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Issue: *Climate Change and Species Interactions: Ways Forward***Get real: putting models of climate change and species interactions in practice**

Lauren B. Buckley

Department of Biology, University of North Carolina, Chapel Hill, North Carolina

Address for correspondence: Lauren B. Buckley, Department of Biology, University of North Carolina, Chapel Hill, NC 27599. buckley@bio.unc.edu

Forecasts of the ecological impacts of climate change are generally focused on direct impacts to individual species. Theory and case studies suggest that indirect effects associated with species interactions may alter these direct responses. How can we tractably predict in which cases indirect effects are likely to be important and appropriately model the interaction of abiotic and biotic drivers? One viable strategy is to characterize partitioning between species along thermal, temporal, and spatial niche axes. The partitioning can be informed by assessing functional traits. Mechanistic models can then be applied to predict how climate change will alter niche partitioning. I illustrate this approach by asking whether competition has altered the responses of Caribbean *Anolis* lizards to recent warming and find that forested habitat has become more suitable for a warm-adapted, open species, and less suitable for a cool-adapted forest inhabitant. Competition may result in competitive displacement of the cool-adapted species as the warm-adapted species moves into the forest. Species interactions may accentuate abundance and distribution shifts predicted in response to climate change along the elevation gradient.

Keywords: competition; elevation gradient; mechanistic niche model; niche partitioning; preferred body temperatures; thermal niche

Introduction

Species are expected to differ in the extent to which they respond to climate change by shifting their phenotypes, seasonal timing, and distribution. These individualistic shifts among species^{1,2} have been commonly observed in response to past climate change and will alter interactions between species and reshape communities. The degree to which interacting species must be accounted for when predicting abundance and distribution shifts of individual species poses substantial uncertainty for efforts to forecast the ecological impacts of climate change.

Forecasts of the ecological impacts of climate change are generally focused on the direct effect of climate on vital rates and, ultimately, abundance and distribution. However, case studies are accumulating, pointing to the substantial influence of indirect effects associated with shifts in the abundance, phenology, and behavior of interacting species.³ These indirect effects can be sufficiently strong to reverse the direct effects of climate change. For example,

a grassland precipitation manipulation initially led to increased diversity and productivity consistent with the predictions of broad-scale vegetation modeling. Subsequently, however, species interactions shifted species composition toward annual grasses, and ultimately decreased diversity of plant and insect communities.⁴ A review of nearly 700 studies found that the influence of climate change on species interactions is often pronounced but varies substantially in magnitude and direction.³ This variability poses a formidable challenge for ecological forecasting, particularly when multiple global change drivers act on complex interaction networks. Hope for our ability to accurately forecast the implications of global change is afforded by cases when the direct effects of climate overwhelm indirect effects.⁵ How can we efficiently predict in which systems species interactions are likely to be central to climate change responses?

One proposed approach⁶ for tractably dealing with complex communities is identifying the interactions between species that are most likely to be altered by climate change and that are central to

community structure and function. Once the key interactions are identified, the complex interaction networks within communities can be broken into manageable subsets. If interactions can be described as functions of abiotic variables, analysis can assess whether the effects of climate change are damped or amplified by interactions within the modules. For example, a community module approach was used⁷ to assess the contrasting effects of stress on disease dynamics via altering both host susceptibility to infection and carrying capacity. More detailed models^{8–10} capturing the temperature dependence of interactions, such as predation, provide insight into the likely trajectories of communities in changing environments. Such mathematical models provide a tractable, process-based approach to understanding the outcome of species interactions. But how can we transfer the insights of these models to make applied predictions for realized rather than theoretical communities?

Shifts in species' distributions are among the most ubiquitous responses to climate change and have been the focus of applied modeling efforts. Most attempts to forecast range shifts rely on correlating species' occurrence to underlying environmental conditions. These environmental niche models (ENMs, or correlative species distribution models) assume that species will move to track their suitable climate space as it moves due to climate change. These models rely on the assumption that the processes setting range limits remain fixed in time and space.^{11,12} Shifts in the strength of species interactions and the reorganization of communities represent a potentially important violation of this assumption. The degree to which species interactions influence the delineation of the environmental niche has not been quantified. If species' localities are constrained by the presence of interacting species, their influence will be included in estimating organism–environmental interactions. Thus, shifts in the presence of interacting species may invalidate these estimated interactions. Including the presence of interacting species in ENMs has been found to increase their performance,^{13,14} but this technique is likely to have limited effectiveness in extrapolation as the interacting species respond individually to climate change.

