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Identifying robust strategies for assisted migration given risks and uncertainties in a stochastic metacommunity

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Abstract

Assisted migration is the translocation of species beyond their historical range to more suitable locations given future climate change. This conservation approach poses risks of establishment failure because of uncertainty in decision making, climate, and interactions with the recipient ecological community. To quantify the risks and benefits of assisted migration under different management decisions, 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, species were vulnerable to climate change if they had a low population sizes, short dispersal, and strong poleword competition. When relocating species that exemplified these traits assisted migration increases 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. Especially when it is difficult to identify a species' optimal climate, 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. 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 in almost all situations. Relocation did not affect the survival of non-target species, suggesting that competitive interactions alone were unlikely cause invasions from assisted migration.

Keywords

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

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Introduction

Global biodiversity is expected to decline at accelerated rates with projected climate change (Urban 2015). Among the species that are most at risk of extinction are those with limited dispersal, narrow ranges, narrow climate tolerance, and low population sizes (Pearson 2006; Parmesan 2006; Tewksbury et al. 2008). Moreover, 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 expected to be more suitable under projected future climates (McLachlan et al. 2007; Schwartz et al. 2012). By allowing these species to reach favorable climates in densities that they would not be able to reach on their own, AM might improve a species' chance of persistence in ways that traditional conservation strategies, such as direct restoration, cannot (McLachlan et al. 2007; Lawler & Olden 2011).

Moving a species into a novel ecosystem incurs many risks (Mueller & Hellmann 2008; Ricciardi & Simberloff 2009; Hewitt et al. 2011). Most frequently raised is the risk that relocated species might become invasive (Hewitt et al. 2011). For example, relocating one species would artificially increase its effective dispersal, creating higher variation in metacommunity dispersal ability and impeding other species' ability to track of climate change (Urban et al. 2012).

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Another risk is the possibility that a relocated population could fail to establish (Chauvenet et al. 2013; Plein et al. 2016). Establishment failure could further contribute to the extinction of species that are already threatened by climate change by reducing the population size and genetic diversity of the species while also incurring an economic cost to the limited available resources for conservation (McDonald-Madden et al. 2008). The challenges inherent to translocation are evident in the low-to-intermediate success of previous conservation-based translocations within species' historical ranges across a wide range of taxa (Fischer & Lindenmayer 2000; Godefroid et al. 2011; Bellis et al. 2019). The risk of establishment failure 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 has led 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 are likely to be 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 (Regan et al. 2005; McDonald-Madden et al. 2008) for the array of decisions involved in AM. This involves deciding 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

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species are already being relocated (McLachlan et al. 2007; 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; 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 risk of invasiveness and uncertainty in the drivers of species ranges. In this paper, we quantify the benefits and risks of AM given species 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. 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

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stochasticity. For simplicity, all species in this metacommunity are annuals competing over the same resources at the same trophic level. The model cycles through the processes of 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 and quantified how these decisions affected species' persistence and community diversity.

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

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

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(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, $n_i^*(x,t) \sim \text{Poisson}(n_i(x,t)b_i(T(x,t))$ (Melbourne & Hastings 2008).

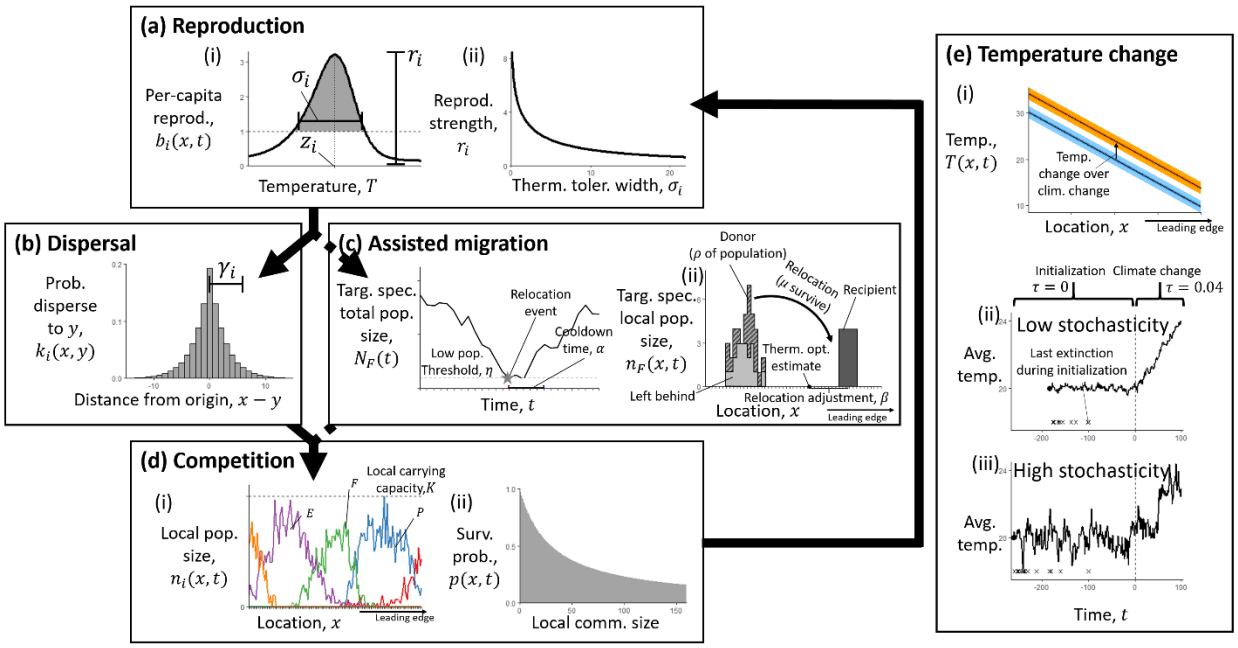

Figure 1: During each time step of the model, all extant species cycle through (a) reproduction, (b) dispersal, and (d) competition before (e) the temperature changes and the next time step continues. The target species also experiences (c) assisted migration during certain time steps. (a.i) Per capita 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.

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Next, each propagule disperses from its origin (Fig. 1b). We adapted the Laplace dispersal kernel (Neubert & Caswell 2000; Urban et al. 2012) 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

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

To incorporate demographic stochasticity, all propagules of species i disperse from patch x throughout all space X with the random vector $M_i(n_i(x,t),x,t) \sim \text{Multinomial}\left(n_i^*(x,t), k_i(x,X)\right)$, and the total metapopulation after dispersal is $n_i^{**}(X,t) = \sum_{x\in X} M_i(n_i(x,t),x,t)$.

