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Moving forward: dispersal and species interactions determine biotic responses to climate change

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We need accurate predictions about how climate change will alter species distributions and abundances around the world. Most predictions assume simplistic dispersal scenarios and ignore biotic interactions. We argue for incorporating the complexities of dispersal and species interactions. Range expansions depend not just on mean dispersal, but also on the shape of the dispersal kernel and the population's growth rate. We show how models using species-specific dispersal can produce more accurate predictions than models applying all-or-nothing dispersal scenarios. Models that additionally include species interactions can generate distinct outcomes. For example, species interactions can slow climate tracking and produce more extinctions than models assuming no interactions. We conclude that (1) just knowing mean dispersal is insufficient to predict biotic responses to climate change, and (2) considering interspecific dispersal variation and species interactions jointly will be necessary to anticipate future changes to biological diversity. We advocate for collecting key information on interspecific dispersal differences and strong biotic interactions so that we can build the more robust predictive models that will be necessary to inform conservation efforts as climates continue to change.

Keywords: dispersal kernels; movement; community ecology; landscape fragmentation

Introduction

Global climate change is already altering the distribution and diversity of species.[1–4] Society now calls on ecologists to forecast how climate change will alter species diversity and distributions in order to ameliorate future effects. Dispersal is perhaps the single most important process determining how species will respond to shifting climates and avoid the negative consequences of climate change. Yet most models predicting future species distributions and persistence assume a simplistic caricature of dispersal. Models usually assume that dispersal abilities do not differ within or among species and that dispersal is "perfect" because it allows all species to track their optimal climates regardless of their actual dispersal abilities.[5–7] Models also assume that species move without regard to their interactions with other species.[8–10] Clearly, most species move, they move at different rates, and they interact strongly with some other species. We argue that this interplay between interspecific dispersal variation and species interactions will often determine how climate change will change future species ranges, abundance distributions, and persistence.

We review work that predicts multispecies responses to climate change, examine evidence for dispersal variation within and among species, and explore how both dispersal differences and species interactions can mediate future responses to climate change. We rely on observed range shifts and emerging insights from theoretical models. Further, we apply insights from invasion biology to expand the generality of our understanding, which might otherwise be constrained by biases in study organisms and the shorter time scale of observed climate change responses. Our take-home message is that just knowing a species' mean or maximum dispersal distance is insufficient to understand its response to climate change—we must understand the effects

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of realistic dispersal kernels, interspecific variation in dispersal, and species interactions.

Climate speeds

Many climates will simply move along latitudinal and altitudinal gradients. For species to track their optimal climate, they will need shift their ranges as fast as the climate changes. Although past climate change spurred numerous range shifts, the current rate of climate change is faster than any rates during the past 50 Myr,[11] and today, species face unprecedented effects from humans.[12] These conditions present an extreme challenge to today's species. Assuming that local climates change linearly, Loarie *et al.*[13] calculated that thermal environments are moving 420 m/year on average. Climate velocities vary inversely with topographical relief, with the lowest rates in tropical and subtropical coniferous forests on mountains at 80 m/year and the highest rates in flat grasslands and savannas at 1,260 m/year.[13] Hence, climates are rapidly ascending in latitude and altitude, and if species cannot adapt to rapidly changing conditions, they must track these shifting targets through dispersal while navigating a human-dominated environment.[14–16]

Modeling biotic responses to climate change

We searched for studies that modeled the responses of multiple species to future climate change with the terms *climate change, extinct*, and *predict* in Web of Science. We read the abstracts of each study returned by the search and eliminated studies that did not evaluate multiple species or model future responses to climate change. Forty studies met these criteria (Table 1). We averaged biodiversity outcomes based on a wide range of methods and assumptions about climate change and dispersal and estimated the median value when a range was given. On average, models predict that 19% of species will become extinct and species will lose 60% of their range area during future climate change (by 2050–2100). However, the predicted outcomes varied considerably depending on their assumptions about dispersal and species interactions. We next analyze the influence of these assumptions, each in turn.

Modeling dispersal

To understand how dispersal determines the potential for range expansion in response to climate change, we must first understand how individual dispersal abilities translate into range expansion. We define dispersal as the spatial displacement between an adult and its offspring during one generation. A dispersal kernel characterizes the distribution of dispersal distances among individuals in a population. To translate individual dispersal into range expansion, we integrate the dispersal kernel with demography. For Gaussian dispersal kernels and homogeneous environments, an expanding range front develops as a traveling wave[17,18] with approximate constant velocity (c):

$$c = \sigma\sqrt{2r} \tag{1}$$

where σ is the standard deviation of the Gaussian distribution and r is the population's rate of increase.[19] For a Gaussian distribution, the mean displacement from the parent (μ) equals $\sigma\ \sqrt{(2/\pi)}$ or $\sim 0.8\sigma$. By substituting the mean into the traveling wave equation, we can predict that a range will expand at a rate of $\sim 1.8\mu\sqrt{\mathrm{r}}$. Just knowing dispersal is insufficient to predict range expansion—a population's growth rate matters just as much. Unfortunately, we often have poor estimates of dispersal and its distribution and even worse estimates of population growth rates. In empirical studies, about half the species demonstrate decreasing population growth rates toward range edges[20]—exactly where they matter most for range expansion.[21] Range-wide variation in population growth rates will also cause temporal variation in range expansion rates during climate change. One model shows how range expansion at the leading (e.g., cold) range edge could gradually accelerate, as edge populations with low dispersal ability would experience increasingly suitable climates that would normally only be experienced by interior populations.[22]