Mechanistic niche models (MNMs) are emerging as an alternative bottom-up approach to predicting distributions, and are based on explicit relationships

between environmental conditions and organismal performance.^{11,12} Approaches include translating environmental conditions into biologically relevant metrics (e.g., potential duration of activity¹⁵), models that capture environmental sensitivities of survivorship and fecundity, and models that use energetics to link environmental conditions and demography. In contrast to ENMs, which estimate the realized niche, the predictions of MNMs represent the fundamental niche.^{16,17} MNMs can thus be used as null models for potential constraints on distributions such as species interactions (see below). Mechanistic models that include demography provide a link to the existing body of population and community ecology theory. They thus provide a framework for considering species interactions in addition to phenotypic variation and evolution.^{18–20}

Here I assess the progress and prospects for applying process-based models to understand the influence of species interactions on ecological and evolutionary responses to climate change. I review methods to predict shifts in thermal, temporal, and spatial niches among interacting species due to climate change and then address how species interactions can be included in mechanistic definitions of the niche. I highlight a suite of MNMs based on foraging energetics that enable accounting for resource partitioning between species. I illustrate such approaches by applying an MNM to predict the responses of two species of *Anolis* lizards, which compete for resources, to recent climate change along an elevation gradient in Puerto Rico.

Thermal niches

The temperature dependence of development and performance may differ among interacting species, which can drive climate change to alter species interactions.²¹ For example, rainbow and westslope cutthroat trout exhibit similar thermal optima, but rainbow trout have a broader tolerance curve and higher upper temperature tolerance (critical thermal maxima, CT_{max}). Consequently, increasing stream temperatures have increased growth rates of rainbow trout relative to cutthroat trout, which may account for the competitive displacement of cutthroat trout at lower elevations.²² Thermal tolerances generally exhibit local adaptation to environmental conditions such as temperature seasonality. Deutsch *et al.*²³ used these geographic gradients to generalize the temperature dependence of

insect fitness and predict that the fitness implications of climate change would be more severe for tropical species due to their narrow thermal safety margins.²³ Generalizing and comparing thermal niches across trophic levels may be a feasible approach for understanding shifts in species interactions. A theoretical model of species with differential thermal niches along an elevation gradient found that temperature dependent competition and dispersal differences led to community reorganization and diversity declines.²⁴ Competition slowed establishment in new locations to track climate.

Climate change directly alters rates of predation by altering consumption, assimilation, and metabolic rates as well as pursuit and escape speeds. Shifts in predation rates can be estimated based on the differential thermal dependencies of these processes between trophic levels and as a function of traits such as ectothermy or endothermy.^{25,26} Marine systems provide numerous examples of how thermal niches result in both direct and indirect effects of climate change with implications for community structure.²⁷ Fish speed when pursuing prey, and even how wide they can open their mouths (which constrains prey size), are temperature dependent. Thermal stress events may alter survival at egg, juvenile, and adult development stages, which has indirect effects on food webs. Growth rates of larval fish are dependent on water temperature, which in turn depends on when hatching occurs. The spawning areas utilized by fish differ between warm and cold years with implications for spatial overlap with interacting species.²⁷ The temperature dependence of development and performance provides a solid foundation for predicting shifts in species interactions in response to climate change, but the paucity of laboratory and field data quantifying temperature dependence tends to limit such analyses.

Several examples highlight how such data can enable ecological forecasts. Laboratory data on the temperature dependence of larval duration enabled the prediction of dispersal distance for planktivorous marine larvae as a function of temperature.²⁸ These predictions could be compared among species to address spatial overlap and potential shifts in marine communities. The thermal tolerances of both symbionts and coral hosts were used to model symbiont population dynamics, which in turn determined coral growth and mortality.²⁹ Whether the

symbionts' thermal tolerance adapted to warming was a crucial determinant of shifts in population dynamics. Although the model was parameterized with empirical data, such modeling has yet to be applied to forecast the fate of corals symbiosis in particular locations. Location-specific bleaching response curves as a function of temperature have been developed and applied to predict coral bleaching,³⁰ and such approaches could incorporate response curves for both mutualistic partners. Such explicit modeling would address whether switching symbionts can enable corals to cope with climate change. Examining changes in which species interact should prove interesting as corals with the greatest propensity for symbiont switching have been found to be the most thermally sensitive.³¹ Similar modeling approaches could be used to address the population impacts of temperature-associated shifts in disease virulence and coral susceptibility.³²

Thermal niches may also be informative for understanding how abiotic stress alters species interactions. For example, a shift from competition to facilitation among alpine plants was experimentally observed as abiotic stress increased along an elevation gradient.³³ Thermal niche differences may enable temporal and spatial niche partitioning, as discussed below. Whether thermal adaptation will be able to keep pace with climate change will be central to how much climate change alters species interactions.^{19,34}

Temporal niches

Climate change leads to relatively predictable phenological shifts via the influence of temperature on rates of development or altering the timing of environmental cues.³⁵ Phenology thus provides a robust basis for estimating shifts in the overlap of daily and seasonal timing among species. Accumulated heat above a lower temperature for development can effectively predict phenological³⁶ and distribution³⁷ shifts in response to recent climate change. Using species' specific estimates of lower development temperature to estimate the time available for development improved predictions of recent range shifts in butterflies³⁸ and could be used to predict phenological mismatches between interacting species as well as novel interactions. How and when temperature influences seasonal timing may be distinct across trophic levels. For example, models attribute recent decreases in synchrony between

oak and winter moths to increasing spring temperatures without a decrease in the incidence of winter freezing.³⁶