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).

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Spatial structure

Metacommunity dynamics occur across a one-dimensional, linear temperature gradient of L patches (Fig. 1e), representing a 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 on the edges, 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 the total metapopulation size $N_F(x, t)$ is below a threshold at the beginning of a time step. 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. From the propagules chosen for AM, only a proportion μ of them

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survive relocation, and those are relocated uniformly around a patch β spaces poleward of the patch that most closely matches the species' estimated thermal optimum.

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

Parameterization and implementation

Simulations occurred on a temperature gradient with $L = 512$ patches, where initial temperatures linearly varied over space from 9.78 °C to 30.22 °C. We considered two types of environments, defined by their stochasticity. Low-stochasticity environments had an annual temporal standard deviation of $\psi = 0.1639$ °C, equal to the standard deviation of mean combined global land-surface air and sea-surface water temperature anomalies from 1880 to 1979 (GISTEMP Team 2019; Lenssen et al. 2019), and high-stochasticity environments had four times that amount. Both had an annual temporal autocorrelation of $\kappa = 0.767$, also from temperature anomalies from 1880 to 1979. We used skewness constant $\lambda = -2.7$ (Urban et al. 2012) and carrying capacity $K = 30$ individuals.

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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

Before simulating climate change, we performed an initialization phase to assemble a metacommunity with multidecadal coexistence under background environmental stochasticity. First, we generated a pool of $S = 32$ randomized species, each with unique dispersal distances γ_i, thermal optima z_i, and thermal tolerance breadths σ_i, all randomly generated from default 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

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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.

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 that there were few false positives (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 (species F) that could be considered vulnerable to climate change, including: the species with the shortest dispersal, the species with the narrowest thermal tolerance breadth (specialists), the species with the closest (or lowest difference in thermal optimum with its) poleward neighbor, and the species with the lowest initial population size. For comparison, we also chose 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. The species with closest thermal optimum below the target species was the poleward neighbor (species P) and the closest species on the other side was the equatorward neighbor (species E). We simulated each

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combination of target species type, fraction relocated ρ from 0 to 1, 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 (extinction/persistence) after climate change, and 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 (extinction/persistence) 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

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specifically benefited from AM, we only included simulations in which the target species went extinct without AM. To simplify analysis, we only considered 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 based on random forest classifications (out-of bag error: 8.09% low stochasticity, 11.27% high stochasticity) (Fig. 2c-d, Appendix S2). Persistence was lowest when a species had low initial population sizes $N_F(0)$, short dispersal distances γ_F, and a close poleward neighbors $z_{\mathrm{diff},P}$. Under low stochasticity, persistence depended on the thermal tolerance of the poleward neighbor σ_P, such that specialists (species with narrow thermal tolerance breadth) with specialists on their leading edge were less likely to persist than specialists with generalists on their leading edge (Appendix S2). Comparatively, dispersal and the measured standard deviation in temperature (s_T) were more important for persistence under high stochasticity. Altogether, competition largely determined persistence under low stochasticity, whereas dispersal largely determined persistence under high stochasticity.

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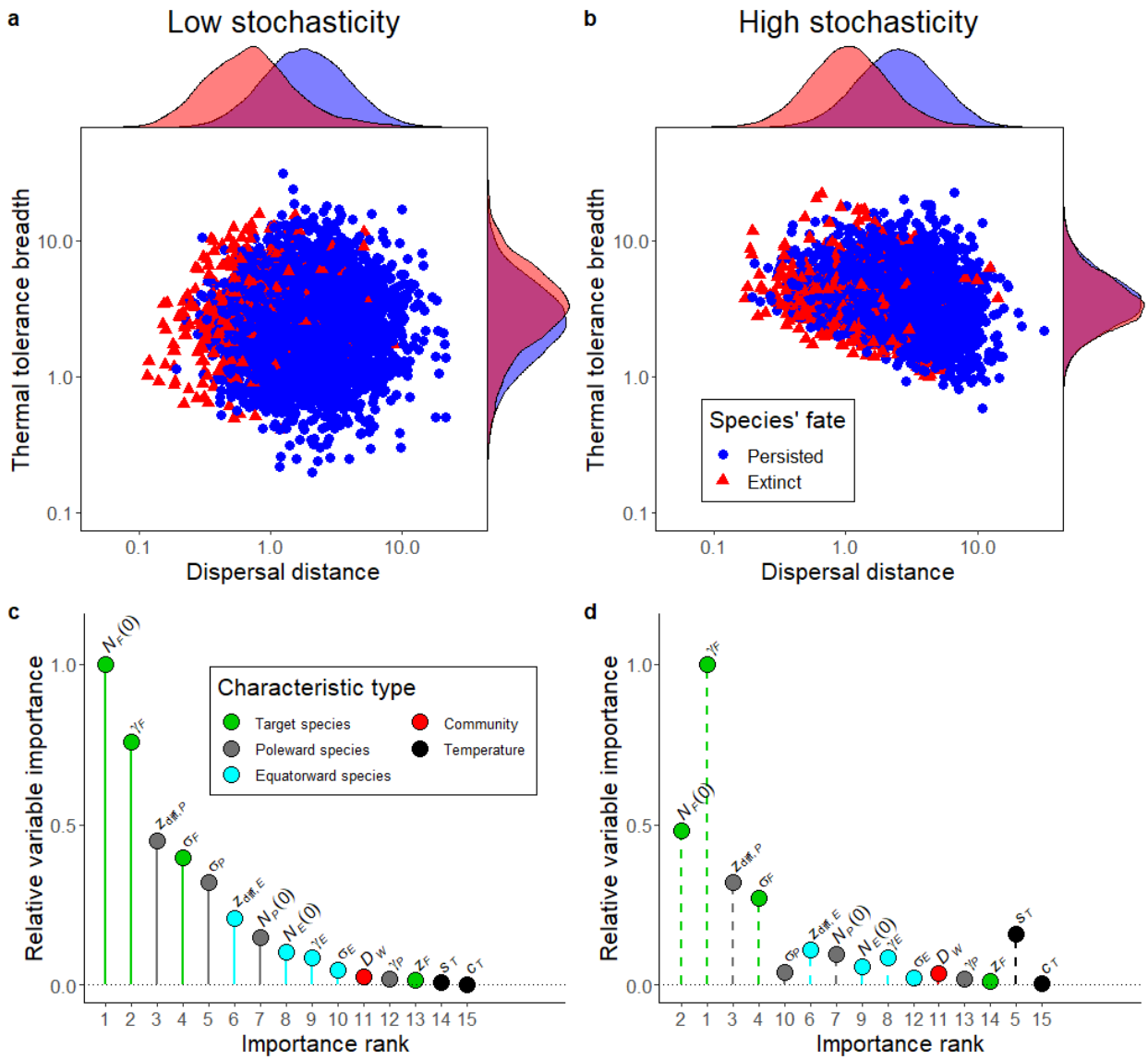

Figure 2: Species' persistence and the characteristics that predicted persistence varied with environmental stochasticity. (a,b) Each point shows the fate of a single species (triangle: extinction; circle: persistence) following climate change from a subset of unique simulations plotted over dispersal 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 shaded 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.