When we measure real dispersal kernels, they usually contain more long-distance dispersers than the Gaussian distribution, leading to a fat-tailed distribution.[23,24] As the tails of the dispersal kernel become fatter, mean dispersal rates increasingly underestimate range expansions because long-distance dispersers determine the range expansion rate rather than the individuals in the shoulder of the distribution.[25] When tails become fatter than those in an exponential distribution, range expansion accelerates rather than stabilizes at a constant speed. This acceleration occurs because long-distance dispersers establish isolated frontier

Table 1. Models predicting multispecies losses in response to climate change and their assumptions about dispersal and species interactions

Study	Year	Region	Taxa	Dispersal[a]	Species interactions?	Effect of no dispersal relative to perfect dispersal	Predictions
40	2002	Mexico	Multiple: birds, mammals, butterflies	P, LC, N	No	Up to 2.4% increase in extinction risk	0–2.4% of species lose ≥ 90% range 5–20% of species lose ≥ 50% range
6	2004	Global	Multiple: plants, mammals, birds, frogs, reptiles, invertebrates	P, N	No	26% more extinctions	24% (15%–37%) mean species committed to extinction[b]
5	2006	25 global biodiversity hotspots	Multiple: terrestrial biomes	P, N	No	1–17% more endemic extinctions	11.6% (<1%–43%) mean species extinction rate[c]
99	2008	Costa Rica	Multiple: plants, moths, ants	P, B	No	–	0–3% extinction rate, lowland attrition, range-shift gaps
100	2009	North and South America	Multiple: birds, mammals, amphibians	P, N	No	41–74% more loss of local richness	11–17% mean species extinctions; 25–38% mean species turnover
53	2010	Kenya	Multiple: birds and trees	P, N (trees); P (birds)	Facilitation	43% more loss of bird richness	36% (33–39%) median loss in bird richness
61	2011	Global mountain transects	Multiple: birds, beetles, reptiles, amphibians	P, SS, N	No	–	0–40% extinction rate
101	2011	Austria	Multiple: vascular plants, spiders, beetles, butterflies, snails that live above treeline	P	No	–	77% lost range area
102	2012	Mediterranean sea; global seas < 200-m depth between the latitudes of 45°N and 45°S	Multiple: non-native fish, molluscs, crustaceans	SS	No	–	2–9% extinction rate
103	2002	Europe	Plants	P	No	–	32% (> 20%– > 50%) mean species turnover
104	2003	Cape Floristic Region, South Africa	Plants: Proteaceae	P	No	–	90% (27%–99%) median range loss. 61% species had range contraction; of these, 18% species had range elimination; 39% species expand range
105	2004	Europe	Plants: herbs	LC	No	–	17–61% loss of suitable range for 75% of species

Continued

Table 1. *Continued*

Study	Year	Region	Taxa	Dispersal[a]	Species interactions?	Effect of no dispersal relative to perfect dispersal	Predictions
106	2005	Europe	Plants	P	No	–	27–42% mean species loss and 45–63% mean turnover; overall range across CC scenarios: 2.5%–90% species loss
107	2006	Global	Plants	P	No	–	–
108	2006	Europe	Plants: woody species	P, N	No	42% more lost range area	7–49% median lost range area
109	2006	Europe	Plants: trees & tall shrubs	P, N	No	Up to a loss of 11% more species	>60% mean loss in habitat (boreal, Iberian, temperate species)
110	2008	North America	Plants: trees	SS	No	–	21% (19–22%) mean extinction rate
111	2008	Southwest Australia	Plants: Proteaceae	P, F, N	No	7% increase in extinction	66% species decline (5–25% species extinct)
112	2009	Western Swiss Alps	Plants: mountain plants	P, SS, N	No	25% increase in extinction	11% (0–53%) median species extinction rate
62	2012	Europe	Plants: high-mtn. plants	P, SS, N	No	33% more lost range area	6–8% extinction rate
113	2013	Mediterranean mountains	Plants: trees	P	No	–	80–100% loss in range; up to 350% gain in range
114	2011	North America	Insects: ants	P, N	No	Less community dissimilarity	Up to 30% species become extinct
115	2011	Southern Germany	Insects: grasshoppers & bush-crickets	P, SS, N	No	–22 to + 200% change in range area	Full dispersal overestimated range expansion by 85–494%
116	2004	Mexico	Amphibians: 2 Plethodontid salamanders	B	No	–	Species' range could reduce by 12–15% or 65–75%
117	2006	Europe	Amphibians and reptiles	P, N	No	64–69% more species lost range area	5–35% of species contract range; 26–44% species expand range
118	2010	Global, based on Mexico	Reptiles: lizards	P	Competition	–	36% (10–69%) mean extinction rate
119	2012	Swedish lakes	Fish	P	Competition	–	73% loss in range area
120	2003	North America (Great Plains & Rocky Mountains)	Birds	P, LC, N	No	–	35% mode range loss; 0–400 km shift in range centroid
121	2006	Central and South America	Birds: manakins	N	No	–	20% of species potentially become extinct; 50% of species would lose > 80% of range, 11% lose > 95%
							76% (35–100%) mean loss in range area