Translating shifts in synchrony into demographic impacts can be challenging.³⁹ However, organisms have generally exhibited greater performance when their phenologies have tracked recent climate change.⁴⁰ Examining phenological shifts across life stages⁴¹ and applying stage-structured models⁴² offers promise for understanding abundance and distribution impacts. In recognition of the importance of temporal overlap with interacting species, studies are increasingly examining a species' phenology relative to the phenological yardstick of interacting species, rather than date.⁴³

Species interactions may also be disrupted when warming drives interacting species to differentially shift their daily activity patterns. Biophysical models use energy budgets to predict body temperatures (operative environmental temperatures, T_e)⁴⁴ based on organismal phenotypes and environmental conditions. The T_e can be compared to thermal limits on activity (such as the preferred body temperature range, T_p) to estimate whether climate change will force changes in daily activity patterns. The degree to which ectotherms will face shorter activity durations in the summer and longer activity durations in winter will depend on the range of temperatures over which they can remain active and the extent to which they can use thermoregulatory behavior to buffer shifts in environmental conditions.⁴⁵ Daily activity patterns may result from competitively partitioning the temporal niche axis.⁴⁶ For example, the diurnal golden spiny mouse, *Acomys russatus*, can shift into nocturnal activity in the absence of its congener. Levy *et al.*⁴⁷ used a biophysical model to evaluate the hypothesis that the golden spiny mouse was competitively driven into diurnality with associated thermoregulatory costs.⁴⁷ The model found that the golden spiny mouse actually reduced energy expenditure by foraging during the day due to adaptations that may reflect the "ghost of competition past." Shifts in daily activity time associated with climate change may disrupt temporal niche partitioning.

A similar biophysical modeling approach had been used to evaluate differential shifts in daily activity time between predators and prey. Warming was found to result in rattlesnakes becoming less diurnal and altering their overlap in activity time with

two small mammal prey.²⁵ The shift in activity time of the rattlesnake was predicted to shift predation from one prey species to the other. The availability of shade in the landscape was also predicted to differentially alter activity patterns of the rattlesnake and its prey.

Spatial niches

Climate change may alter the overlap in spatial niches between species via habitat selection at local scales and range shifts at broad scales. Behavioral thermoregulation is likely to be important for buffering climate change.⁴⁵ Biophysical models reveal that body temperatures (T_b) can vary by 10 to 20 °C across local scales based on topography and vegetation cover.^{48,49} Interacting species of different size, shape, coloration, and composition may differ substantially in T_b s even within a microhabitat. Such temperature differences are observed between intertidal mussels and their sea star predators.⁵⁰ The differences may lead to shifts in spatial niche overlap or partitioning as a result of climate change. A population model incorporating density dependence predicted shifts in habitat selection by three species of arctic rodents as the frequency of xeric and mesic habitats changed due to climate change.⁵¹ Competition was expected to intensify among the two mesic specialists and decrease with the third species, which has a different fitness landscape, with the increase of xeric habitat. Observed shifts over the past 15 years have been consistent with this model.

Range shifts may be either hindered or facilitated by interacting species. Shifts may be restricted by the presence of hosts, prey, pollinators, or mutualists. For example, butterflies exhibited decreased fitness when fed novel host plants that they might encounter during a range shift.⁵² Such fitness decreases or the availability of associated species might be incorporated into process-based models. Conversely, range shifts may be enabled by release from enemies or competitors. A process-based model of plant community assembly illustrates how escape from host-specific pathogens and parasites may have enabled beech trees to rapidly expand after glacial retreat despite the presence of the competing hemlock trees slowing the range expansion.⁵³

Mechanistic niche partitioning

One approach^{18,54} that incorporates estimates of thermal tolerance, and the temperature dependence

of locomotion, metabolic rates, and assimilation in a population dynamic model based on optimal foraging, illustrates how mechanistic niche partitioning can be employed to predict abundances and distributions. The population dynamic framework enables linkage to existing community ecology theory. In the following discussion, I review how this framework has been applied to examine how abiotic and biotic constraints interact to determine abundance and distribution.

The model estimates the potential duration of activity by comparing the range of T_{cs} and T_{ps} . Energetic yield, $E(d)$, is calculated using an optimal-foraging model for a territorial, central place forager.⁵⁵ The energetic yield ($J s^{-1}$) is partially a function of metabolic rate and running velocity, both of which are estimated from body size. Energetic yield is also a function of prey density and prey size. The intrinsic rate of population increase, r_0 , was calculated as births minus deaths, $bE(d) - \lambda$. Here, b is the reproductive rate per unit of net energetic yield ($b = mt_f$) and λ represents mortality and the reproductive cost of metabolism while not foraging [$\lambda = \mu + m(24 \times 3600 - t_f)e_w$]. When calculating the reproductive rate, the parameter m equals the quantity of eggs produced per joule multiplied by the probability of surviving to adulthood (eggs J^{-1}), t_f equals the duration of foraging (s), μ equals the daily mortality rate (day^{-1}), and e_w equals the resting metabolic rate.

