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Climate change and species interactions: ways forward

Amy L. Angert,[1] Shannon L. LaDeau,[2] and Richard S. Ostfeld[2]

[1]Departments of Botany and Zoology, University of British Columbia, Vancouver, British Columbia. [2]Cary Institute of Ecosystem Studies, Millbrook, New York

Address for correspondence: Amy L. Angert, Departments of Botany and Zoology, University of British Columbia, Vancouver, BC, V6T 1Z4. amy.angert@botany.ubc.ca

With ongoing and rapid climate change, ecologists are being challenged to predict how individual species will change in abundance and distribution, how biotic communities will change in structure and function, and the consequences of these climate-induced changes for ecosystem functioning. It is now well documented that indirect effects of climate change on species abundances and distributions, via climatic effects on interspecific interactions, can outweigh and even reverse the direct effects of climate. However, a clear framework for incorporating species interactions into projections of biological change remains elusive. To move forward, we suggest three priorities for the research community: (1) utilize tractable study systems as case studies to illustrate possible outcomes, test processes highlighted by theory, and feed back into modeling efforts; (2) develop a robust analytical framework that allows for better cross-scale linkages; and (3) determine over what time scales and for which systems prediction of biological responses to climate change is a useful and feasible goal. We end with a list of research questions that can guide future research to help understand, and hopefully mitigate, the negative effects of climate change on biota and the ecosystem services they provide.

Keywords: climate change; species; ecosystems; ecology; biota

Introduction

Anthropogenic climate change is profoundly affecting Earth's biota. Perhaps the most obvious manifestations of the effects of climate change are recent and rapid alterations in abundance and geographic distribution of many species.[1,2] Such observed changes will have cascading effects, including (1) some species will be threatened with extirpation, with important conservation implications;[3] (2) other species will spread, with important consequences for ecological integrity and human health;[4] and (3) communities will change in their abilities to perform important ecosystem functions, including those on which humans rely (ecosystem services).[5] Thus, with continuing climate change, major challenges for ecologists are to predict how individual species will change in abundance and distribution, how biotic communities will change in structure and function, and the consequences of these climate-induced changes for ecosystem functioning.

A number of factors complicate efforts to predict how species will respond to climate change. Direct responses to climate can be dramatically affected by physiological acclimation and other kinds of phenotypic plasticity,[6,7] evolutionary changes in species–environment relationships,[8] and interactions among different limiting resources.[9] Moreover, recent research across terrestrial, freshwater, and marine ecosystems demonstrates that the indirect effects of climate change on species abundances and distributions, via climatic effects on interspecific interactions, can outweigh and even reverse the direct effects of climate.[10–16] However, understanding the relative importance of species interactions is complicated by the observations that current climatic ranges for species occurrences can be much broader than the climatic range for commonness,[17] and that the strength of top-down and bottom-up regulation can change with a changing climate.[18,19] Such complications are not limited to efforts to project the distribution and abundance of species within communities; they also hinder most

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current efforts to predict future ecosystem function, which tend to ignore critical links between physiological responses and population and community dynamics.

Given these complexities, it is clear that the ecological and evolutionary community needs new concepts, models, and empirical approaches to project where individual species will move, how new ecological communities will assemble, and how those communities will change in structure and function as the climate continues to change. Stronger predictive power will be critical for mitigating the effects of climate change on biodiversity, community dynamics, ecosystem functioning, and species of conservation concern. But, whether prediction is an attainable goal, and if so, the nature and extent of efforts to achieve it are not well established. To this end, we held an interactive conference to address the state-of-the-art and ways forward, with results of the conference disseminated in this issue of *Annals of the New York Academy of Sciences.*[a]

The conference

The conference "Climate Change and Species Interactions: Ways Forward" was held November 14–15, 2012 at the Cary Institute of Ecosystem Studies in Millbrook, New York. Presentations in the mornings were followed by breakout-group discussions in the afternoon. The goal of the breakout groups was to engage discussion from all participants and to promote interdisciplinary networking and collaboration. Presenters spoke in four sessions, and many of their contributions are included in this issue. Below we briefly summarize those contributions.