Continued

Table 1. ***Continued***

Study	Year	Region	Taxa	Dispersal[a]	Species interactions?	Effect of no dispersal relative to perfect dispersal	Predictions
122	2007	Europe	Birds	P	No	–	more long-distance dispersers
123	2008	Western Hemisphere	Birds: land birds	P	No	–	12–16% extinction rate (in intermediate CC scenario) (low CC: 1.3% extinction; high CC: 30% extinction)
124	2009	South Africa, Lesotho and Swaziland	Birds	P, N	No	14% more lost range area	32% species lose > 50% of range area; 38% increase range area
125	2010	Cerrado region, Brazil	Birds	P, N	No	34% more lost range area	46,000–70,000 km^2 current & future range overlap
126	2012	Australian tropical savannas	Birds	P, SS, N	No	23% more lost range area	67% of species lose range area
127	2012	Europe	Birds	P, SS, N	No	10% reduction in richness; 4% more lost range area	8–14% lost range area (61% loss to 72% gain)
128	2007	Europe	Mammals	P, N	No	8.1% increase in extinction	1–7% extinctions; 32–78% of species become severely threatened; 40–140% range expansion in Mediterranean species
129	2009	Europe, Mediterranean	Mammals: bats	P	No	–	50% (0–100%) species contract range; 50% (0–100%) species expand range (based on 2 intermediate CC scenarios)
37	2012	Western Hemisphere	Mammals	SS	No	9% increase in extinction	9% extinction rate (up to 39%)
130	2012	Subarctic Europe	Mammals	P, N	No	–	0% extinction rate, 30% of species contract range, 70% of species expand range
131	2012	Southeast Asia	Mammals: bats	P, N	No	1–3% increase in extinction	2–9% extinction rate

NOTE: Wherever applicable, we chose the intermediate climate change scenarios analyzed. Range values are in parentheses. [a]P = perfect, B = accounts for landscape barriers, LC = least-cost, SS = species-specific, N = no dispersal, F = fixed rate; [b]assumes mid-range climate change; [c]assumes narrow biome definition and specificity, MAPSS GVM, using SAR method, averaging across plants and vertebrates.

populations, which expand outward and eventually coalesce into an accelerating range boundary.[26] Hence, we need to know not just dispersal and population growth rates, but also the distribution of dispersal among individuals.

Fat-tailed dispersal kernels occur frequently in nature, especially owing to biotic interactions. For instance, many trees have fat-tailed dispersal kernels, which provides one explanation for Reid's paradox.[18] Reid's paradox states that trees expanded quicker after deglaciation than predicted by their mean dispersal distances.[25] Pollen records indicate that trees dispersed 100–1000 m/year[25] during rapid shifts in climate.[27,28] Passive dispersal cannot explain these high rates.[25] Instead, broad-ranging animals most likely transported seeds, thus enabling long-distance dispersal and fattening the trees' dispersal tails. Hence, heavy-seeded oaks could shift their ranges northward just as fast as wind-dispersed trees.[29] Fat-tailed dispersal kernels, often owing to animal-mediated dispersal, might enhance the capacity to track climatic changes better than expected based on mean or median dispersal rates—the statistics most commonly used in models of range expansion.

Much of the evidence for fat-tailed distributions and accelerating range expansions can be traced to longstanding work in invasion biology.[17,18] Evidence from species invasions countered the original assumption of linear rates of spread and limited the use of classical traveling wave models in real situations.[30,31] Real patterns of invasion are complex and idiosyncratic. Rare, long-distance movements often determine range dynamics.[32] These rare events are sometimes driven by stochastic fluctuations, which are not captured well by deterministic traveling-wave solutions.[33] Dispersal ability also might commonly evolve during range expansions, changing both the mean, variance, and skew of the dispersal kernel.[34,35] Yet discussion of movement under climate change generally has not yet assimilated these advances, even though they follow patterns similar to those observed for biological invaders.[36] Predictive models for climate change still mostly rely on average or median rates of spread and follow the classical paradigms of species movement modeling.[37]

Most theory depicts a species range as an unbroken mass set upon a homogeneous landscape. Few ranges or invasions match this clean abstraction. Species distributions reflect the patchy nature of the environment, and environmental heterogeneity strongly influences the rate and pattern of range expansion.[31,38] Given that many of the species most vulnerable to climate change have small and patchily distributed ranges, successful forecasts of their fate will depend on how they move across available environments. For instance, a simulation study demonstrated that the best landscapes for range expansion are those with corridors, whereas the worst landscapes are highly aggregated patches surrounded by unsuitable habitat.[39] Straight-line distances lose their utility in these types of realistically patchy landscapes. One solution is to apply landscape resistance models of movement, which model the circuitous routes that species must take to circumvent unsuitable habitat.[40]

The greatly modified landscapes of today will inhibit dispersal for many species, requiring them to detour around human-created barriers.[41] For still other species, anthropogenic landscapes will facilitate their dispersal and survival. These include weedy species, invasive species, and species that humans protect, cultivate, and carry. Humans will move these species long distances, on purpose and by accident, which can allow them to track climate changes.[42,43] For instance, garden plants are regularly planted outside their natural ranges, thus already assisting their migration into regions of newly suitable climates.[43] Humans also accidently move seeds and microscopic organisms on muddy or felt-soled shoes,[42] car tires,[44,45] and boats. Humans could be the greatest source of long-distance migrants and fat-tailed dispersal kernels.