The model was initially developed and parameterized to compare abundance patterns of *Anolis* lizards along elevation gradients on Caribbean islands with one and two species.⁵⁴ The model predicted decreasing abundance with elevation due to decreasing foraging duration. The predicted decreases in abundance varied with lizard size and thermal tolerances and matched observations on one-species islands. However, abundance patterns diverged from the predictions on two-species islands: one species predominated in abundance at low elevation whereas the other reached peak abundance at mid elevations.⁵⁴ *Anolis* species compete for insect prey and habitat. Abundance data for the two-species islands enabled estimating Lotka–Volterra competition coefficients as a function of elevation and incorporating competition in the model. They applied the model to predict the occurrence of coexistence on nearby smaller islands. Coexistence is restricted to the two largest of the islands, which

the model predicts have substantially greater carrying capacities than the smaller islands.⁵⁶ The model could be extended to include prey partitioning explicitly in the foraging energetic model.

The modeling framework was adapted to account for moisture in addition to thermal constraints and applied to predict the elevation range limits of montane salamanders in the Appalachian Highlands.⁵⁷ The model suggests that physiological constraints drive the lower elevational limits of the higher-elevation species, but that competition sets the upper range limit of the lower-elevation species.

The model was then applied to predict distribution shifts of North American lizard species in response to climate change. The model predicts more pronounced and individualistic range shifts in response to climate change than do ENMs.^{12,18} Phenotypic differences between populations were found to have implications for current distributions and distribution shifts.¹⁸ MNM predictions of a species' fundamental niche can be compared with ENM predictions of the realized niche to develop hypotheses for the influence of biotic constraints on distributions. The model predicts similar fundamental niches for closely related *Sceloporus* lizard species, which have similar thermal physiology but disjoint ranges, suggesting the importance of histories of niche partitioning in constraining distributions. Hypotheses for the influence of biotic constraints can be evaluated by incorporating the constraints into the model. Buckley⁵⁸ showed how habitat constraints can effectively refine predicted distributions. Competition has not been incorporated previously when forecasting responses to climate change. Here, I apply the model to ask how species interactions will modify responses to climate change among *Anolis* lizards along an elevation gradient in Puerto Rico.

Case study: elevation and abundance shifts of competing Puerto Rican Anolis lizards in response to climate change

Huey *et al.*⁵⁹ recently revisited studies from the early 1970s of *Anolis* thermal biology in lowland Puerto Rico. At El Verde, *Anolis gundlachi* was a forest-dwelling, non-basking species. *Anolis cristatellus* occupied open and edge habitats and had higher T_b , T_p , and CT_{max} . In 1972, T_{cs} were well aligned with the T_p range of *A. gundlachi*, but too cool for *A. cristatellus*. Following 2.1 °C warming in the

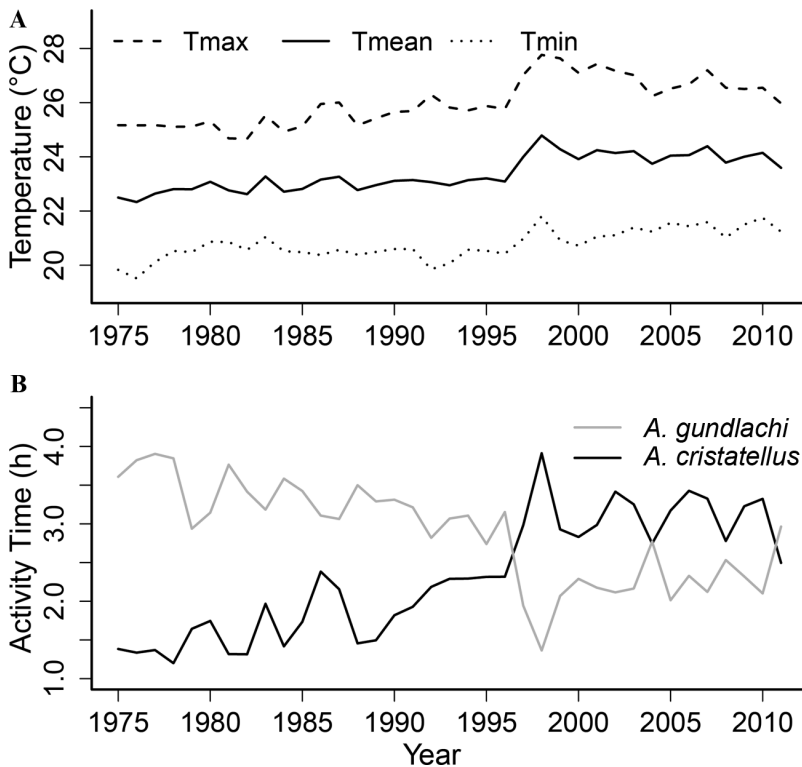


Figure 1. (A) Average annual minimum, mean, and maximum temperatures have increased at El Verde forest (elevation: 400 m) since 1975. (B) Consequently, we predict that the average daily activity duration (h) available to the forest-dwelling, cool-adapted *A. gundlachi* has decreased and that available to the open-habitat, warm-adapted *A. cristatellus* has increased.

summer since 1975, Huey *et al.*⁵⁹ predicted that forest T_e s would now be too hot during summer for *A. gundlachi*, but would coincide with the T_p range of *A. cristatellus*. They suggested that *A. cristatellus* may move into the forest and potentially displace *A. gundlachi*. Here, I estimate shifts in activity time and population size for each species at El Verde since 1975 and then include competition in the model to explore the interaction of abiotic and biotic constraints. Finally, I extend the analysis along the elevation gradient in Puerto Rico.

