent relocation events that occurred over the course of the simulation. Here we show the number of simulations that fall into these categories (colored differently) depending on the fraction of the population moved during assisted migration (horizontal axis). The center line in each sub-figure separates simulations where the target species survives (below the line) and where it goes extinct (above the line). Simulations shown here use the shortest disperser as the target species and the initial distribution (realized niche) estimate of the species' thermal optimum.

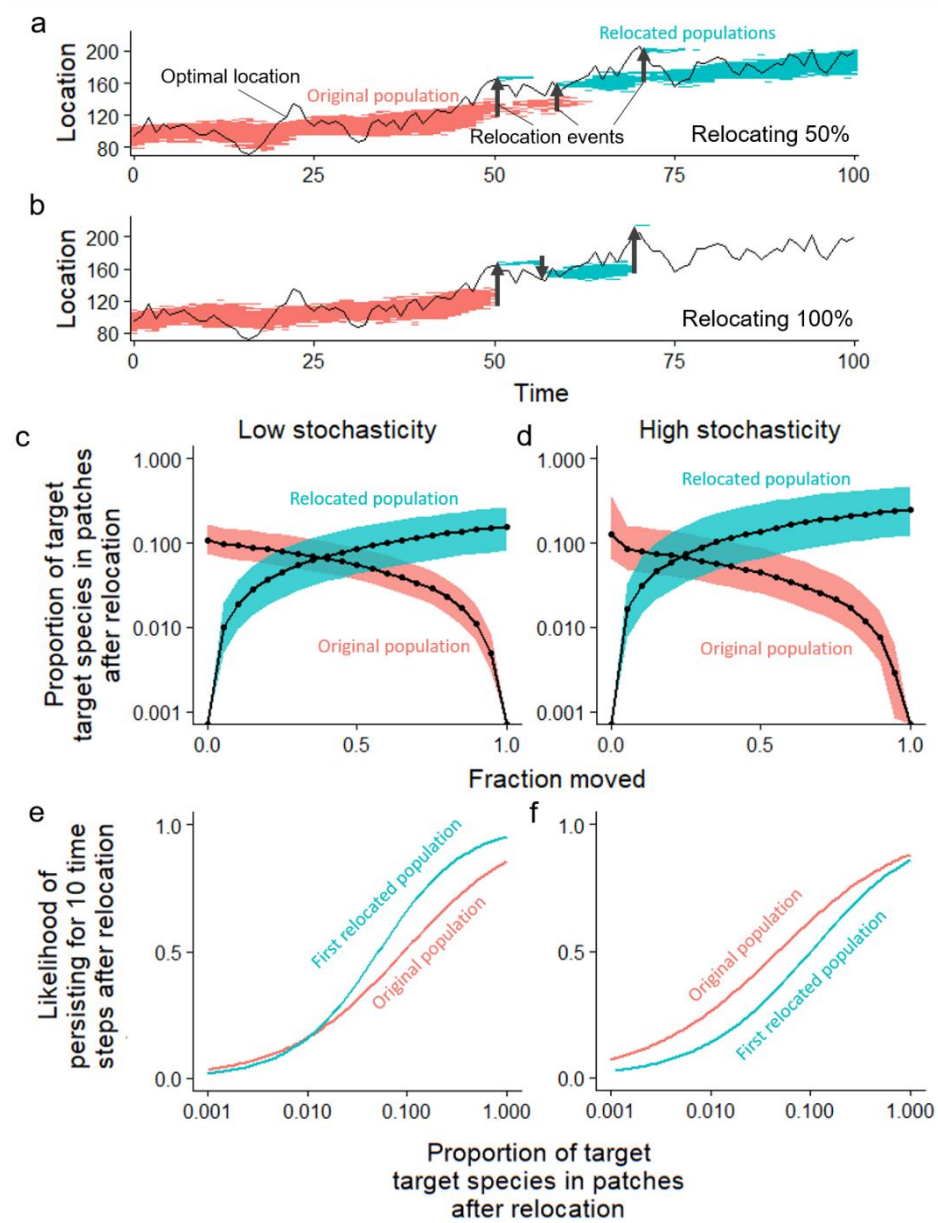

Figure 5: The dynamics and fate of original and relocated populations depend on what fraction of the total population is relocated. (a-b) Example simulations showing how the shortest dispersing species' range changes over time in a high stochasticity environment. The population follows its optimal climate (thin solid line) as it moves poleward (higher location number). If the total population size falls below a low threshold η, a fraction is relocated (thick arrows) based on the estimated thermal optimum. Original and relocated populations are colored separately. (c-d) After relocation, the composition of the donor and recipient communities depend on what fraction of the target species was relocated (horizontal axis). Solid lines represent the median value for the fraction of propagules in the community that are the target species, while the surrounding ribbons represent 25% and 75% quantiles. (e-f) The donor and recipient populations are more likely to persist for at least 10 time steps after relocation (vertical axis) if the target species makes up a higher fraction of the surrounding community (horizontal axis). Lines correspond to predictions from logistic regression.

Of the possible target species, the shortest dispersers experienced the greatest benefit from AM (Fig. 3a-b). For most treatments, AM also increased persistence of target species with the lowest population sizes, species with the closest poleward neighbors, and randomly picked species. However, AM usually decreased persistence of species with the narrowest thermal tolerances (specialists).

On average, AM had a similar effect on persistence regardless of how we estimated the species' thermal optimum (Fig. 3c-d). Under high stochasticity, AM was most successful with perfect knowledge of species' thermal optima, but under low stochasticity, AM was most successful with realized niche estimates. This difference suggests stronger competition in low-stochasticity environments such that competition set species limit more than species' inherent thermal tolerances.

For both levels of stochasticity, three of the top four most important variables for predicting AM success of the shortest disperser were the target species' initial population size $N_F(0)$, the target species' thermal tolerance breadth σ_F, and the difference in thermal optimum between the target species and its poleward neighbor $z_{\mathrm{diff},P}$ (random forest classifications; out-of-bag error: 25.27% low stochasticity, 30.56% high stochasticity) (Fig. 6a-b). AM was most successful when the values of these characteristics were higher (Fig. 6c-e), suggesting that AM is most likely to benefit generalists with higher population sizes and less poleward competition. Under low stochasticity, AM was less successful if the poleward neighbor was a specialist with narrow thermal tolerance breadth σ_P (Fig. 6f), implying that poleward competition limited AM success under low stochasticity but not as much under high

stochasticity. AM was also more successful when thermal optimum estimates were warmer than the true value (positive deviation of $z_{\mathrm{est,dev}}$) (Fig. 6g), and this effect was stronger under high stochasticity. Colder estimates placed target species further along the climate gradient, often beyond temperatures under which they can survive, so extreme year-to-year temperature change under high stochasticity would be more likely to drive the relocated population extinct if they are placed into the wrong location.