In the first session, "Beyond traditional models of climate change and species responses," Robert Anderson (City University of New York) discussed how to make correlative distribution models more useful. In his paper, Anderson[20] describes a class of correlative distribution models that couple a statistical estimation of environmentally suitable habitat with simulations of dispersal and demography. The advantage of such coupled models is that, like other correlative modeling approaches, they use data that are readily available data for most organisms, yet they incorporate greater realism about dispersal limitation and establishment. Anderson's thorough overview of the assumptions of the modeling framework, principles for selection of occurrence data and environmental variables, and transferability of outputs across space and time create a valuable guide for practitioners. Anderson also discusses possible approaches for incorporating biotic interactions into coupled models, most notably using biotic variables as additional environmental predictors during niche modeling versus incorporating biotic interactions during latter simulations of demography and dispersal. A major challenge to distribution modeling approaches such as those outlined by Anderson is validating the potential future responses that they project. John Williams (University of Wisconsin) offered a unique and powerful perspective from paleoecology, where models can be challenged to accurately predict past changes that have been observed. In his paper, Williams discusses the challenges of predicting responses to climate change, given inherent ecological complexity and the particular difficulty of forecasting into "no-analog" environments and communities.[21]

The second session, "Neglected issues in climate change/species interactions research," included Mark Urban (University of Connecticut), who spoke about the importance of dispersal ability in affecting species and community responses to climate change. Drawing on lessons from recently observed range shifts, invasion biology, and theoretical models, in their paper here, Urban and coauthors conclude that we must fine-tune the way that dispersal is considered in forecasts of range shifts by incorporating realistic dispersal kernels and interspecific variation in dispersal.[22] Moreover, they show that species interactions can drastically alter the outcome of range shifts predicted from individual species' dispersal responses alone. Oswald Schmitz (Yale University) argued that evolution, though traditionally underappreciated in ecosystem ecology, could critically influence responses of ecosystems to climate change in contemporary time. In his paper, Schmitz chooses one concept from evolutionary ecology, phenotypic plasticity, and describes how plasticity in the physiological responses of animals to warming can propagate up to influence ecosystem processes like elemental cycling.[23]

In a session entitled, "Ways forward: Concepts," Chris Harley (University of British Columbia) presented a conceptual framework linking environmental and body temperature to individual performance, population growth, species interactions, and

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community structure. In his paper, Harley reviews key case studies that demonstrate how the effects of temperature on individual species and their interactions can be complex, for example when temperature affects both per capita interaction strength and population size.[24] Jessica Hellmann (University of Notre Dame) spoke about how evolutionary history can affect biotic responses to climate change. Bocedi, Hellmann, and coauthors describe a simulation model exploring the joint effects of local adaptation and competition on range shifts.[25] In this model, two species can coexist indefinitely without climate change, and each species can track climate change when not experiencing competition. However, competition during climate change reduces genetic diversity, slows the rate of range shifting, and reduces range size, particularly when there is asymmetry between the species in degree of local adaptation and breadth of climatic tolerance. Thus, the model reveals that the interaction between local adaptation and competition yields qualitatively different outcomes than either factor in isolation. Finally, Mary O'Connor (University of British Columbia) focused on the interplay of local and regional processes that is the hallmark of metacommunity approaches. In their paper, Benjamin Gilbert (University of Toronto)[26] and O'Connor outline how climate-induced changes in regional processes such as dispersal and habitat configuration can influence local abundance within communities, and conversely how changes in individual performance and species interactions within local communities can alter the movement and distribution of species at the regional scale. Building on metacommunity theory, Gilbert and O'Connor highlight key processes and approaches that should be fruitful avenues for empirical research.