Methods

I used daily minimum and maximum temperature data from the El Verde (18.15N, 64.75W) weather station from 1975 to 2011 (Long-Term Ecological Research (LTER) Climate database, <http://climhy.lternet.edu>). I subsequently extended the analysis along the elevation gradient (sea level to 1200 m) using daily data since 1975 for 28 weather stations in the Global Historical Climate Network (GCHN; stations listed in Table S1 and accessible at [\[ncdc.noaa.gov/oa/climate/ghcn-daily/\]\(http://www.ncdc.noaa.gov/oa/climate/ghcn-daily/\)\). The few instances of missing data were approximated by averaging the two previous and two subsequent measurements. I estimated hourly air temperatures \(\$T_a\$ \) using a diurnal temperature variation function based on maximum and minimum temperatures, and the Julian date.⁶⁰ Daytime temperatures were fit using a sine wave, while night time temperatures were modeled using an exponential function.](http://www.</p>
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I translated T_a into T_e by assuming that temperatures near the surface are 2 °C higher than air temperatures. This value is intermediate among comparisons of air and surface temperatures at U.S. Department of Agriculture (USDA) National Resource Conservation Service weather stations.⁶¹ Further, I assumed that lizard T_e s are 0.6 °C above surface T_a , consistent with past observations at El Verde.⁶² Both lizards are approximate thermoconformers, but *A. cristatellus* sometimes exhibits basking behavior to elevate its body temperature in open habitats.^{48,62,63} Available meteorological and habitat data are insufficient to compute surface or body

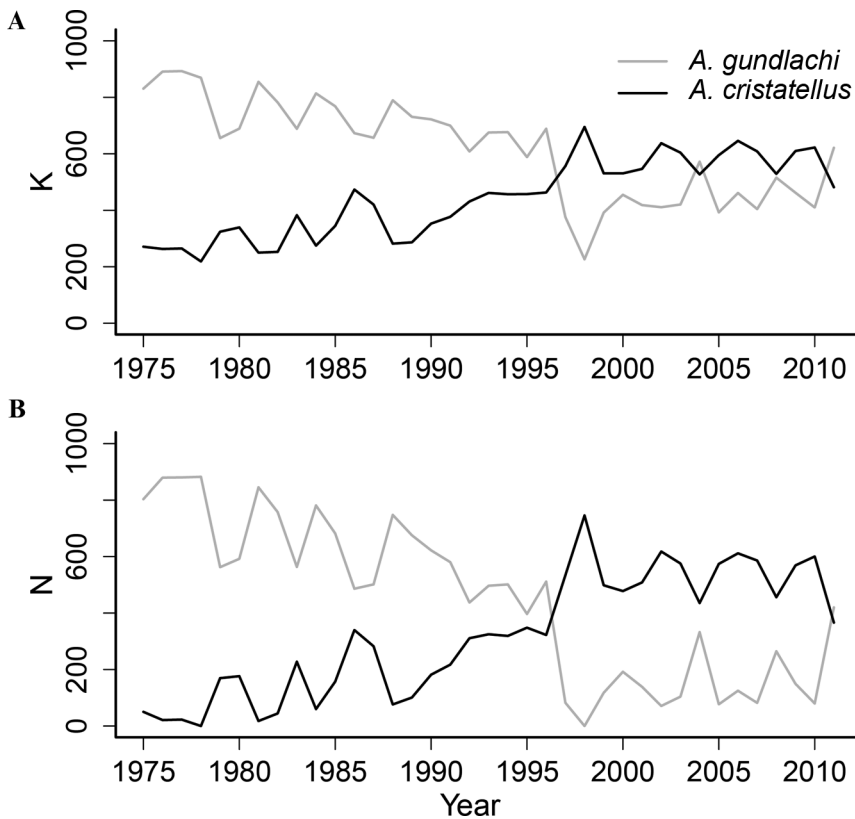


Figure 2. (A) Warming since 1975 is estimated to have altered rates of energy acquisition and use such that the carrying capacities (K) of the cool-adapted *A. gundlachi* have decreased and those of the warm-adapted *A. cristatellus* have increased. (B) The trend in population size (N) is accentuated when including competition (N). The movement of *A. cristatellus* into the forest to avoid overheating in open habitat may result in the competitive displacement of *A. gundlachi*.

temperatures. These assumptions enable implicit accounting for determinants of body temperature such as microhabitat choice.