One additional note is that dispersal is a trait of organisms that can evolve.[34,46] Changing climates could select for greater dispersal ability, especially for species at the leading edge of a range where suitable habitat exists beyond the range boundary that might be less crowded with conspecifics[47] or lack interspecific competitors or enemies. The evolution of greater dispersal can occur through spatial selection, whereby the best dispersers are the first to colonize newly suitable habitats, and through their spatial isolation from poorly dispersing individuals, they quickly evolve greater dispersal ability.[47] Simulations show that the evolution of dispersal in leading-edge populations can rescue a species by allowing it to track a rapidly changing climate.[48] Although relatively poorly understood in nature, the evolution of dispersal offers another way that species might respond to climate change and mitigate its effects.

Interspecific dispersal variation

Multispecies analyses of climate change effects generally ignore interspecific variation in dispersal and instead contrast models assuming no dispersal and perfect dispersal (Table 1). The perfect dispersal scenario predicts fewer extinctions, but this scenario might offer an unrealistically positive outcome. To what degree do species within and among taxonomic groups differ in dispersal ability? How wrong are we when we assume perfect and equal dispersal?

We examined four taxonomic syntheses of dispersal distances that include plants,[49] ant-dispersed plants more specifically[50], amphibians,[51] birds,[52] and mammals[52] (Fig. 1). Unfortunately, we did not find sufficient data on dispersal kernels for these species, so we only could analyze differences in mean dispersal abilities. We find strong variation in dispersal ability both among and within taxonomic groups. Ant-dispersed plants move little compared to birds and mammals, setting the stage for interactions between these taxonomic groups.[53]

The dispersal differences vary just as much within taxonomic groups. Mean dispersal rates within a taxonomic group usually follow a log-normal distribution because most species disperse poorly and a few species disperse really well.[54] For instance, the Townsend's vole (*Microtus townsendii*) moves 5 m per generation whereas the gray wolf (*Canis lupus*) disperses 140 km, revealing a 28,000-fold difference in dispersal ability.[52] These differences among and within taxonomic groups in dispersal can alter species interactions and create no-analog communities,[55] or sets of interacting species that have never co-occurred before.

Dispersal abilities are also likely to differ by region. Janzen[56] posed that barriers to dispersal would be larger in the tropics relative to temperate regions because in the tropics within-site temperature varies little during the year whereas thermal regimes differ strongly with altitude.[56] Thus, tropical species should evolve narrower tolerances to temperature variation than their temperate counterparts that experience seasonal temperature fluctuations.[56] For a given altitude, this narrower tolerance makes any dispersal up or down in elevation a potential fitness liability.[56] Therefore, tropical species generally have

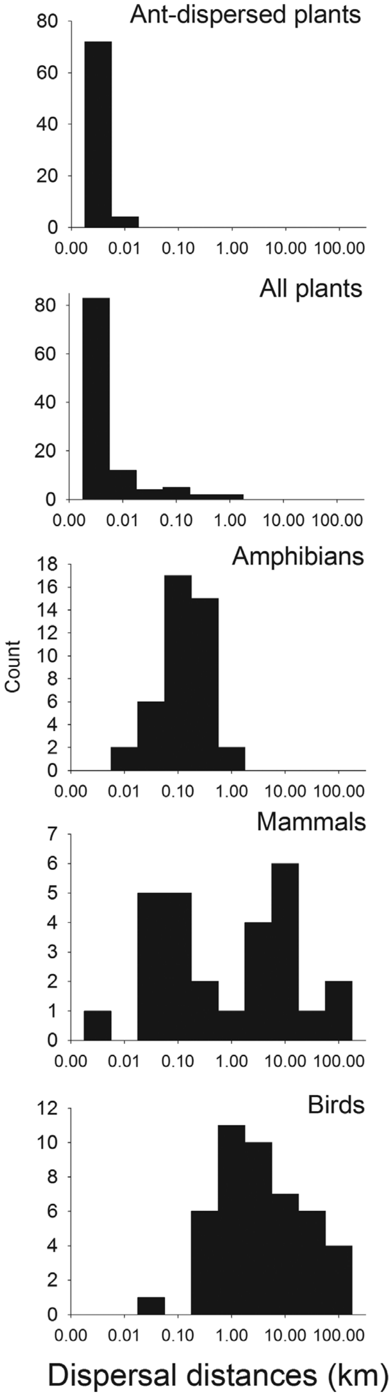

Figure 1. Histogram of the central tendencies of dispersal distances among species across a broad set of taxonomic groups, including ant-dispersed plants, plants, amphibians, birds, and mammals. We used the mean, median, or mode of dispersal distances, depending on what statistic was reported. Note that data are not corrected for generation length. See Figure 2 for corrected mammal data.

lower thermal breadth.[57,58] Lower dispersal ability might have evolved as well,[59] but this prediction requires further evaluation.

Human affiliation provides an additional way to differentiate species in terms of their dispersal capacities. We will intentionally move the species that we use in commerce[43] and some threatened species through assisted migration.[60] As we currently do with invasive and weedy species, we will also move a subset of species unintentionally and support them in human-modified environments.[42,45] These human-associated species are likely to expand their range rapidly, setting up their interactions with those species that are not associated with humans.