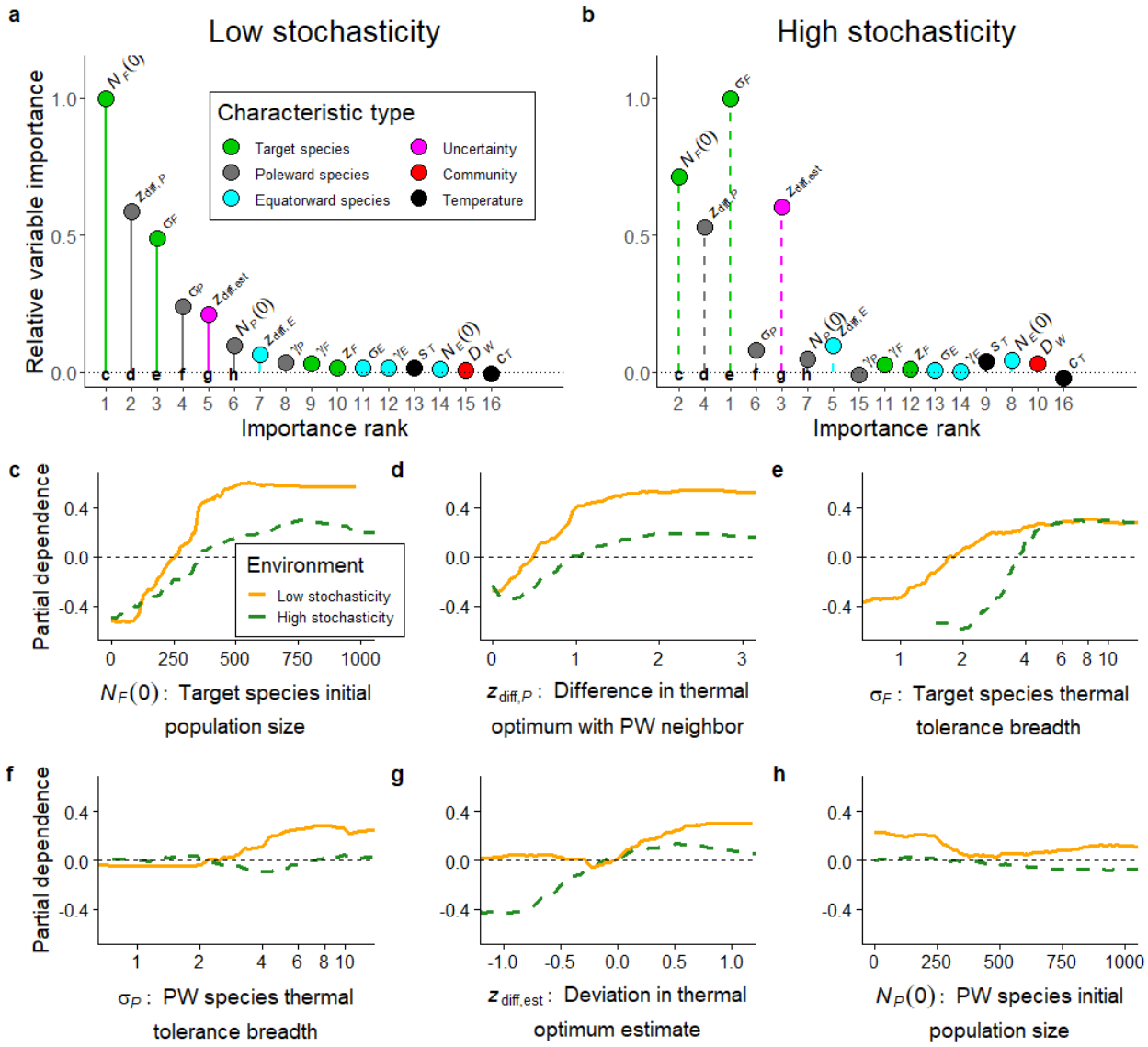

Figure 6: Importance of ecological characteristics from random forest classifications in determining whether assisted migration was successful for the target species (relocating 50% of the shortest dispersing species population with a realized niche estimate thermal optimum). (a,b) Relative unscaled permutation importance of independent variables of whether or not assisted migration improved species' persistence under low stochasticity (a) and high stochasticity (b). The horizontal axis shows the rank of the variable importance compared to other variables (1 being the most important), arranged in the same order for both plots. Each characteristic is colored depending on whether it is a characteristic of the target species, its neighbors, the full community, the environment, or uncertainty around the thermal optimum estimate. (c-h) Partial dependence of the values of 6 independent variables (corresponding to the top 6 important variables for low stochasticity labeled in panel (a) and (b)) on whether or not assisted migration will increase the shortest disperser's persistence. The vertical axis is the log-odds of whether assisted migration increases persistence of a species (higher being more likely to persist). Solid lines represent the low stochasticity environment and dashed lines represent the high stochasticity environment. See Table 1 for definitions of symbols.

313 ## Discussion

314 Our model suggests that assisted migration (AM) can be effective at increasing species'
315 persistence under climate change if the species is limited by short dispersal, small population
316 sizes, and competition (Fig. 3). However, like many related conservation translocations (Fischer
317 & Lindenmayer 2000), we found that AM often fails when the relocated population does not
318 establish, especially for narrow thermal tolerance species. Relocating an intermediate fraction
319 of the population was consistently an optimal strategy (Fig. 3) due to multiple possible drivers,
320 such as allowing additional relocation attempts after establishment failure (Fig. 4) and reducing
321 the degree of negative density dependence in both the donor and recipient populations (Fig. 5).

322 *Choosing species for AM*

323 Species are vulnerable to climate change for a variety of reasons, ranging from
324 dispersal-limitation (Pearson 2006), to narrow thermal tolerance (Tewksbury et al. 2008), to
325 competitive interactions (Gilman et al. 2010; Urban et al. 2012). Our model suggests that the
326 effectiveness of AM as a management strategy depends on the driver of vulnerability. In
327 particular, AM might not be appropriate for specialist, narrow-tolerance species. Because
328 specialist species usually persisted under climate change without AM (Fig. 2), narrow thermal
329 tolerance was not a limiting factor for persistence in this model. This arises because of our
330 assumption of a jack-of-all-trades-master-of-none trade-off (Levins 1968), where specialists had
331 a high reproductive performance over a smaller range of temperatures. Because of this trade-
332 off, specialists were stronger competitors under lottery competition (Chesson & Warner 1981),
333 and this competitive advantage could outweigh any costs from narrow thermal tolerance. We

334 also found that specialist species were less likely to benefit from AM (Fig. 3). With only a
335 narrow range of temperatures under which specialists can replace themselves, any error in
336 identifying a species' optimal climate would disproportionately affect specialists. Removing this
337 tradeoff would reduce specialists' competitiveness which could make them more vulnerable to
338 climate change, but it would also weaken specialists' competitive ability, further limiting the
339 effectiveness of AM.