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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). Moreover, target species persistence was typically lower we relocating 100% of the total population than under no relocation (except when the target species was the shortest disperser). More often than not, AM involved multiple relocations (Fig. 4a-b) and higher AM success when relocating intermediate fractions required more individual relocation events (Fig. 4c-d). Assisted migration had little effect on the persistence of non-target species and final community diversity (Appendix S2), so the remaining results focus on persistence instead of invasion risk.

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).

Assisted migration 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.

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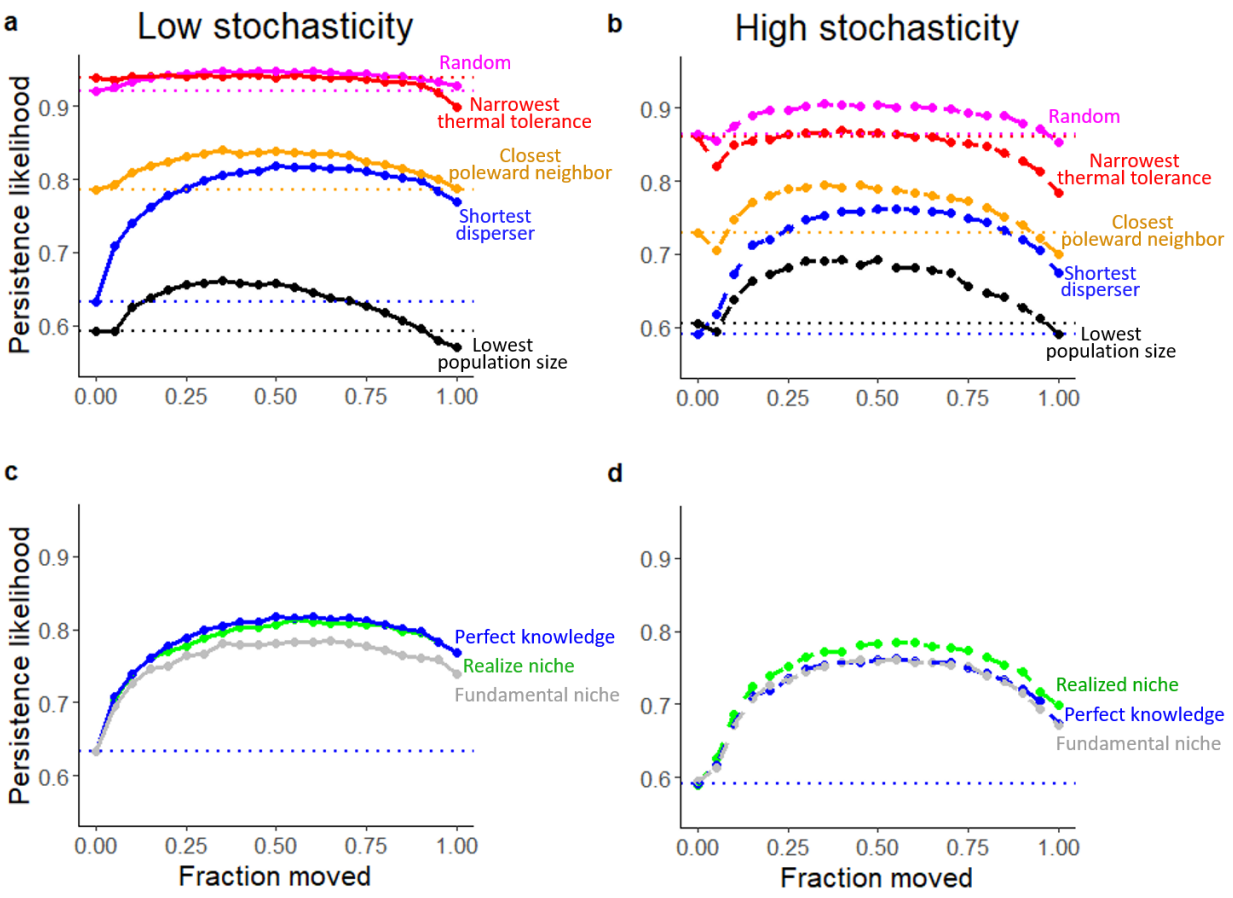