Tracking climate changes: models

Most researchers apply a climate envelope approach where they model the species' current ranges based on current climate variables and then project new ranges based on the future climate (Table 1). Most of these models assume either perfect or no dispersal. In the perfect dispersal scenario, the species is assumed to possess sufficient dispersal ability to facilitate its exact shift into the new range. In the no-dispersal scenario, the species is expected not to move at all and persist only in the overlap of its current and predicted range. This scenario requires that locally adapted populations evolve *in situ* to altered conditions. We use the difference between these two extremes to highlight the importance of dispersal in reducing extinctions.[5,6] From our literature review, contrasting scenarios with and without dispersal leads to 18% more extinctions (range: 2.4–57.5%) and 25% smaller ranges (range: 4–42%) under future climates (i.e., by 2050–2100). A total of 28% of studies assumed perfect dispersal only and 33% assumed just perfect and no dispersal scenarios. Ten percent of reviewed studies incorporated barriers or used least-cost modeling to understand landscape connectivity. A growing number (23%) of models incorporate species-specific dispersal differences.

In one model with species-specific dispersal rates, Schloss *et al.*[37] evaluated the annual rate at which mammals could disperse and compared it against local climate change velocities. They found that 9% of mammals, on average, would fall behind local climate change (Fig. 2). Not surprisingly, shrews and moles were least likely to track climatic change whereas large carnivores and ungulates were more likely.[37] By using median dispersal, the study might underestimate range expansion rates for mammals with more fat-tailed dispersal kernels or higher rates of increase. To see the upper limit of climate tracking, we also plotted maximum dispersal velocities in Figure 2 for the same set of mammal species. All species' maximum dispersal velocities fell above the 0.42 km/year mean climate change velocity. Hence, this upper limit to dispersal suggests that the dispersal kernel could play a substantial role in allowing climate tracking for those species with fatter-tailed distributions.

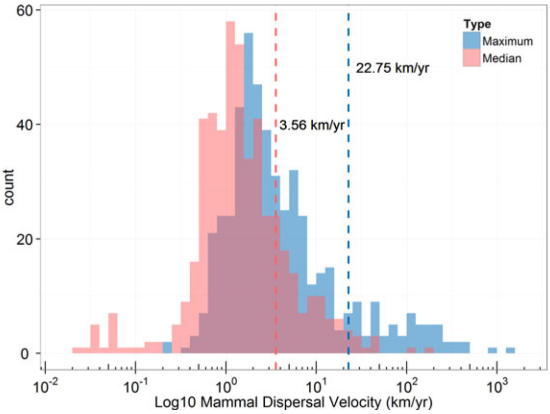

Figure 2. Median (blue) and maximum (red) dispersal velocities (km/year) for mammals[37] on a $\log_{10}$ scale. Blue and red dotted lines indicate mean dispersal rates for median and maximum dispersal, respectively. Based on median dispersal velocities of mammals versus the velocity of climate change calculated from the emissions scenario A2, Schloss *et al.*[37] predict that on average 9% of mammals will not keep track with climate change. We include maximum dispersal distances for comparison. The range expansion of some species with fatter-tailed dispersal kernels might track climate much faster than their mean or median dispersal velocity. In all likelihood, range expansion might occur more quickly than the median values, but slower than the maximum values.

Sheldon *et al.*[61] set dispersal ability proportional to range breadth, assuming that thermal tolerance determines both range size and dispersal. This model produced extinction outcomes intermediate between the no- and perfect-dispersal scenarios.[61] Dullinger *et al.*[62] applied a hybrid approach to predict responses of high-mountain plants. They combined niche-based climate envelope models, the real landscape of soil types and climate factors in the European Alps, and a mechanistic simulation model with species-specific demographic and dispersal data, including fat-tailed seed dispersal.[62] In contrast to what might be expected, the model with high species-specific dispersal resulted in smaller declines in range size than the model with perfect dispersal. But these were dynamic simulations, compared to the static no- and perfect-dispersal simulations. In the dynamic simulations, species could persist in unsuitable habitats even though they were destined for eventual extirpation. These transient dynamics buffer losses in the near term. After accounting for this transient extinct debt, the species-specific results fell between the no- and perfect-dispersal scenarios,[62] as would be expected. These types of approaches offer promising ways forward toward integrating realistic dispersal abilities with climate envelope models.

Tracking climate changes: empirical observations

We next turn to the empirical literature on climate change–induced range expansions. On average, species ranges are expanding toward higher latitudes at 1.7 km/year (95% confidence intervals = –1.1–4.6 km/year).[1,63] Although this value surpasses the average climate velocity of 0.42 km/year,[37] these data sets are biased toward mobile taxa such as birds, mammals, and flying insects. The mean also disguises a great deal of variation in range expansions among species: some species have expanded their range to great distances whereas other species have not expanded at all or have even decreased in range.[1,4,64,65] Explaining this variation in range responses to climate change is critical to predicting which species are most at risk.[36]