340 AM was most successful for dispersal-limited species because, in these cases, AM
341 directly mitigated the driver of their vulnerability to climate change (McLachlan et al. 2007;
342 Schwartz et al. 2012). Not only was short dispersal a strong predictor of extinction (Fig. 2), but
343 the shortest dispersers also had the strongest proportional increase in persistence with AM
344 (Fig. 3). Moreover, the shortest dispersers were the only target species with increased average
345 persistence in every variation of AM that we modeled. We also found that species with low
346 initial population sizes and species with close poleward competitors were also likely to be
347 vulnerable to climate change and to benefit from AM (Fig. 3). Though these species also had
348 lower-than-average dispersal (Appendix S7), they were likely to be strong AM candidates
349 because of their other vulnerabilities (Thompson & Gonzalez 2017). For example, species with
350 low population sizes might disperse far but not produce enough offspring to realize the full
351 extent of their dispersal potential. Given the possibility that climate change could select for
352 increased dispersal, fecundity, and climate tolerance in relatively short timeframes (Nadeau &
353 Urban 2019), ignored here for simplicity, the traits associated with AM success could change
354 over time. Rapid evolution might act as another source of uncertainty that can affect AM
355 decisions, such as the choice of source locations or whether declining populations reliably

356 indicate the persistence risk that motivates AM (as the "evolutionary rescue" process of
357 adapting to novel environments often entails a period of population decline before eventual
358 adaptation and growth; Carlson et al 2014). For the case of close poleward competitors also
359 affecting extinction risk, note that our focus on lottery competition amongst the many possible
360 drivers of competitive coexistence (Chesson 2000) ignores the niche differentiation for
361 environmental characteristics beyond temperature, which might reduce the impact of
362 poleward competitors. While acknowledging these assumptions inherent to our simple model,
363 our results suggest that AM might be considered for conserving a variety of species beyond
364 those that are directly dispersal limited.

365 Even under optimal conditions, AM did not prevent the extinction of nearly 20% of
366 short-dispersing species (Fig. 3). For specialists, AM failed because suitable environments were
367 sparse and narrow, but for other species, AM failed because they had a combination of
368 characteristics that limited establishment success (such as a species with both short dispersal
369 and narrow thermal tolerance) (Fig. 6). In these cases, managers might combine alternative
370 management strategies, like increasing connectivity, removing barriers, or creating new
371 reserves (Heller & Zavaleta 2009; Lawler & Olden 2011). For example, we also found that
372 species relocated into smaller communities were more likely to persist (Fig. 5), suggesting that
373 managers could prepare the recipient ecosystems by controlling the populations of resident
374 species (Godefroid et al. 2011). This approach might limit competitive pressure, reduce the risk
375 of establishment failure, and temporarily increase the realized niche of the relocated species,
376 but it would come with additional risks to resident species.

377 Both for understanding the options for species for which AM failed and for
378 comprehensively for incorporating the balance of risks and benefits of AM in management
379 decisions, an important next step, beyond the scope of this study, is to compare the outcome of
380 AM to alternate management approaches (Lawler & Olden 2011). Our initial investigations into
381 this question as a next step involve extending our model to incorporate variable carrying
382 capacity and a two-dimensional landscape to model the effects of protection and restoration.
383 While crucial for comparing AM to alternate management approaches, preliminary results
384 indicate that variable carrying capacity and two-dimensional landscapes do not affect the
385 qualitative take-homes on AM decision-making that are the focus here.

386 *Fractional relocation*

387 We found that AM was most successful when we relocated an intermediate fraction of
388 the total population (typically around 50-60%; Fig. 3), as this was most robust to uncertainty
389 that could cause AM actions to fail. By leaving donor population to persist temporarily, this
390 approach retains a source for future conservation actions in case relocation occurs at the wrong
391 time or into the wrong place and ends in establishment failure (Fig. 4). Fractional relocation
392 also buffers against the risk of falsely identifying a target species for AM, in which case leaving
393 some individuals behind could allow the species to recover those individuals that might be lost
394 during AM. This contrasts with past AM models that assume the optimal strategy is to move the
395 entire population, as the lagging donor population would eventually go extinct without
396 management (McDonald-Madden et al. 2011). Though relocating more individuals should
397 increase the chances that a species establishes (Godefroid et al. 2011; Blackburn et al. 2015),

398 this could have diminishing returns with negative density dependence (Fischer & Lindenmayer
399 2000). Instead, our simulations suggest that, in some cases, relocating a fraction of a species
400 could create two smaller populations, each with less negative density dependence than a single
401 unmanaged population (Fig. 5). However, creating two smaller populations could increase
402 extinction risk in some situations. Though our model accounted for the extinction risk through
403 demographic and environmental stochasticity (Lande 1998), we did not include additional
404 extinction risks from Allee effects or explicit genetic factors that could cause inbreeding
405 depression (Gilpin & Soulé 1986). Note that this conclusion is robust to different values of
406 threshold population size for movement η and carrying capacity K that influence the likelihood
407 of engaging in AM and degree of density dependence, respectively (Appendix S2).

408 Fractional relocation could also be robust to other risks that we did not directly model,
409 such as the risk of invasion beyond that arising from competitive interactions. Though fractional
410 relocation relies largely on repeated translocations, which repeatedly expose the recipient
411 ecosystem to potential invasion events (Kolar & Lodge 2001; Lockwood et al. 2005),
412 intentionally relocating fewer individuals into a well-monitored ecosystem could also make it
413 easier to detect and prevent invasions before they occur. Similarly, smaller releases could be
414 easier to control if funding, planning, or societal opinions change, and reversal is necessary
415 (Haight et al. 2000).

416 *Community ecology of AM*

417 Our model builds on past research that suggests competition can prevent some species
418 from tracking climate change (Urban et al. 2012). Though species were vulnerable to extinction

419 if poleward species were strong competitors (Fig. 2), AM was also less successful when we
420 relocated species into an area occupied by stronger competitors (Fig. 5, Fig. 6). The effect of
421 competition was higher in competition-driven, low-stochasticity communities where AM
422 success depended on characteristics of the poleward species than in dispersal-driven, high-
423 stochasticity communities where success depended more on the ability to accurately place
424 species into their optimal climates. This difference suggests that historical climate variability
425 and community assembly could inform management decisions about AM. For example, limiting
426 competitive interactions (Godefroid et al. 2011) might be more effective for species from
427 environments with low historical variability, whereas relocating species into climate refugia
428 (Morelli et al. 2016) might be more effective for species from environments with higher
429 historical variability.