Figure 3: During climate change simulations, the persistence likelihood of a target species chosen for assisted migration (vertical axis) depended on the fraction of that population that was relocated (horizontal axis), and the level of environmental stochasticity (a,c: low, b,d: high). The dotted lines correspond to persistence with no management action and are shaded to match each comparison. (a,b) The effect of assisted migration on 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 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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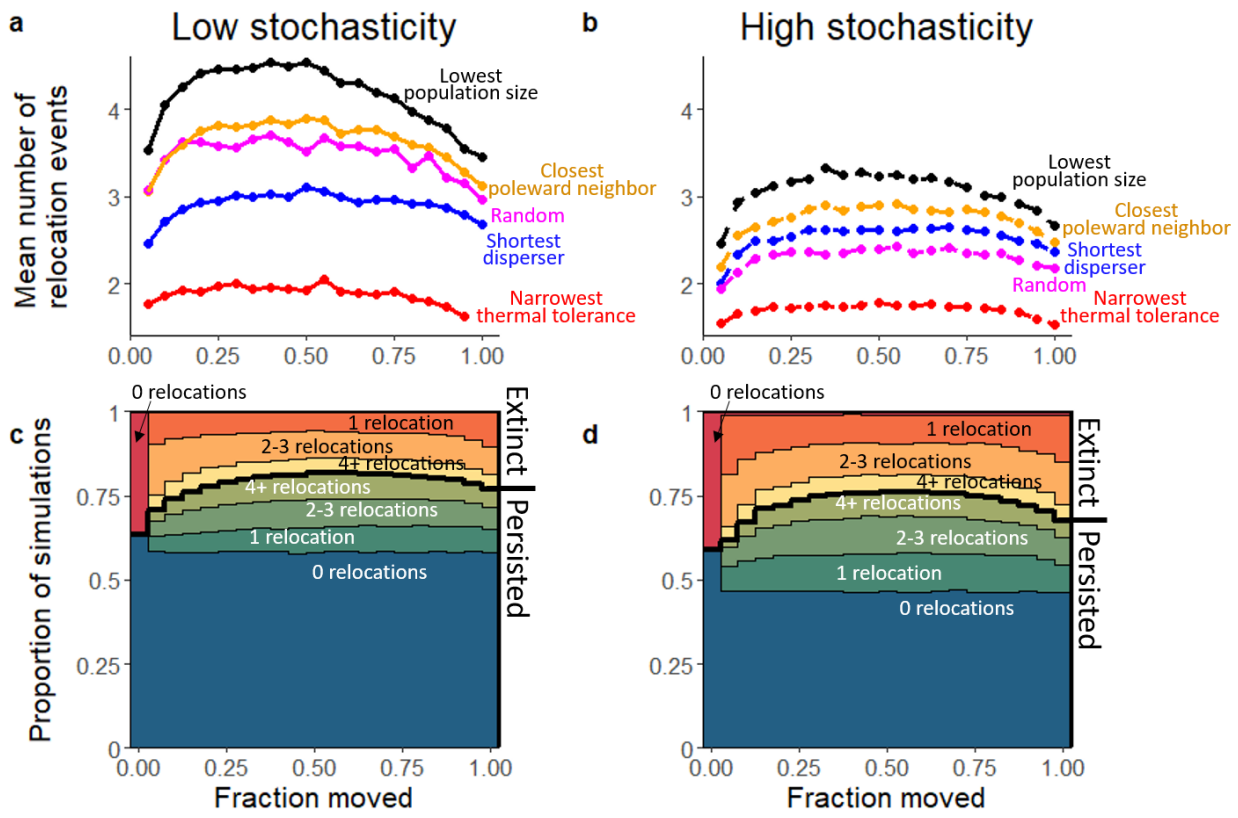

Figure 4: The number of independent relocation events that occurred during assisted migration simulations for low stochasticity (a,c) and high stochasticity (b,d) environments. (a,b) Among species that were relocated at least one time, the mean number of independent relocation events (vertical axis) that occurred under a range of values for the fraction of the population that was relocated each time (horizontal axis). 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 proportion simulations that fall into these categories (shaded differently) depended on the fraction of the population moved during assisted migration (horizontal axis). The thick black 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.

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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 $z_{\mathrm{diff},P}$, based on random forest classifications (out-of bag error: 25.27% low stochasticity, 30.56% high stochasticity) (Fig. 5a-b). Assisted migration was most successful when the values of these characteristics were higher (Fig. 5c-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. 5f), implying that poleward competition limited AM success under low stochasticity but not under high stochasticity. Assisted migration was also more successful when thermal optimum estimates were warmer than the true value (positive deviation of $z_{\mathrm{est,dev}}$) (Fig. 5g), 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.

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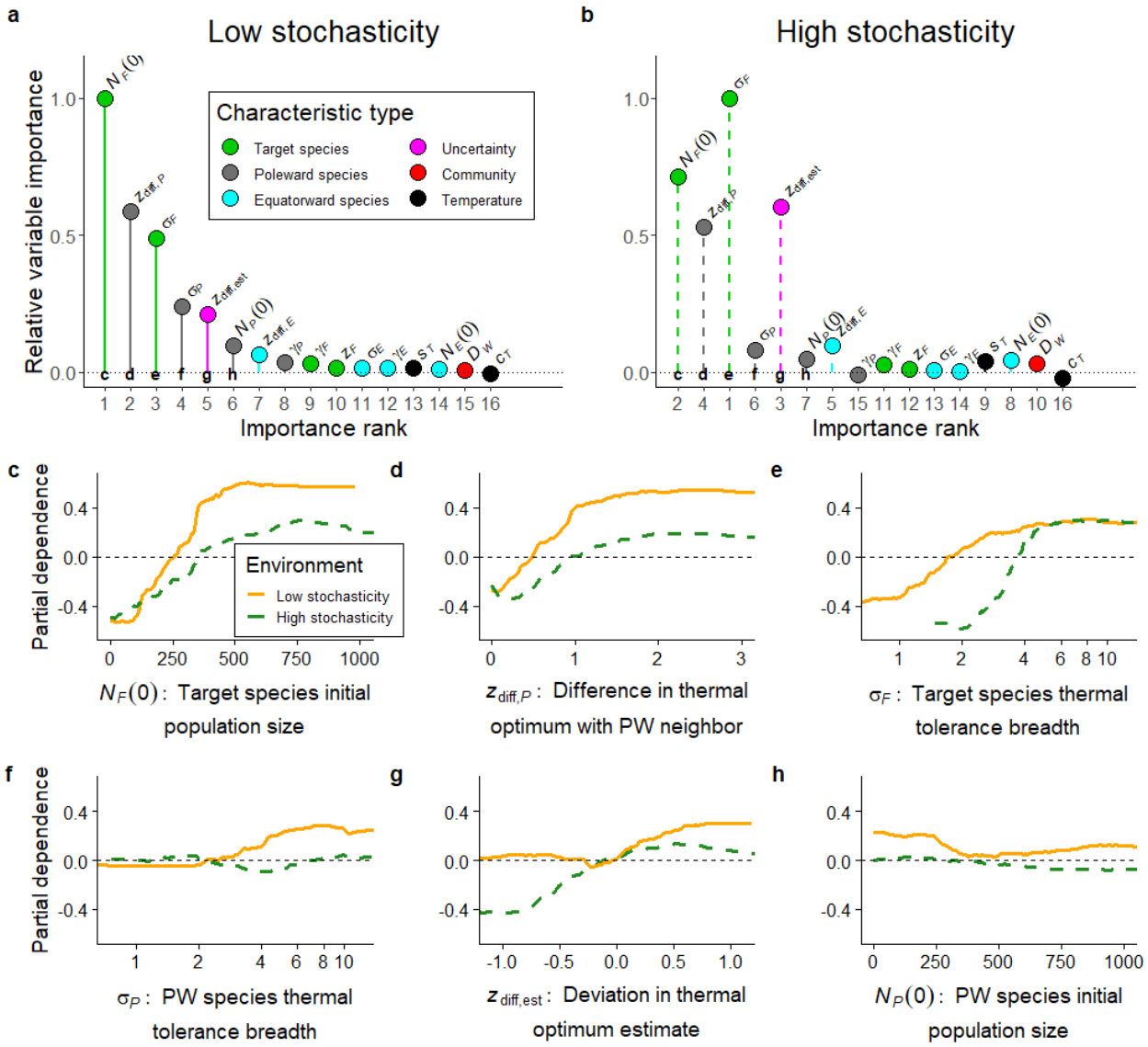

Figure 5: Importance of ecological characteristics from random forest classifications in determining whether assisted migration was successful for the target species (relocating 50% of the shortest dispersing species population with a realized niche estimate thermal optimum). (a,b) Relative unscaled 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 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 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.