Toward this end, Angert *et al.*[36] used a trait-based approach to evaluate if dispersal could explain the variation in range responses to climate change in birds, dragonflies, plants, and mammals. If dispersal strongly determines range responses to climate change, as suggested by current dogma, then a strong relationship between dispersal-related traits and recent range expansions should exist. However, dispersal traits did not consistently explain range responses. Dispersal traits were not related significantly to range shifts in mammals based on body mass, which is correlated with dispersal ability,[52] and in dragonflies based on dispersal behavior and duration. Migratory status and seed dispersal period were retained in the best models for birds and Alpine plants, but were not significant by themselves, and the best bird and plant models explained only 6% and 14%, respectively, of the variation in range shifts.[36] Another study found a significant relationship between expert characterizations of butterfly mobility and range shifts.[66] One explanation for these different outcomes is that the second model used expert knowledge on dispersal in butterflies, and this expert knowledge might incorporate a more holistic view of dispersal by aggregating behavior, philopatry, and phenology than is captured by the limited subset of dispersal traits available in the literature.[36]

Overall, these results suggest that dispersal by itself does not strongly determine range responses to climate change. Paradoxically, dispersal does appear to explain variation in species invasions.[67] This difference might stem from a lack of statistical power to detect the effect of dispersal traits in climate-induced range expansions. We know a lot more about successful species invasions, on average, than we know about species studied for climate change effects. Also, invasions that require survival during cross-continental translocation might place a greater emphasis on traits associated with long-distance dispersal (e.g., desiccation resistance). Alternatively, the high rates of movement of the study organisms favored for climate change biology might lessen the role of dispersal. Here, we will concentrate on a fourth reason: species interactions might alter the importance of dispersal.[36] This explanation could explain the divide between observed outcomes in climate change and invasion biology because the expansion of native ranges usually occurs in a similar biotic context whereas biological invaders leave behind many of their strongest species interactions.[68]

Biotic limitations to range expansion

Even though a species might be capable of dispersing far enough and fast enough to remain in a suitable climate, species interactions might still prevent climate tracking and explain the high variance in range responses to climate change.[10,69] Longstanding research has shown that biotic interactions influence niche breadth and species ranges.[8,70–73] Elegant experiments involving *Drosophila* demonstrated that interactions with competitors and parasitoids determine the ranges of temperature habitats colonized by different species. For instance, *D. simulans* was eliminated from the hottest temperature environment when *D. melanogaster* was introduced.[8] *D. melanogaster* reaches its highest population density at hot temperatures, whereas *D. simulans* does best at intermediate temperatures. Although both species can maintain relatively high densities by themselves across the experimental range of temperatures, competition narrows the temperature range at which each species can maintain positive population growth. Field observations suggest that species interactions modify responses to changing climates.[74,75] Yet, only three modeling studies in Table 1 incorporated biotic interactions in their predictions.

Depending on their type, species interactions can either hinder or augment range responses to climate change.[10] Specialized mutualists or predators cannot expand without their partner species. For example, Schweiger *et al.*[76] showed that a specialist butterfly, *Boloria titania,* could lose more than half its current range if its host plant does not disperse as rapidly as it does. Any species that depends on other species for food or habitat will experience similar constraints. Kenya's bird species richness was predicted to decrease by 36% if the woody plants that structure the birds' habitat lagged behind bird range expansions, as would be expected based on their slower dispersal rates.[53] In contrast, assuming the same and perfect dispersal results in a 7% gain in bird species richness, showing the striking difference that assumptions about dispersal can make.[53] Again, interspecific dispersal differences play a strong role in preventing climate change responses. For these dependent species, we must consider the intersection of multiple ranges, each potentially changing asynchronously with climate. The most severely affected species will determine the fates of all other dependent species.

Species interactions do not just create losers. Prey, hosts, or competitors can outrun their enemies by expanding their range and entering enemy-free space. Within this space, population growth rates could increase, possibly allowing species to increase their rate of range expansion in response to climate change.[54,77] For instance, expanding into pathogen-free space allowed a tree to invade a resident tree population in one model.[77] Invasion biology provides support for this phenomenon, in which fewer predators or pathogens allow invasive species to fill their broader fundamental niches in new places.[78,79] However, humans transport invasive species far from their native range, creating a greater potential for lost species interactions. Will it also happen with climate-induced expansions of native ranges? Menendez *et al.*[80] provide one example where the Brown Argus butterfly (*Aricia agestis*) experiences lower mortality from parasitoids in regions recently made suitable by warmer conditions. Hence, even native range expansions could result in a biotic advantage for the good disperser.

Theoretical approaches that combine dispersal and species interactions

Thus far, scientists have presented mostly verbal arguments about how biotic interactions affect climate change responses.[10,69] A few models have begun to address this question quantitatively. The three major findings to date are that species interactions can (1) slow the tracking of climate change, (2) increase extinction risks and changes in species distributions, and (3) reduce the potential for dispersal evolution.

In models, competitors can slow down the advance of species by occupying habitats and reducing the fitness of individuals at the invasion front.[54,77,81] For instance, in the absence of a competitor, a tree colonizes new habitat at 200 m/year in one model, but this rate is reduced to 2 m/year when a competing tree species is already established.[77] Mutualists slow down the expansion of competitors during rapid climate change in another model.[81] In a model of 40 competitors along a warming climate gradient, competition substantially increased the lag in climate tracking relative to models lacking competition.[54] In this boxcar effect, each species is blocked from colonizing the next cooler habitat by its resident species, slowing the climate responses of all species. The same boxcar effect characterizes locally adapted populations in a single-species model in which the presence of maladapted genotypes blocks better-adapted genotypes from tracking optimal habitat along a warming temperature gradient.[82] Just like boxcars on a train, species might only climb climate gradients as fast as species further up the line.