430 Though we did not find any substantial negative effects of relocated species on recipient
431 communities (Appendix S6), we made several simplifications to our model that could have
432 limited the capacity for invasion impacts to occur. First, the simple spatial structure of our
433 model assumed a single contiguous community that assembled without distinct barriers,
434 making the AM in our model analogous to intra-continental relocations that are less likely to
435 cause invasions (Mueller & Hellmann 2008). Additionally, for the sake of simplicity, our model
436 considered only intra-guild lottery competition without the wider web of species interactions
437 that would naturally occur. Biological invasions usually involve more complex ecological
438 dynamics, many of which are taxon-specific and difficult to generalize (Kolar & Lodge 2001;
439 Lockwood et al. 2005; Simberloff et al. 2013). Enemy-release effects would occur if relocated
440 species escape antagonistic interactions that limits growth within their original range (Prenter

et al. 2004). Also, relocated species might carry pathogens or parasites that spread to other species in recipient community (Simler et al. 2018). A richer set of interactions could also complicate AM success, as relocating a species without a mutualist might limit establishment (Lunt et al. 2013; Plein et al. 2016). Finally, a wider set of interactions would allow analysis of the effects of AM on characteristics of ecosystem structure and function beyond the extreme outcome of extinction analyzed here. Overall, while our simple competitive framework provides a first step toward exploring the uncertainties and community context of AM, a more complete set of interactions will be necessary to understand the full range of outcomes that could follow a relocation event, from establishment failure, to invasion, to the wide-scale restructuring of ecological communities that is already taking place with climate change (Alexander et al. 2015; Thompson & Gonzalez 2017).

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600

601 **Appendix S1: Supplementary methods**

602 *Double geometric distribution*

603 In continuous space models of species dispersal, ecologists often use a Laplace or
604 double exponential distribution kernels (Kot et al. 1996; Neubert & Caswell 2000; Urban et al.
605 2012). This is largely because a Laplace distribution is leptokurtic, or has "fat-tails" compared to
606 a standard Guassian kernel. These fat tails give some individuals a higher chance of dispersing
607 extremely far from their origin, which may explain how some slow-dispersing species could
608 track rapidly changing climates in the past (Clark et al. 1998). Because these rare long dispersal
609 events could play an important role in how dispersal-limited species could track climate change
610 in our model, we used a discrete-space leptokurtic dispersal kernel.

611 Just as the Laplace distribution is a "double exponential" distribution, we considered
612 dispersal kernel that would be a "double geometric" distribution. In other words, this kernel
613 resembles a geometric distribution moving away from 0 in both the positive and negative
614 directions. This kernel is defined by one parameter q_i, the probability of a propagule remaining
615 in any particular patch (besides the origin). Each propagule either stays at its origin with
616 probability $\frac{q_i}{2-q_i}$ or moves one space in the pole-ward or equator-ward direction, each with
617 equal probability $\frac{1-q_i}{2-q_i}$. Then each propagule either stays at that current patch with probability
618 q_i or continues to move one space in the same direction with probability $1 - q_i$. This process
619 continues until the propagule stays. The probability that a propagule disperses from patch x to
620 path y is then,

$$k_i(x,y) = \left(\frac{q_i}{2-q_i}\right)(1-q_i)^{|x-y|}. \tag{1}$$

Using this probability mass function, we can determine the mean dispersal distance of a propagule, γ_i, as the mean absolute value of a random variable $y \sim k_i(x,y)$. That is

$$\begin{aligned}
E[Y] &= \sum_{y=-\infty}^{\infty} |x-y|\, k_i(x,y) \\
&= \sum_{y=-\infty}^{\infty} |x-y| \left(\frac{q_i}{2-q_i}\right)(1-q_i)^{|x-y|} \\
&= \left(\frac{1}{2-q_i}\right)\left[\sum_{y=-\infty}^{x-1} |x-y|\, q_i(1-q_i)^{|x-y|} + 0 + \sum_{y=x+1}^{\infty} |x-y|\, q_i(1-q_i)^{|x-y|}\right] \\
&= 2\left(\frac{1}{2-q_i}\right)\sum_{y=0}^{\infty} y\, q_i(1-q_i)^{y} \\
&= \frac{2(1-q_i)}{q_i(2-q_i)}.
\end{aligned} \tag{2}$$

Low population threshold

As we implemented a reactive approach to assisted migration, we had to determine a threshold population below which the population would be relocated. Deciding on appropriate thresholds required us to weigh certain management priorities. If these thresholds were too low, there would likely be only a narrow time window in which managers could react to population decline and relocate the population before extinction. Alternatively, if thresholds are too high, managers might relocate species that are temporarily in decline but not at risk of

extinction, risking management funds and effort while potentially creating some extinction risk during an inappropriate relocation.

To find a threshold that balanced these priorities, we analyzed time series of population sizes in the 2^{16} high stochasticity simulations in which no management actions were taken. We considered a range of potential population size thresholds from 1 to 100. For each species, if the population fell below the threshold, we determined whether or not the population went extinct following the first instance it fell below the threshold. Those that fell below this threshold but did not go extinct were false positives. Those that fell below the threshold and went extinct in less than 5 time steps were true positives, but impractical to relocate before extinction. Those that fell below the threshold and went extinct in more than 5 but less than 10 time steps were true positives that were practical for relocation. The maximum percentage of practical true positives occurred with a threshold of population size of $\eta = 42$ (Figure S1.1), which we used as the low population threshold throughout our AM simulations.

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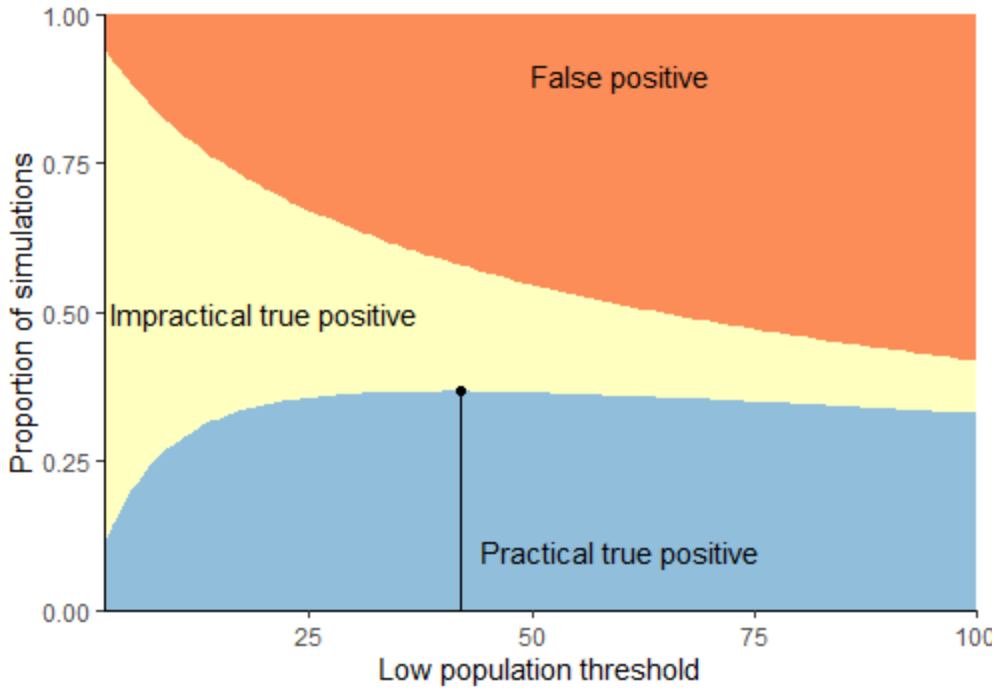

653

Figure S1: When simulated under climate change without assisted migration, species fell into three categories (shaded) depending on their fate following the first time they fell below a low population threshold. We compared threshold values to determine when we could detect a species was likely to go extinct, but with enough time to take management action to prevent that extinction. “False positive” species continued to persist until the end of the simulation. “Impractical true positive” species went extinct within 5 time steps. “Practical true positive” species went extinct in more than 5 time steps but less than 10 time steps. The threshold value that optimizes the percentage of practical true positives (42) is marked by the vertical line.