I assumed that lizards forage during daylight hours when they could reach a temperature within their T_p range (defined as the central 50% of body temperatures selected in a thermal gradient; *A. gundlachi*: 24.3–26.1 °C; *A. cristatellus*: 28.6–30.7 °C; Table S2).⁶⁴ Assuming a different quantile of body temperatures for the T_p range does not qualitatively influence the results. I used allometric relationships with mass and snout-vent length (svl) to estimate other model parameters (*A. gundlachi*: 6.9 g, 65.2 mm; *A. cristatellus*: 8.4 g, 67.3 mm).⁵⁹ Resting metabolic rate (e_w , $J s^{-1}$) was estimated as a function of temperature (T_e , °C) and body mass (M, g): $e_w = 0.0056 \times 10^{(0.038T_e - 1.771)} M^{0.82}$ (Ref. 65). I multiplied this expression by a factor of 1.5, which is the activity scope appropriate for a non-foraging

iguanaid lizard.⁶⁶ Metabolic rates of *A. gundlachi* did not vary altitudinally or exhibit compensation to thermal variation.⁶⁷ For the active metabolic rate e_p ($J s^{-1}$), I assumed an activity scope of 3 (Ref. 68) and calculated sprint speed ($m s^{-1}$) as a function of svl: $1.54 \text{svl}^{0.3}$ (Ref. 69).

I estimated the energy content of insect prey (*A. gundlachi*: 6.76 J; *A. cristatellus*: 7.29 J) based on empirical observations of prey size as a function of lizard svl and energy density (as described in Ref. 54). I discounted energy content per insect by assuming that lizards could assimilate 76% of this energy⁷⁰ and that lizards catch 50% of insects that they encounter. I estimated an insect abundance of $0.016 \text{insects m}^{-1} \text{s}^{-1}$ based on empirical measurements across several Caribbean islands.⁵⁴ I assumed daily mortality rate, $\mu = 1/365 \text{day}^{-1}$, and $m = 1/e \times 10^{-4} \text{eggs J}^{-1.61}$ (Ref. 55). Previous implementations of the model have examined sensitivity to

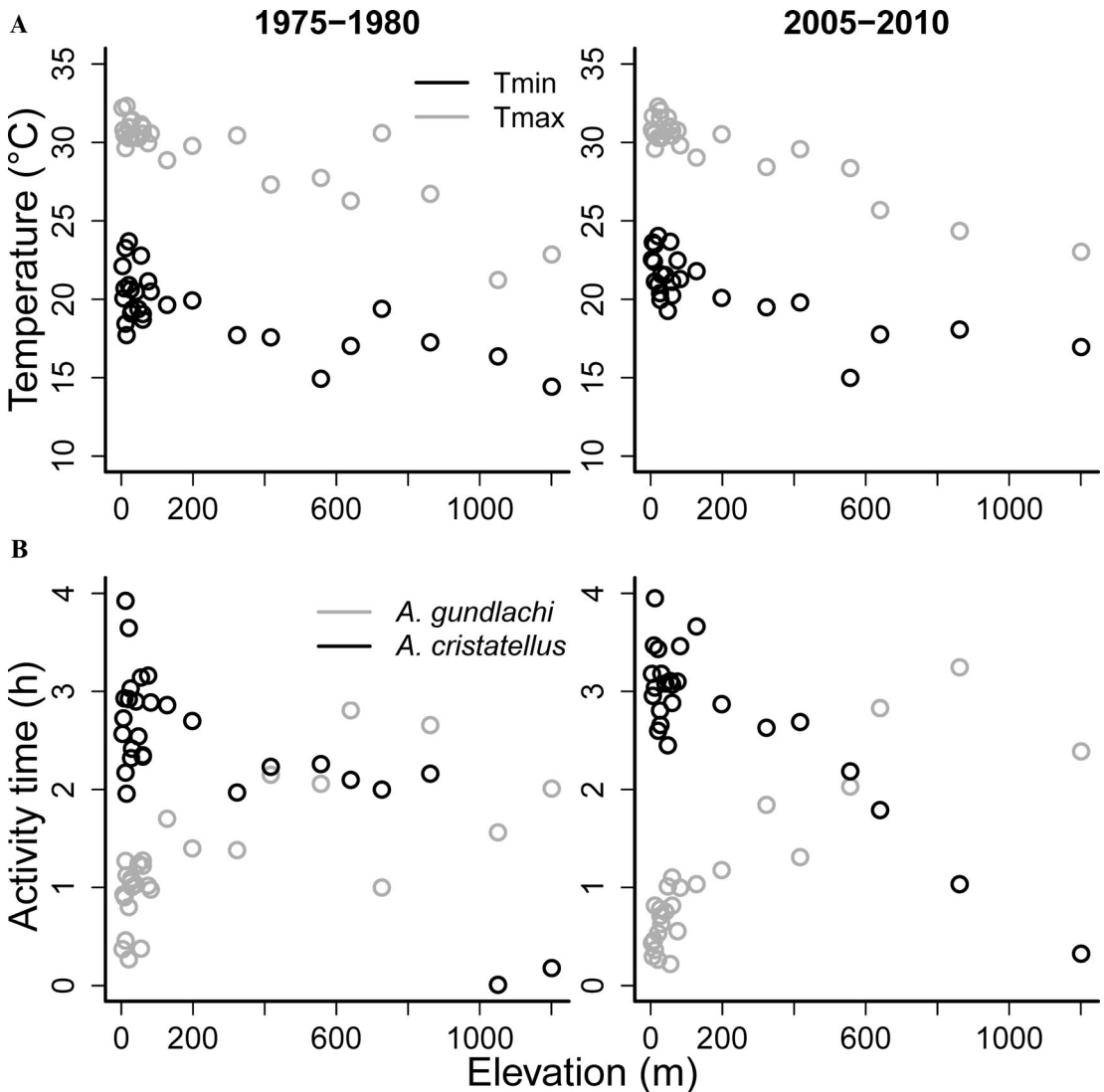


Figure 3. Warming along the elevation gradient (A) has likely increased the activity time of *A. cristatellus* across the elevation gradient and of *A. gundlachi* at high elevations (B).

these parameterizations.^{54,58} While parameter values do influence abundance estimates, they should not influence the relative abundance differences between species.