Competition, together with higher interspecific dispersal variation, is predicted to produce more extinctions, greater reductions in diversity, and more no-analog species interactions. In a model of multispecies competition, more than half the species went extinct after assuming moderate dispersal variation among species[54] (Fig. 3). This result occurred even when the majority of species could disperse

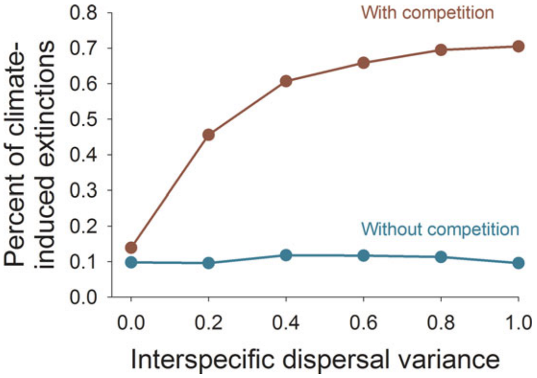

Figure 3. Percentage of climate-induced extinctions with (red) and without (cyan) interspecific competition depending on the variance among species in dispersal.[54] Standard error bars are plotted but are smaller than the size of symbols. Absent competition, only the 10% of species with ranges closest to the mountaintop become extinct. With competition, extinctions increase, most dramatically when interspecific dispersal variance is greatest. Both performance and competitive niche breadth standard deviations were set to 5.0° C and the mean dispersal distance is 0.3. Data from Ref. 54.

perfectly. In the absence of competition, extinctions were fewer and changes in species diversity were less dramatic.[54] The influence of competition becomes most evident when the best dispersers track their optimal climates and encounter slower dispersing species (boxcars) ahead of them. Because these fast-dispersing species successfully track their optimal climate, they also were fitter and better able to outcompete the slow-dispersing residents in their path. The slow-dispersing species thus faced not only the threat of falling behind their optimal thermal niche, but also the lower fitness that accompanied the arrival of a fast-dispersing competitor in their habitat. Competition also produced many more mountaintop extinctions than simulations without competition. Without competitive interactions, a species could persist at the cold mountaintop or Pole as long as its thermal niche was broad enough to allow positive population growth rates. As soon as competitors arrive from behind, population growth rates become negative and these species become extinct.

The evolution of dispersal can rescue species from extinction owing to climate change. Yet competition can theoretically prevent this evolution.[48] In a simulation model, populations of a range-expanding species evolved to invest much less in dispersal ability when invading a region filled with competitors than when invading an empty landscape.[83] This outcome occurs in the model as populations shift investment into traits that aid competition over dispersal.

Discussion

Climate change is shifting habitats at an unprecedented rate. Species will need to adapt *in situ* or disperse to track their climatic niches. Our ability to understand how dispersal translates into range expansion with climate change is modest at best. One reason is that we rarely incorporate interspecific variation in dispersal, realistic dispersal kernels, and biotic interactions. Are climate change outcomes sensitive to the details of these factors, or are we just delving into the details? We find that incorporating these details produces more specific predictions. Moreover, biotic interactions and interspecific dispersal distances, when combined, can produce qualitatively different dynamics than those produced by simpler models.

Instead of predicting a wide range of outcomes by comparing the perfect- and no-dispersal scenarios, models that assume species-specific dispersal differences can produce more specific predictions about changes in species ranges and extinctions. The difference between the no- and perfect-dispersal cases in Table 1 resulted in an average 18% difference in extinction rates and 25% difference in diversity. This range in outcomes would likely be significantly narrowed by incorporating species-dispersal differences. Approaches that include species-specific dispersal also can pinpoint more exactly which species are most at risk. For instance, Schloss *et al.*[37] specified that shrews and moles face the greatest risks from climate change.

We did not find any models that compared responses between normal and fat-tailed dispersal kernels. However, including fat-tailed distributions should increase range expansion and lead to outcomes closer to the perfect dispersal scenario. For instance, the maximum dispersal abilities of mammals are sufficient to track climate change for all species, but only 9% of species will track climate based on their median dispersal rate. Incorporating information about among-species differences in dispersal kernels will likely facilitate insights about the individual species that are most at risk.[62]

We advocate for applying more realistic dispersal kernels derived from observed dispersal patterns that often are substantially fatter than normal dispersal kernels. But this is just the first step. To make further progress, we need to model dispersal mechanistically.[7,84] Mechanistic dispersal models can improve upon an empirical dispersal kernel if the empirical distribution is not well characterized, which is often the case for rare long-distance dispersers or dispersal that depends on environmental factors.[85,86] A key feature of mechanistic dispersal models is that they directly incorporate how the environment alters dispersal. For instance, rising temperatures can increase wind turbulence, which subsequently elevates long-distance dispersal of seeds and the potential for range expansion in trees.[85] Another mechanistic model indicates that wind-dispersed North American trees are unlikely to keep pace with climate change unless wind speed and seedling survival significantly increase.[7] Mechanistic models have also been developed for animal movement behavior. In these models, dispersal kernels emerge from simple movement rules that describe correlated random walks across landscapes with varying biases toward patches and different times spent moving.[84] These mechanistic models offer a more robust way to predict movement, especially when dispersal depends on changing climatic factors such as wind speed.