Appendix S2: Global sensitivity of η and K

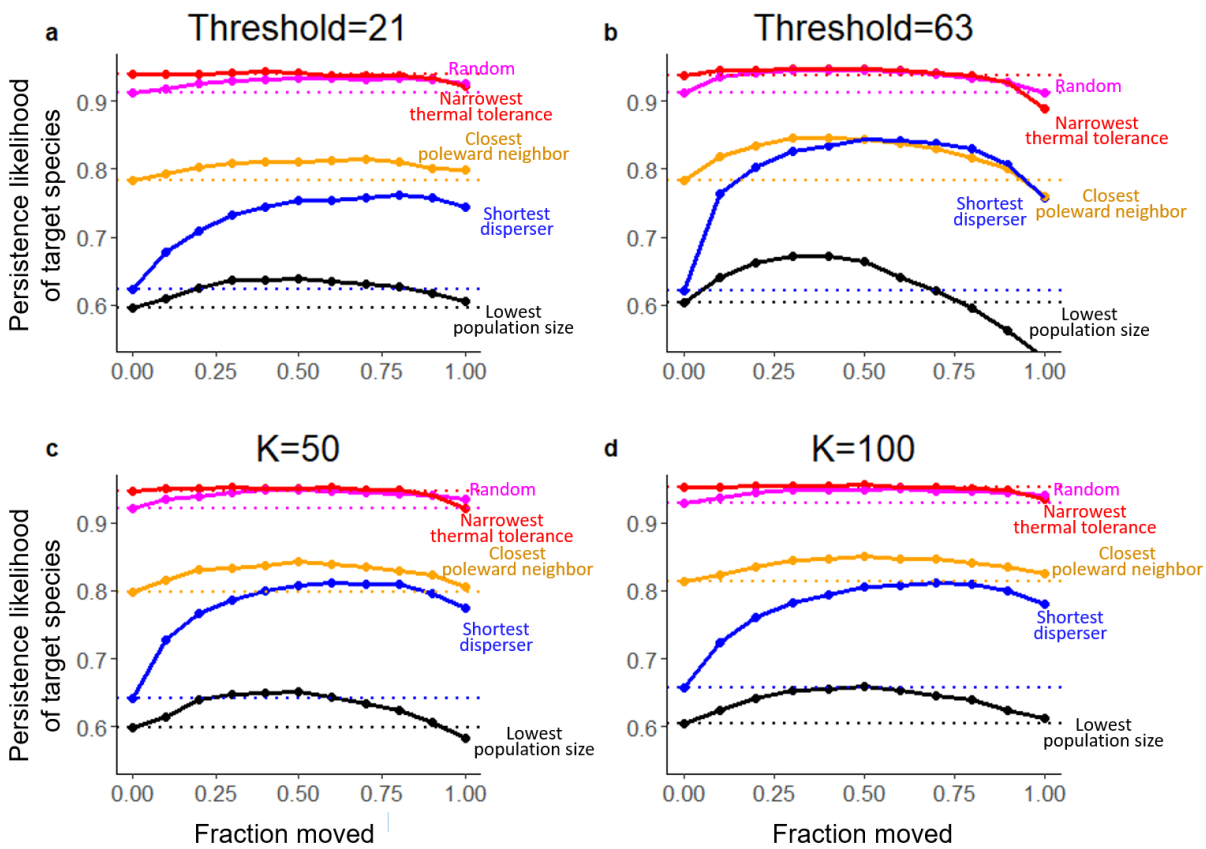

Figure S2: Based on 10000 climate change simulations, the persistence likelihood of a target species chosen for assisted migration (vertical axis) depended on the fraction of that population that was relocated (horizontal axis). In this figure, we compare variations on parameter values for the low population threshold for assisted migration (η) and the community-wide patch carrying capacity (K). Comparative default parameter simulations are found in Figure 3 in the main text. In (a) and (b) we use variations on the low population threshold $\eta = 21$ and $\eta = 63$ (compared to a default of $\eta = 42$) while keeping all other parameters at default values and low stochasticity ($\psi = 0.1639$). In (c) and (d), we use variations on the carrying capacity $K = 50$, and $K = 100$ (compared to a default of $K = 30$) while keeping all other parameters at default values. In each set of simulations, the target species chosen for relocation were random, narrow thermal tolerance, closest poleward neighbor, shortest dispersal, or lowest population size. The thermal optimum estimate used in each of these was the realized niche estimates (based on the species initial distribution). The dotted horizontal lines correspond to persistence likelihood without AM (zero moved, or no management action) and are colored to match each comparison.