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Discussion

Our model suggests that assisted migration (AM) can be effective at increasing species' persistence under climate change if the species is limited by short dispersal, small population sizes, and competition. However, like many related conservation translocations (Fischer & Lindenmayer 2000; Godefroid et al. 2011), we found that AM often fails when the relocated population does not establish, especially for narrow thermal tolerance species. Relocating an intermediate fraction of the population was consistently an optimal strategy (Fig. 3) because it allowed repeated AM events, compensating for potential establishment failures (Fig. 4).

Choosing species for AM

Species are vulnerable to climate change for a variety of reasons, ranging from dispersal-limitation (Pearson 2006), to narrow thermal tolerance (Tewksbury et al. 2008), to competitive interactions (Gilman et al. 2010; Urban et al. 2012). Our model suggests that the effectiveness of AM as a management strategy depends on the driver of vulnerability. In particular, AM might not be appropriate for specialist, narrow-tolerance species. Because specialist species usually persisted under climate change without AM (Fig. 2), narrow thermal tolerance was not a limiting factor for persistence in this model. This arises because of our assumption of a jack-of-all-trades-master-of-none (JATMN) trade-off (Levins 1968), where specialists had a high reproductive performance over a smaller range of temperatures. Because of this trade-off, specialists were stronger competitors under lottery competition (Chesson & Warner 1981), and this competitive advantage could outweigh any costs from narrow thermal tolerance. We also found that specialist species were less likely to benefit from AM (Fig. 3).

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With only a narrow range of temperatures under which specialists can replace themselves, any error in identifying a species' optimal climate would disproportionately affect specialists. Removing the JATMN tradeoff would reduce specialists' competitiveness which could make them more vulnerable to climate change, but it would also weaken specialists' competitive ability, further limiting the effectiveness of AM.

Assisted migration was most successful for species that were dispersal limited because, in these cases, AM directly mitigated the driver of their vulnerability to climate change (McLachlan et al. 2007; Schwartz et al. 2012). Not only was short dispersal a strong predictor of extinction (Fig. 2), but the shortest dispersers also had the strongest proportional increase in persistence with AM (Fig. 3). Moreover, the shortest dispersers were the only target species that had increased persistence with every variation of AM that we modeled. We also found that species with low initial population sizes and species with close poleward competitors were also likely to be vulnerable to climate change and to benefit from AM (Fig. 3). These species had lower dispersal than the average species (Appendix S2), but they were likely to be strong AM candidates because of their other vulnerabilities (Gilman et al. 2010; Urban et al. 2012; Thompson & Gonzalez 2017). For example, species with low population sizes might be capable of dispersing far but not produce enough offspring to realize the full extent of their dispersal potential. For the case of species with close poleward neighbors, our analysis reveals that species interactions could identify target species for AM that might otherwise be overlooked. Overall, our results suggest that AM might be considered for conserving a variety of species beyond those that are directly dispersal limited.

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Even under optimal conditions, AM did not prevent the extinction of nearly 20% of short-dispersing species (Fig. 3). For specialists, AM failed because suitable environments were sparse and narrow, but for other species, AM failed because they had a combination of characteristics that limited establishment success (such as a species with both short dispersal and narrow thermal tolerance) (Fig. 5). In these cases, managers might consider combining alternative management strategies, like increasing connectivity, removing barriers, or creating new reserves (Heller & Zavaleta 2009; Loss et al. 2011; Lawler & Olden 2011). For example, preparing the recipient ecosystem by controlling the populations of resident species (Godefroid et al. 2011) could limit competitive pressure, reduce the risk of establishment failure, and temporarily increase the realized niche of the relocated species. However, this approach would come with additional risks to resident species.

Fractional relocation

We found that AM was most successful when we relocated an intermediate fraction of the total population (typically around 50%; Fig. 3), as this increases robustness to uncertainty that could cause AM actions to fail. By leaving a fraction of the population to persist in the original location, this approach retains a source population for future conservation actions in case relocation occurs at the wrong time or into the wrong place. Fractional relocation also buffers against the risk of falsely identifying a target species for AM, in which case leaving some individuals behind could allow the species to recover those individuals that might be lost during AM. This contrasts with past AM models that assume the optimal strategy is to move the entirety of the total population, as the left-behind population would eventually go extinct without management (McDonald-Madden et al. 2011). Though relocating more individuals

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should increase the chances that a species establishes (Godefroid et al. 2011; Blackburn et al. 2015), this has diminishing returns when considering negative density dependence (Fischer & Lindenmayer 2000). Instead, relocating a fraction of a species would create two smaller populations, each with higher growth rates and less negative density dependence than a single unmanaged population. Though we account for the extinction risk of small populations through demographic and environmental stochasticity (Lande 1998), we do not include Allee effects or explicit genetic components that could cause inbreeding depression, which can further increase extinction risk of small populations (Gilpin & Soulé 1986).

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

Community ecology of AM

Our model builds on past research that suggests competition can prevent some species from tracking climate change (Urban et al. 2012). Though species were vulnerable to extinction if poleward species were strong competitors (Fig. 2), AM was also less successful when we relocated species into an area occupied by stronger competitors (Fig. 5). The effect of

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competition was higher in competition-driven, low-stochasticity communities where AM success depended on characteristics of the poleward species than in dispersal-driven, high-stochasticity communities where success depended more on the ability to accurately place a species into its optimal climate (Fig. 5). This difference suggests that historical climate variability and community assembly can inform management decisions about AM. For example, limiting competitive interactions (Godefroid et al. 2011) might be more effective for species from environments with low historical variability, whereas relocating species into climate refugia (Morelli et al. 2016) might be more effective for species from environments with higher historical variability.