I used Lotka–Volterra approximations to the discrete time-logistic growth equations to simulate competition. The equilibrium abundances, N_1 and N_2 , are found from simultaneously solving two linear equations: $N_1 + \alpha_{12}N_2 = K_1$ and $\alpha_{21}N_1 + N_2 = K_2$, where K_i is the carrying capacity of species i , and α_{ij} is the competition coefficient for the effect of species j against species i . I approximated the

competition coefficient for the effect of *A. cristatellus* on *A. gundlachi* as the ratio of interspecific to intraspecific aggressive encounters in field experiments at El Verde ($\alpha = 148/267 = 0.55$) (Ref. 71). As Huey *et al.*'s hypothesis⁵⁹ is that *A. cristatellus* may competitively displace *A. gundlachi*, I assumed that the competition coefficient for the effect of *A. gundlachi* on *A. cristatellus* is half of that of the converse interaction ($\alpha = 0.55/2$). The observations of how competition amplifies abundance differences between species are robust to the assumption of competitive differences.

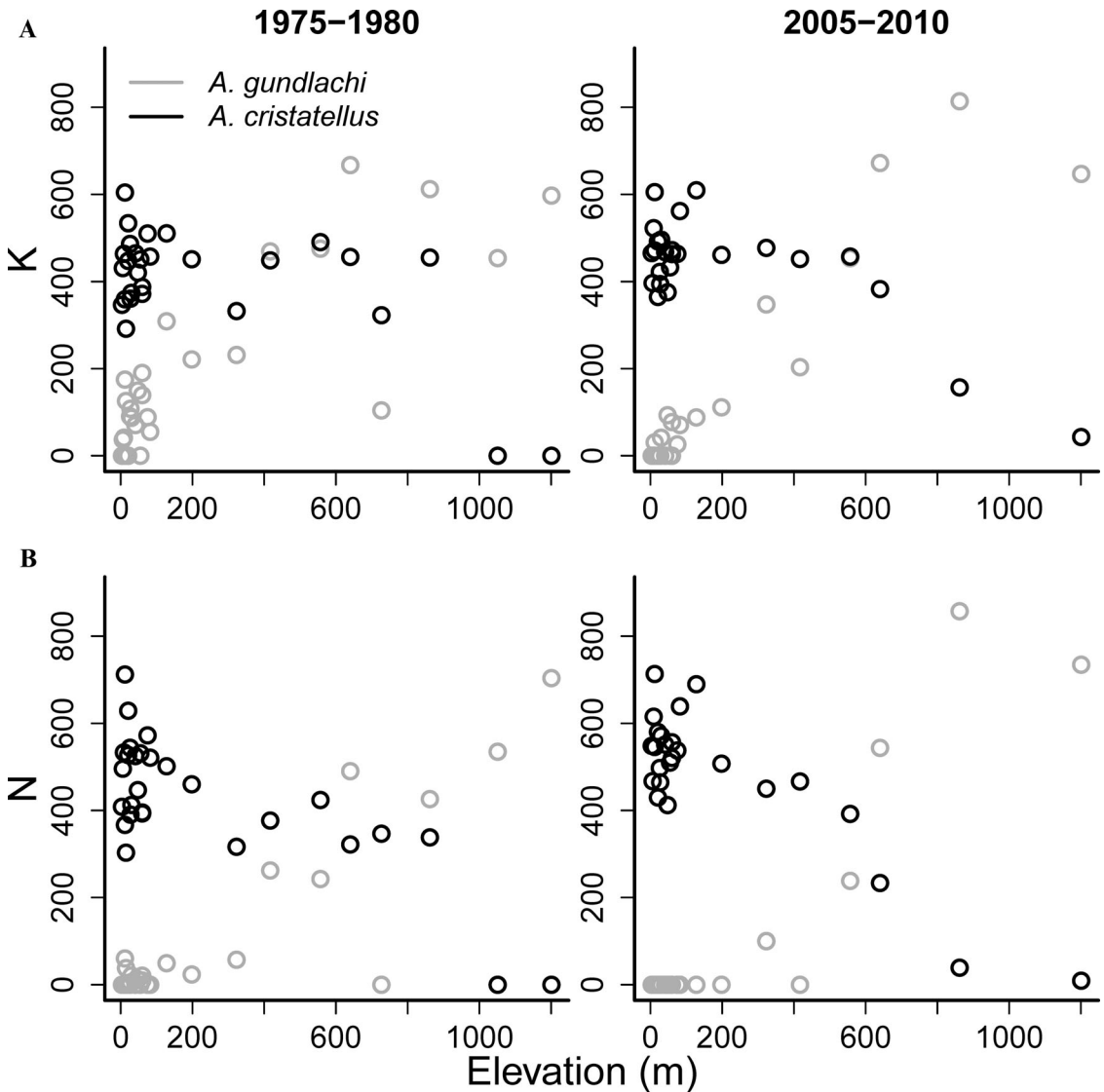


Figure 4. The model predicts that, at low elevations, the carrying capacity (K) of *A. gundlachi* has decreased due to overheating (A). The decrease in population size (N) is accentuated by competition with *A. cristatellus* (B).