Appendix S3: Initialized community data

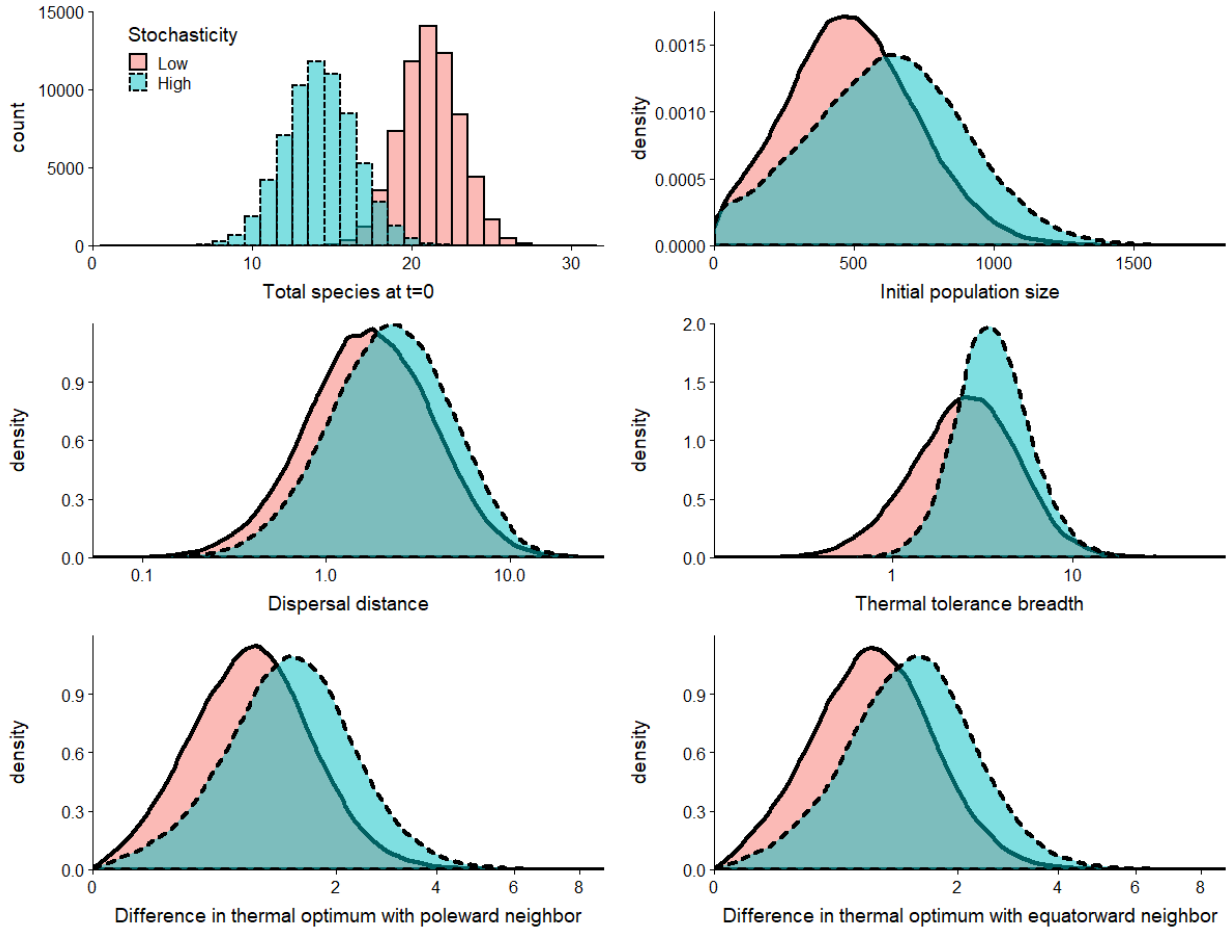

Figure S3: Distribution of initialized community characteristics before 2^{16} climate change simulations, comparing between low stochasticity (salmon colored with solid line) and high stochasticity (teal colored with dashed line). (a) Number of extant species in the entire spatial gradient (not just the interior sub-region W) prior to climate change. (b-f) Characteristics of a species that was randomly picked from those extant in the interior sub-region of the climate gradient W at prior to climate change at time $t = 0$. The horizontal axes are linear in (a-b), log-transformed in (c-d), and square-root-transformed in (e-f).

Appendix S4: No action random forest results

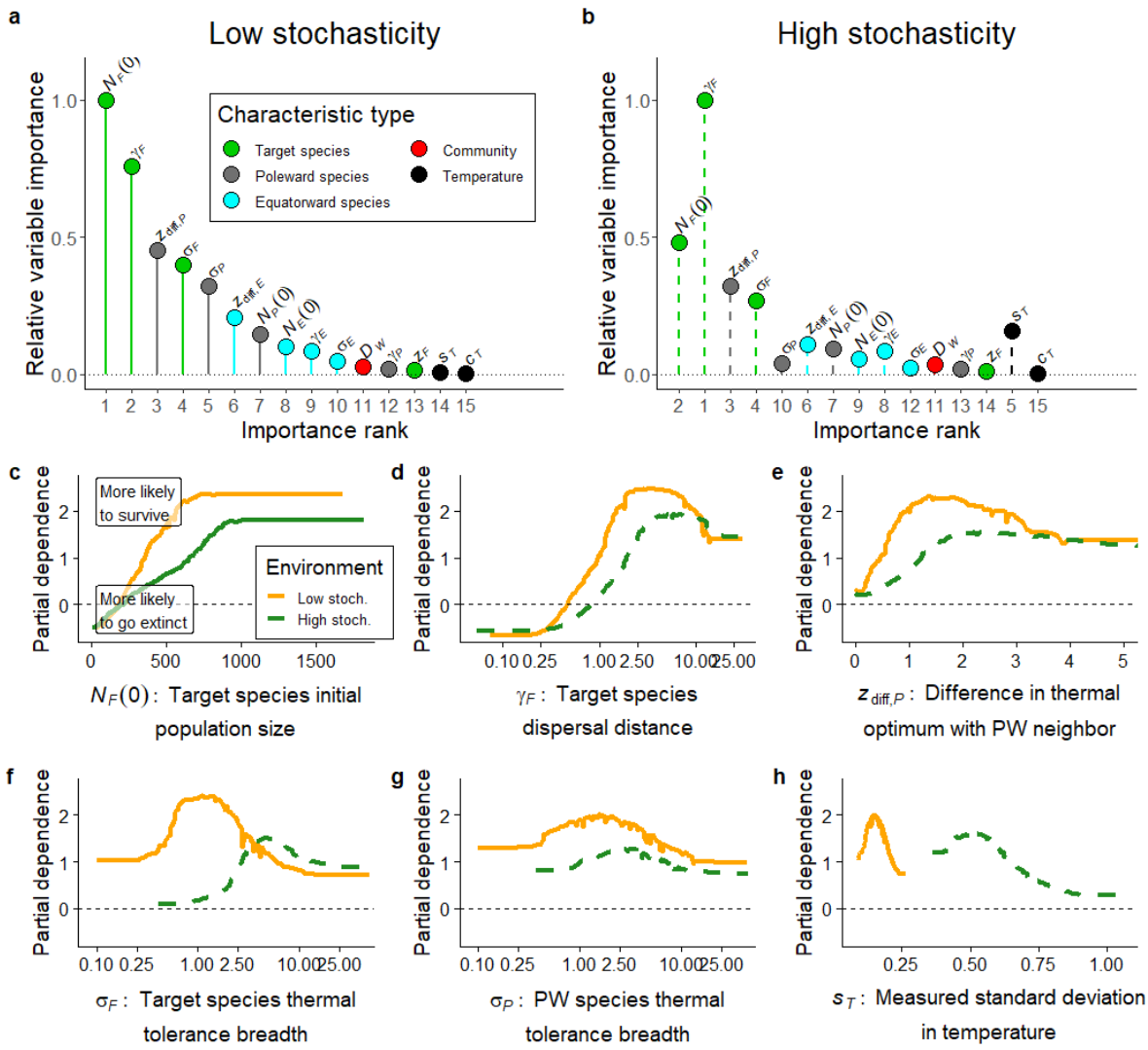

Figure S4: Importance of species, community, and environmental characteristics in determining whether the target species will persist with climate change without assisted migration. (a,b) Relative unscaled permutation importance of independent variables of whether a species persisted through climate change with no management under low stochasticity (a) and high stochasticity (b). The horizontal axis shows the rank of the variable importance compared to other variables (1 being the most important), arranged in the same order for both plots. Each characteristic is shaded depending on whether it is a characteristic of the target species, its neighbors, the full community, the environment, or uncertainty around the thermal optimum estimate. (c-h) Partial dependence of the values of 6 independent variables (corresponding to the top 6 important variables for low stochasticity labeled in panel (a) and (b)) on whether or not assisted migration will increase the shortest disperser's persistence. The vertical axis is the log-odds of whether a species persisted (higher being more likely to persist). Solid lines represent the low stochasticity environment and dashed lines represent the high stochasticity environment. See Table 1 for definitions of symbols.