Habitat fragmentation also plays an important role in determining range-expansion rates.[39] Distinguishing between suitable and unsuitable habitats based on climate and other factors will be necessary to understand this effect.[40] One approach to modeling species dispersal through fragmented landscapes is to apply a conductivity method derived from electrical circuit theory.[87] This method predicts movement more accurately than alternative methods in simulations[39,87] and thus provides a means to predict range expansion in realistically complex landscapes.

If species-specific dispersal mainly improves predictive accuracy, incorporating biotic interactions can generate dramatically different outcomes. These differences are particularly striking when combined with dissimilarities in species dispersal. Species that depend on poorly dispersing species for food or habitat cannot take advantage of their own dispersal ability.[53] Competition plus interspecific dispersal variation greatly increases extinction risks because fast dispersers outcompete slow dispersers for newly suitable habitat.[54] Species interactions also slow range expansion by reducing rates of increase in frontier communities. Species cannot track climate fully because competitors block their forward advance.[77] Empirical data show that lack of pathogens can create enemy-free space and subsequently higher rates of increase that can accelerate climate-induced range expansions.[80] Hence, the few models exploring the intersection between dispersal variation and biotic interactions suggest that this complexity will alter our predictions considerably.

Outlook

Scientists have studied the biological consequences of climate change from four perspectives: inferences drawn from observed range shifts, correlative climate envelope models, mechanistic models, and general theoretical models. The data-driven perspective focuses on the particular responses of species to climate change.[1,63] These studies, though often requiring decades of persistent study by scientists, cover just a small fraction of the Earth's species, and the stories that they tell us are biased toward a subset of study organisms (i.e., plants, birds, mammals, and butterflies). One general lesson to emerge is that the assumptions used in most global forecasts often apply poorly (e.g., Ref. 88). We believe invasion biology can provide important insights about projecting future changes in species ranges in cases where we currently have limited data.[67] For several decades, invasion biologists have considered closely analogous issues including the role of species interactions on movement by a colonizing species as well as the effect of climate variation on invasion pattern and speed. Despite similarly daunting challenges, invasion biologists have developed the means to make predictions about the dynamics of invasion among highly heterogeneous species. An important future direction is to understand when insights from invasion biology can be applied to understand the expansions of native species just beyond their native range.[68]

Most existing models of responses to climate change are correlative climate envelope models. These models have the advantage of being easily parameterized based on available climate and species distribution data. These models also already incorporate the multifarious mechanisms that determine a species' range, including dispersal limits and species interactions. As a result, correlative models often outperform mechanistic models in describing a species' current range.[89] However, the actual mechanisms remain hidden beneath the environmental correlations used to build the models. If correlative approaches mistake correlated factors for mechanisms, then predictions extrapolated to novel future climates and future distributions of interacting species are unlikely to be accurate. Mechanistic models offer an alternative approach.

Mechanistic models of responses to climate change are gaining increasing traction because they generate predictions based on observed mechanisms rather than potentially spurious correlations.[89,90] For instance, dynamic vegetation models offer a mechanistic platform for predicting plant distributions.[91] Many of these models already incorporate competitive interactions among plants, and these models recently have incorporated more realistic assumptions about dispersal.[92] The program TreeMig incorporates explicit space and a dispersal kernel for seeds.[93] The TreeMig model was parameterized for Alpine tree species in Europe and then used to simulate the colonization of the Valais following the last Ice Age. The simulations reveal logical transient dynamics during past climate change, including varying waves of dispersers and replacement of residents with fitter species, and ultimately recreates the current species distribution of the region.[93] Mechanistic models for animals also show great promise in producing better predictions than can be extrapolated into future climates.[94] The remaining issue is that these models require lots of high-quality data, which often does not exist for a given system.[89]

Theoreticians have developed more general multispecies models parameterized on real or generic species to estimate the sensitivity of predictions across a range of parameter space. Currently, only a few such models exist and they focus on simple competitive and enemy–victim interactions. We will need to expand this theory to incorporate other interaction types and greater trophic complexity. For instance, trophic interactions often affect species ranges, and top consumers are often highly sensitive to climatic changes.[95] Changes to top consumers can have wide-ranging effects on food webs.[96,97] However, only a few models address this complexity[98] and seldom do so in a spatial context.[77] Even with these models, the data needed to parameterize these models often outstrip our current knowledge, requiring us to make substantial assumptions about parameter values. These assumptions reduce both the accuracy and precision of our predictions.

We highlight the need for more mechanistic models that incorporate more realistic assumptions about dispersal and species interactions. Before we can reach this goal, we need better data on dispersal and its distribution among individuals within populations. These data almost never exist for entire communities, making inferences about multispecies responses difficult. To make progress rapidly, we might need to categorize species movement patterns based on coarse traits like dispersal syndromes and body size. For instance, patterns in the mammal data in Figure 2 originate from the strong relationship between mass and dispersal ability calculated from fewer species. We might also delineate those species that are facilitated by human activities and that will move into new locations as quickly as climate allows. Future models might take into account these useful dispersal syndromes to make progress where measuring the dispersal of many species will be prohibitive in the short term.

Conclusions

Many global change biologists predict that better dispersers will fare better under warming climates because they will best track the shifting climates. However, this view ignores important mediating factors emerging from environmental heterogeneity and dispersal and fitness variation among species. Species interactions, in particular, provide a powerful force that will alter the responses of species assemblages to climate change. Predicting future effects will require us to understand whether and how entire communities move, not just individual species.

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Conflicts of interest

The authors declare no conflicts of interest.

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