In the final session, "Ways forward: Approaches," Janneke HilleRisLambers (University of Washington, Seattle) discussed the value of space-for-time substitutions in experimental and observation studies. In their paper, HilleRisLambers and coauthors provide an overview of the various ways that negative and positive biotic interactions can create range limits and might cause range shifts to proceed faster or slower than climate change.[27] Using their own case studies for illustration, they describe how to use space-for-time substitutions to quantify the demographic effects of biotic interactions across environmental gradients, and then discuss how such results might be integrated into models of climate-induced range shifts. Lauren Buckley (University of North Carolina) spoke about new directions to move process-based models of species distributions beyond autoecology. In her paper, Buckley describes how to incorporate species interactions into process-based models of species distributions, or models that project potential distributions as a function of physiological and demographic responses to environmental conditions.[28] She illustrates how this approach can be used to evaluate the influence of species interactions on climate-induced range shifts with a foraging energetics model applied to two species of competing Puerto Rican *Anolis* lizards.

Last, Jason Harmon (North Dakota State University) and Brandon Barton (University of Wisconsin) describe how animal behavior can alter how species respond to changing environments and to each other in ecological communities.[29] Behavior is a major component of phenotypic plasticity, allowing quick responses to environmental changes, including climate change. Behavior can mitigate adverse direct impacts of climate change on fitness as well as indirect climate impacts affecting interacting species. They provide a conceptual framework to integrate these direct and indirect effects of climate change and suggest ways that inclusion of behavioral responses can aid in future research.

Post-workshop survey

Following the conference, all attendees were invited to participate in a questionnaire about their expert assessment of ways forward. The questionnaire included a thought experiment where the respondent was asked how best to predict changes in the distribution or abundance for their focal study organism by the end of this century. Focal organisms included insects, plants, herptiles, aquatic invertebrates and mammals. In response to the question, What are the 2–3 most important things you currently understand about your focal species which allow you to predict change?, 85% of respondents listed information on abiotic responses, particularly thermal sensitivities of performance, growth, or demography. Nearly half already had some understanding of key species interactions (e.g., prey communities, host plant requirements, natural enemies) that they thought were important for predicting responses to climate change. Other answers frequently highlighted the importance of basic information on natural history, such as resource and habitat requirements. In response to the question, What are the 2–3 most important things that you don't know but need to make this prediction?, almost all respondents identified the need for more information about evolutionary processes (e.g., genetic variation, local adaptation, or evolutionary potential). Despite often having some information about key species interactions, 57% of respondents wished to have greater information about *changes* in species interactions. Half of the respondents wanted a greater understanding of dispersal dynamics, especially when trying to predict changes in distribution. Finally, several responses highlighted the need for more precise climatic forecasts, recognizing that uncertainty about the direction and magnitude of changes in abiotic variables might be at least as great as uncertainty about ecological responses to such changes.

The questionnaire also asked participants to rank different kinds of observational and experimental data streams that could be potentially useful for predicting biotic responses to climate change. The top selection (based on average rank and number of times as the first-choice pick) was field-based transplant experiments. In a sense, transplants can be viewed as experimentally simulated dispersal events, so their favorability in this ranking is concordant with the impression that a greater understanding of dispersal is necessary to predict changes in distribution and abundance of focal organisms. Other top choices for data types were medium-grained observational data (10 sites, each with a 5-year time series of abundance) and field-based global change manipulations (e.g., experiments altering temperature or rainfall). The bottom three selections (again, based on average rank and number of times as the last-choice pick) were field-based removal experiments, coarse observational data (100 sites, each with abundance at only a single time point), and field-based resource manipulation experiments. Lab-based experimental data on physiological responses were perceived neutrally, rarely being selected as either high- or low-priority data streams. Thus, there is an interesting disconnect between the prevalence versus perceived usefulness of lab-based physiological measurements among this community of researchers. The responses revealed an unsurprising perception of a trade-off between the ease and cost of acquiring data versus their usefulness. For example, coarse observational data were ranked among the least useful for predicting responses to global change, while manipulative field experiments were ranked among the most useful. Nonetheless, there was considerable support for the usefulness of medium-grained observational data, presumably optimizing a trade-off between spatial scope and local detail, at a temporal and spatial scale that would be tractable for many kinds of organisms. It is also interesting to note that not all field experiments were perceived to be equally useful (for example, removal experiments and resource manipulations were not highly favored, though they can be informative for some questions). Unfortunately, a category for data on genetic variation was not included as a potential data stream; presumably many would have ranked this highly based on responses to earlier questions.