Results

The analysis suggests that warming temperatures since 1975 (Fig. 1A) have made the forests of El Verde more thermally suitable for the warm-adapted *A. cristatellus* and less suitable for the cool-adapted *A. gundlachi*. This is evidenced by predicted shifts in the time that falls within each species' T_p range (Fig. 1B). *A. gundlachi* is predicted to have substantially more foraging time available than *A. cristatellus* through 1997, at which point the forest begins to frequently exceed *A. gundlachi*'s preferred temperature range,

and *A. cristatellus* is predicted to have relatively more foraging time available. Consequently, *A. gundlachi* is predicted to maintain considerable carrying capacities and *A. cristatellus* is predicted to maintain low carrying capacities until this warming period (Fig. 2A). Subsequently, the species are predicted to have similar carrying capacities. These trends are accentuated when accounting for competition (Fig. 2B), which may have maintained small population sizes and initially prevented *A. cristatellus* from establishing in the cool forest. *A. cristatellus*

may have then moved into the forest to seek refuge from thermal stress in open habitats. The results support Huey *et al.*'s hypothesis³⁴ that *A. cristatellus* may competitively displace *A. gundlachi*.

I next extended the analysis to examine activity times and abundance along the elevation gradient. Temperatures have increased across the elevation gradient since 1975 (Fig. 3A). Consequently, activity time available to *A. cristatellus* has increased, and that available to *A. gundlachi* has decreased, at low elevations (Fig. 3B). The separation in activity time between the species along the elevation gradient has increased since 1975. The dominance of *A. cristatellus* at low elevations, and that of *A. gundlachi* at higher elevations, is predicted to have increased (Fig. 4A). I estimated that the elevation range over which the two species are present at approximately equal abundance has narrowed. In both time periods, competition may lead to exclusion of *A. gundlachi* at low elevation and *A. cristatellus* at high elevation (Fig. 4B).

Discussion

The case study illustrates how species interactions can accentuate abundance and distribution shifts in response to climate change. Abiotic and biotic constraints are likely to interact in determining responses along elevation gradients for numerous taxa.⁷² These constraints may shift over time in ways not accounted for in the case study, resulting in idiosyncratic responses to climate change. For example, shifts in vegetation cover and humidity may be influencing the response of Puerto Rican anoles to recent climate change (R. Huey and L. Otero, personal communication). Modeling approaches such as those presented here are central to assessing how climate change will shift abiotic and biotic constraints and drive changes in abundance and distribution.

Applying theoretical models of species interactions to particular systems requires close interplay with empirical work. A major limitation in developing process-based models is the scarcity of quantitative studies of the strength of species interactions, particularly in the context of abiotic conditions. Even in the well-studied *Anolis* lizard system, I was only able to crudely approximate the strength of competition. Transplants studies to assess interactions between species that may come into contact following individualistic responses to cli-

mate change are an important potential resource for building process-based models. A reciprocal transplant study of two species of salamanders at the edge and core of their adjacent distributions highlights the potential of such an approach.⁷³ Competition was found to be more intense in the stressful abiotic conditions at the range edge contact zone than in the range interiors. Furthermore, core populations were more harmed by competition in the contact zone than local populations, illustrating the likely complex interactions of abiotic and biotic constraints on responses to climate change. Field and lab studies of the energetic and fitness consequences of species interactions will yield informative data. Such empirical data can refine uncertain model predictions, which stem from limitations in parameterization, such as whether competition will result in competitive exclusion along the elevation gradient in our case study.

Empirically quantifying species interactions pose logistical challenges. However, quantifying species traits and using them to estimate the degree of species interactions and how they may be altered by climate change provides a tractable approach. Partitioning along thermal, temporal, and spatial niches is likely to be particularly important in the context of climate change. However, how behavior modifies the implications of phenotypes is an important consideration. The degree of stabilizing niche differences between species may be an important determinant of the relative strength of the direct and indirect impacts of climate change.⁷⁴ Greater niche differentiation may lead to direct effects overwhelming the indirect effects of climate change. In many cases, indirect effects may be crucial to understanding responses to climate change. Applied models informed by empirical measurements and manipulations are necessary to extrapolate abiotic and biotic constraints into the novel environments created by climate change and to understand how direct and indirect effects interact to determine abundance and distribution shifts in communities.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. Global historical climate network stations used in the analysis

Table S2. Parameters used in the mechanistic model

Conflicts of interest

The author declares no conflict of interest.

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