Despite concerns about the potential of AM to cause invasive species (Mueller & Hellmann 2008; Ricciardi & Simberloff 2009), we did not find evidence of invasions with our model (Appendix S2). However, we made several simplifications that could have limited the capacity for invasion to occur. First, the simple spatial structure of our model assumed a single contiguous community that assembled without distinct barriers, making the AM in our model analogous to intra-continental relocations that are less likely to cause invasions (Mueller & Hellmann 2008; Thomas 2011; Bellemare et al. 2017). Additionally, for the sake of simplicity, our model considered only intra-guild lottery competition without the wider web of species interactions that would naturally occur. Biological invasions usually involve more complex ecological dynamics, many of which are taxon-specific and difficult to generalize (Kolar & Lodge 2001; Lockwood et al. 2005; Simberloff et al. 2013). Enemy-release effects would occur if relocated 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

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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). Also, novel interactions in the recipient ecosystem could counteract any physiological benefits the species would receive by reaching an optimal climate. 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).

Acknowledgments

We would like to thank L. Bay, C. Clements, R. Gates, S. Harrison, C. Logan, M. McClure, C. Muhlfeld, S. Sawyer, M. Schwartz, R. Waples, and A. Whipple for their thoughtful conversations at the managed relocation workshop at UC Davis that informed this manuscript. This project was funded by the National Science Foundation, grant #1655475.

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Appendix S1: Supplementary methods

Double geometric distribution

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

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

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

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

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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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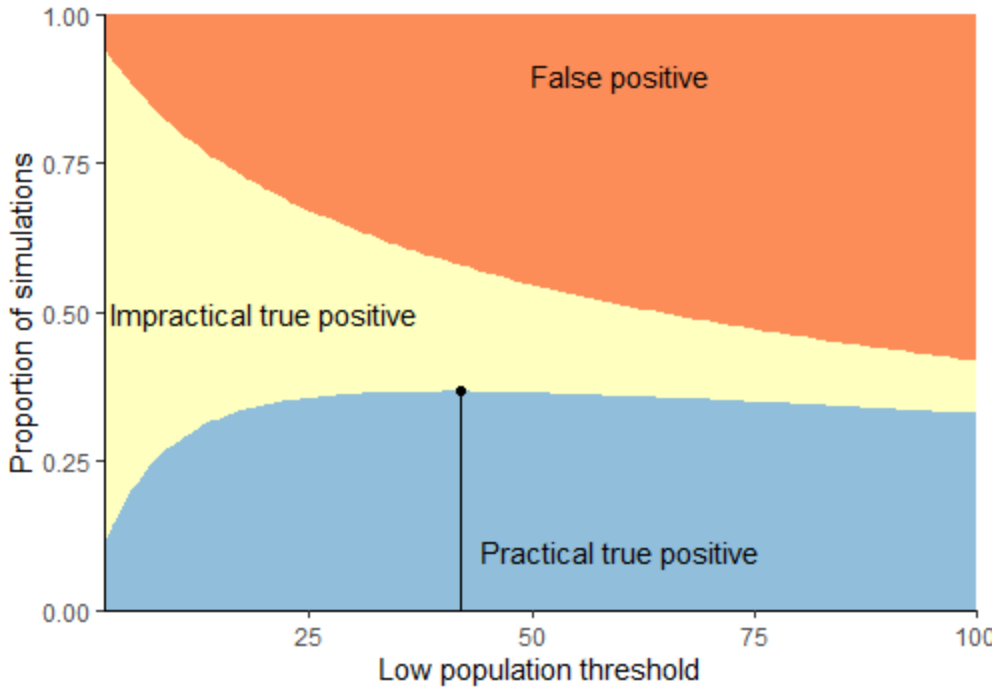

Figure S1.1: When simulated under climate change without assisted migration, species fell into three categories (shaded) depending on their fate following the first time they fell below a low population threshold. We compared threshold values to determine when we could detect a species was likely to 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.

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Appendix S2: Supplementary tables and figures

Table S2.1: 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

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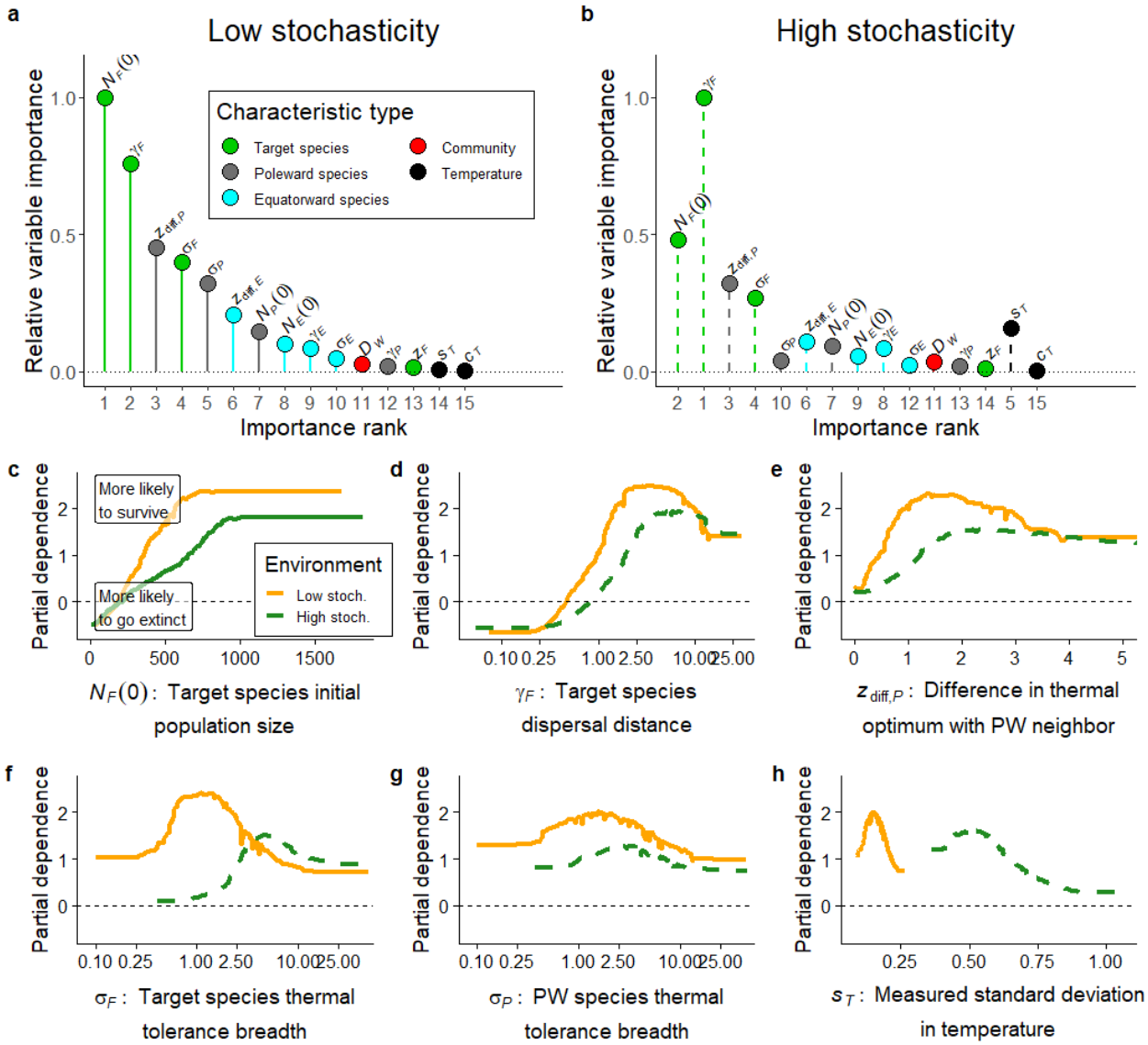