659 **Appendix S5: Thermal tolerance extinction trends**

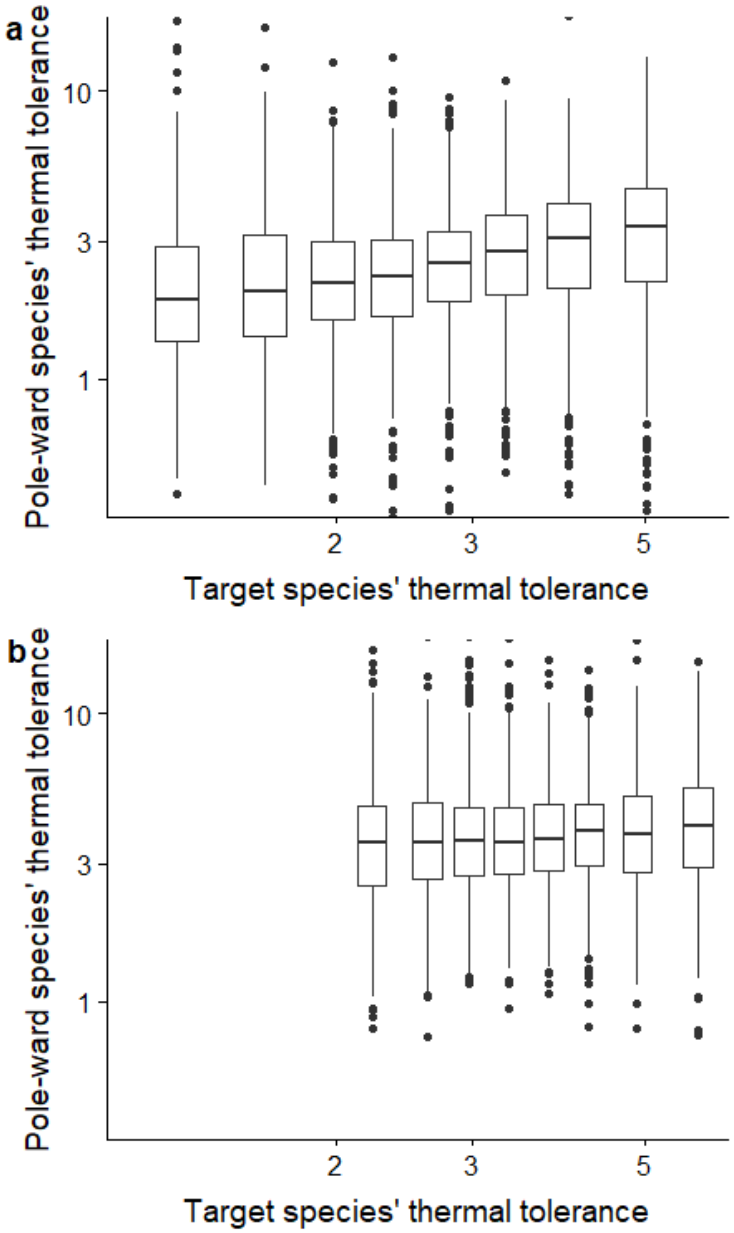

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Figure S5: Comparison of the thermal tolerances of target that went extinct during simulations without assisted migration and with the species on their pole-ward side (a) under low stochasticity and (b) under high stochasticity. Target species are grouped into 10% quantiles of their thermal tolerances with the bottom and top quantiles removed to limit the scale of the figure. Among these species that went extinct, those with higher thermal tolerances had pole-ward neighbors with higher thermal tolerance, with a stronger relationship in lower stochasticity environments.