Figure S2.1: Importance of species, community, and environmental characteristics in determining whether the target species will persist with climate change without assisted migration. (a,b) Relative unscaled permutation importance of independent variables of whether a species persisted through climate 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.

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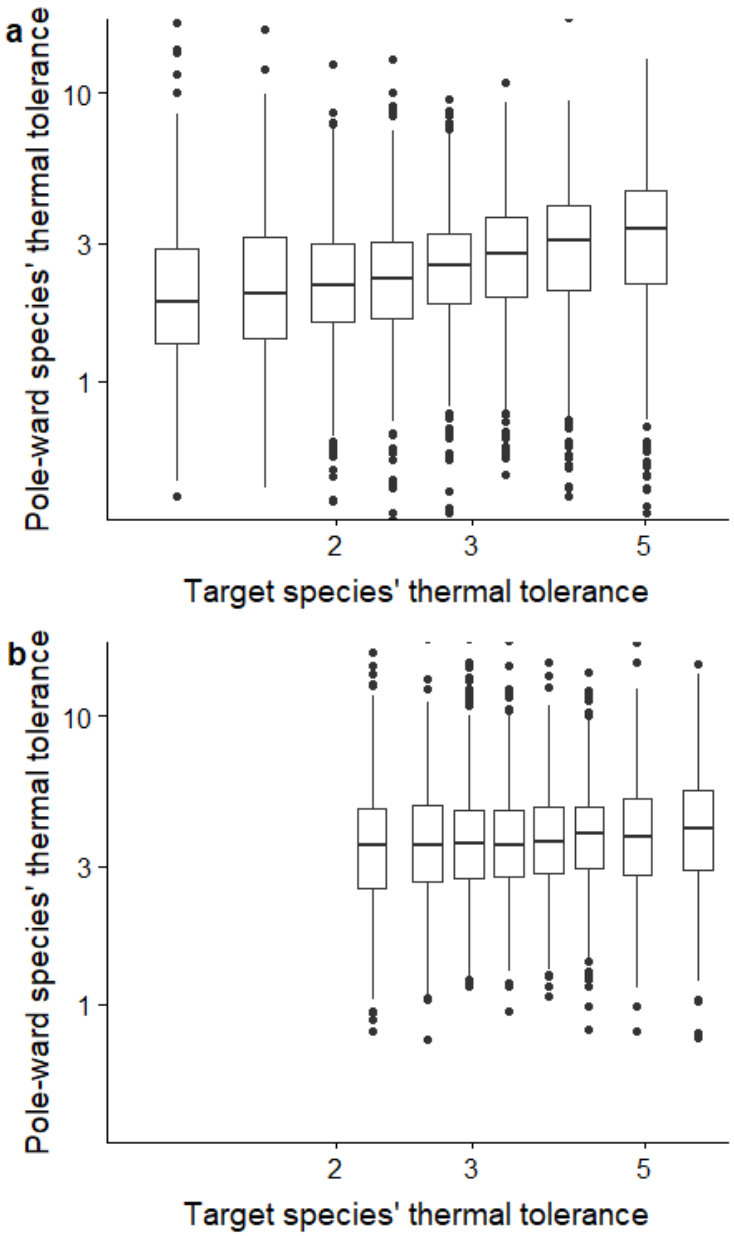

Figure S2.2: Comparison of the thermal tolerances of target that went extinct during simulations without assisted migration and with the species on their pole-ward side (a) under low stochasticity and (b) under high stochasticity. Target species are grouped into 10% quantiles of their thermal tolerances 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.

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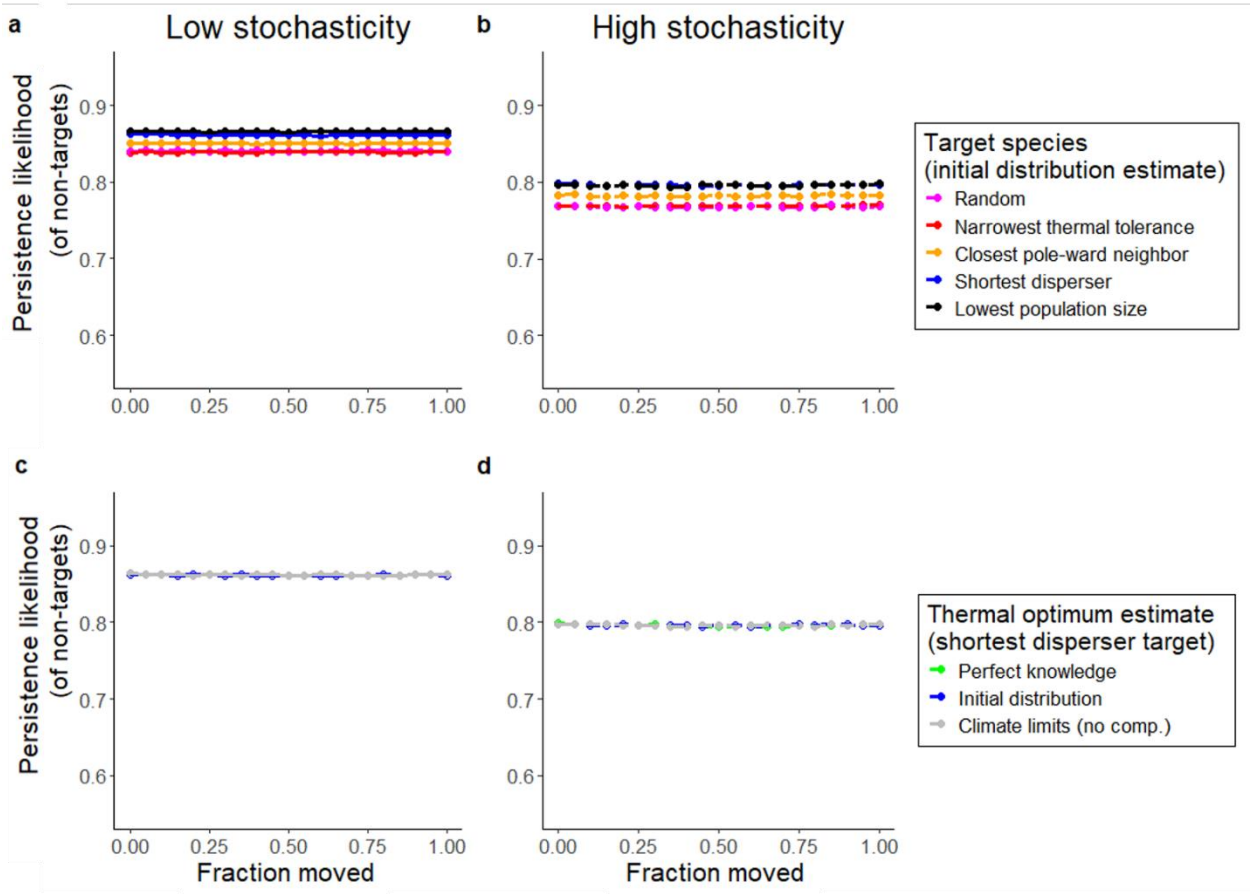

Figure S2.3: During climate change simulations, the persistence likelihood of non-target species that were not chosen for assisted migration (vertical axis) did not depend on the fraction of that population that was relocated (horizontal axis). The dotted lines correspond to persistence with no management 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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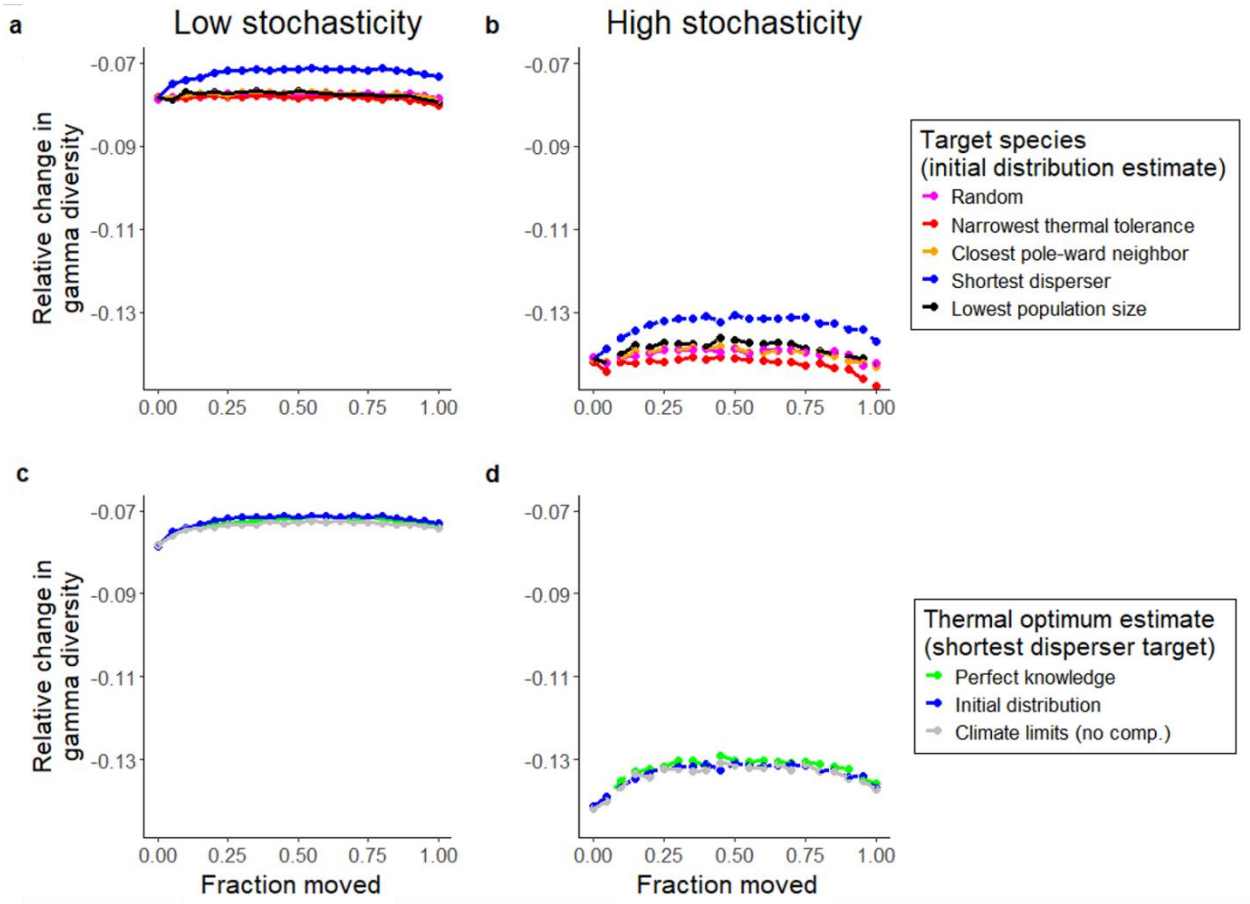

Figure S2.4: During climate change simulations, the relative change in gamma inverse Simpson's diversity index (vertical axis) depended on the fraction of the target population that was relocated (horizontal axis). The dotted lines correspond to gamma diversity with no management action and are shaded to match each comparison. (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.

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Appendix S3: R code

Sample R code can be accessed at: https://figshare.com/s/3325b51ed75d159e035e