Appendix S6: Effects of assisted migration on non-target species and community

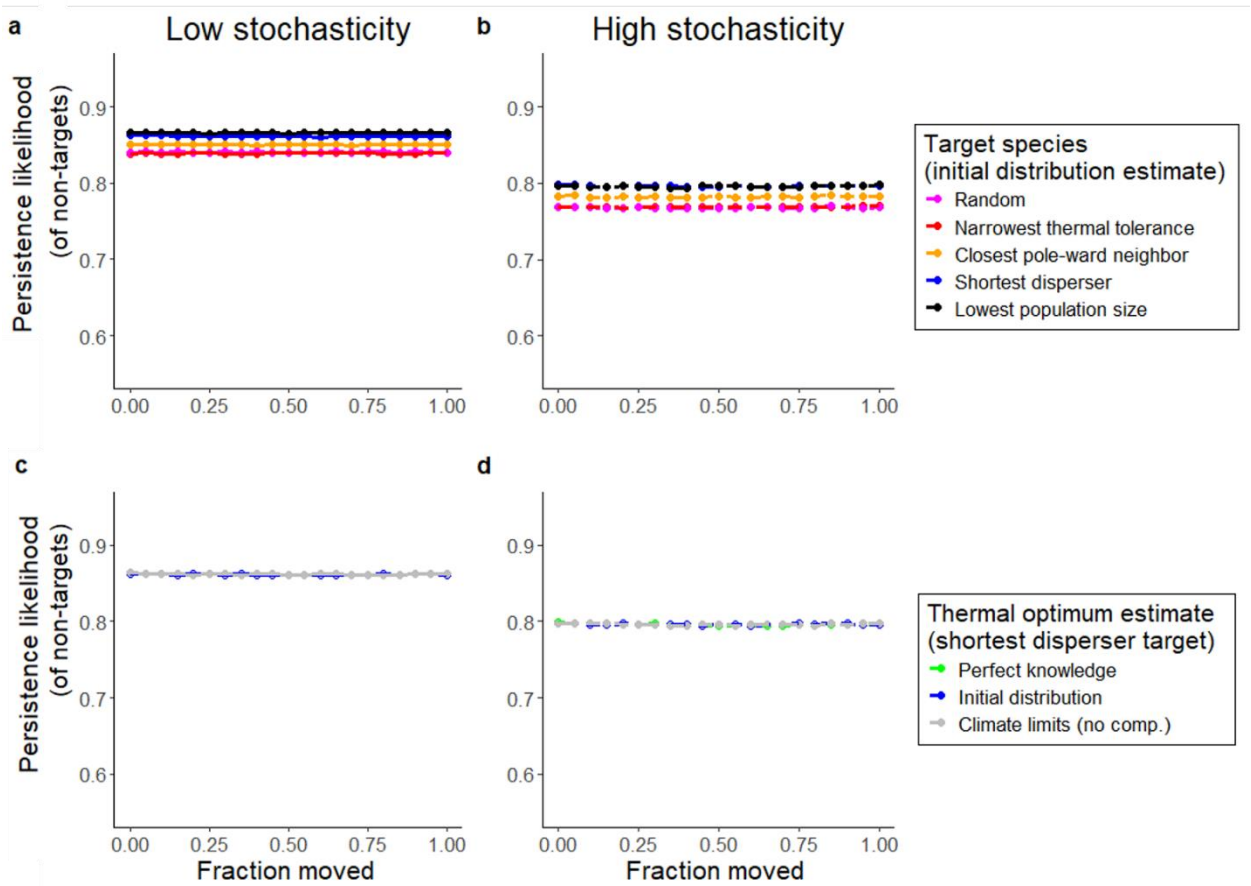

Figure S6.1: During climate change simulations, the persistence likelihood of non-target species that were not chosen for assisted migration (vertical axis) did not depend on the fraction of that population that was relocated (horizontal axis). The dotted lines correspond to persistence with no management action and are shaded to match each comparison. (a,b) The effect of assisted migration on non-target species' persistence with different types of target species chosen for relocation. The thermal optimum estimate used in each of these was the realized niche estimates (based on the species initial distribution). (c,d) The effect of assisted migration on non-target species' persistence with different types of thermal optimum estimates. The target species in each of these simulations was the species with the shortest dispersal.

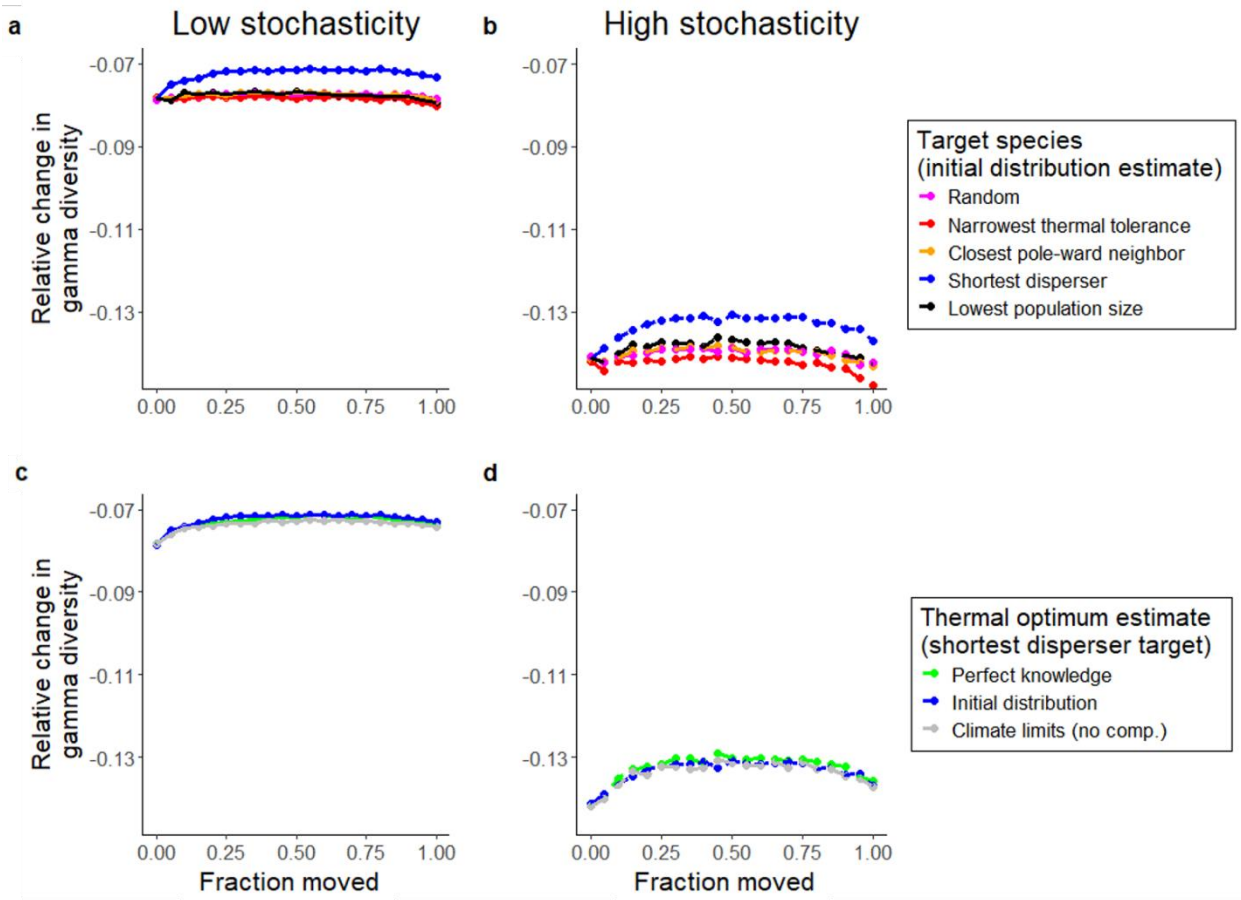

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Figure S6.2: During climate change simulations, the relative change in gamma inverse Simpson's diversity index (vertical axis) depended on the fraction of the target population that was relocated (horizontal axis). The dotted lines correspond to gamma diversity with no management action and are shaded to match each comparison. Because the persistence likelihood of non-target species is constant across simulations (Fig. S561), the small differences in gamma diversity observed here are likely due to the differences in persistence of the target species. (a,b) The effect of assisted migration on gamma diversity with different types of target species chosen for relocation. The thermal optimum estimate used in each of these was the realized niche estimates (based on the species initial distribution). (c,d) The effect of assisted migration on gamma diversity with different types of thermal optimum estimates. The target species in each of these simulations was the species with the shortest dispersal.

Appendix S7: Table of relative values of target species

Table S7: Mean value of characteristic values for different types of target species relative to mean values from randomly chosen species in both low and high stochasticity environments.

Target	Shortest γ_F		Narrowest σ_F		Lowest $N_F(0)$		Closest $z_{\mathrm{diff},P}$	
Stochasticity	Low	High	Low	High	Low	High	Low	High
z_F	1.00	1.01	1.00	1.00	1.00	1.01	1.00	0.99
γ_F	0.22	0.27	1.06	1.48	0.85	0.83	0.90	0.97
σ_F	0.98	1.10	0.28	0.47	1.49	1.24	0.92	0.99
$N_F(0)$	0.85	0.84	0.88	0.99	0.29	0.39	0.73	0.77
$z_{\mathrm{diff},P}$	0.98	1.01	0.86	0.99	0.70	0.73	0.17	0.28
$z_{\mathrm{diff},E}$	0.97	1.01	0.85	0.99	0.74	0.77	1.19	1.19

Appendix S8: R code

Sample R code can be accessed at:

https://anonymous.4open.science/r/9e80ce08-9937-4e71-8a77-73e47fac8f15/