Synthesis and prospects

The contributions to this volume and the responses to the questionnaire all highlight the fact that predicting how biological systems will respond to a changing climate is a complex and multifaceted problem. Those working at the forefront of this field identified an extensive wish list of necessary data, including physiological responses of focal organisms to the abiotic environment, key species interactions and their environmental dependencies, genetic variation in important traits for both focal and interacting species, and dispersal dynamics. Moreover, this will require a combination of experimental and observational studies in both lab and field settings and an analytical framework to link data across scales. Certainly this will not be possible for most organisms. What, then, are our prospects for progress and some realistic goals for the research community?

We suggest that one goal is to utilize tractable study systems as case studies to illustrate possible outcomes, test processes highlighted by theory,[23,26] and feed back into modeling efforts.[22,25] Even when potential outcomes vary across disparate study systems, it can be useful to begin to place bounds on the range of potential outcomes[30] and to highlight ecological surprises.[24] Some of the contributions in this volume illustrate ways to work toward a detailed, mechanistic understanding within select study systems, for example by drilling down into detailed biophysical ecology[28] and dissecting communities into smaller subsets of strongly interacting species.[27] Such approaches are particularly valuable for identifying mechanisms and projecting responses into novel conditions. The accumulation of detailed case studies might eventually help identify generalities.

A second main goal is to develop a robust analytical framework for projecting species and community responses to climate change. Even for the most well-developed study systems, it remains difficult to link physiology, demography, and species interactions and to project responses across an environmentally variable landscape. Analytical frameworks that allow for better cross-scale linkages are clearly needed.[26] Furthermore, statistical methods that are applicable to more readily available data types (e.g., time series) and a wider range of organisms are promising, especially when coupled with targeted experiments.[20,27,31] Analytical synthesis has traditionally relied on either model-based (e.g., mathematical simulation) or data-based (e.g., statistical hypothesis testing) approaches to develop understanding and generate predictions of ecological dynamics.[32] However, efficient data-model integration is crucial to support both inference and forecasting of how climate influences species and interspecific interactions. Analytical approaches that combine data and mechanistic models (using either Bayesian or maximum likelihood methods) are gaining prominence across ecological disciplines.[33–35] When implemented in a Markov chain Monte Carlo (MCMC) framework these models can accommodate multiple types of data, cross-scale linkages, and stochasticity.[36,37]

Third, ecologists must confront the magnitude of uncertainty that faces efforts to forecast biological responses to climate change. Recognizing that one of the largest sources of uncertainty in biological responses is in fact uncertainty in climate projections, a productive line of research might be to focus on scales and processes that will help improve global circulation models (for example, vegetation and soil feedbacks to the atmosphere).[38] Another avenue forward is to focus on near-term ecological dynamics, which are arguably most relevant for immediate conservation decisions, before uncertainties in both climatic and biological responses become too magnified. More broadly, the research community must grapple with whether prediction is a useful and feasible goal, and if so, over what time scales and for which systems.

Notably, many of these same issues were raised 20 years ago by contributors to a similarly themed conference and edited volume, *Biotic Interactions and Global Change*.[39] Though we have made progress on many fronts, some issues are as yet unresolved. As we move forward, we suggest the following list of critical research questions that can serve as guideposts for future studies:

1. How will range shifts of individual species be affected by differences in the degree to which other community members shift with them? Can we predict which communities will maintain integrity versus show idiosyncratic responses by individual species?
2. To what extent do specific biotic interactions (e.g., competition, parasitism) accelerate versus decelerate rates of range shift under climate change? How will climate change affect trophic interactions, particularly the relative importance of top-down and bottom-up forcing?
3. What are the consequences of integrated versus disintegrated community shifts for various metrics of community stability? Will new communities that are formed as species shift their ranges be more or less resilient than the "ancestral" communities?
4. What are the relative roles of plasticity and genetic adaptation in response to novel abiotic and biotic challenges? How does the capacity for rapid evolutionary response vary across life histories and habitats?
5. As some organisms adapt to changing climate, how will the phenotypic changes affect their biotic interactions and role in ecological functions? How will differences in evolutionary potential among interacting species affect community (dis)assembly and ecosystem function?

Ecologists from diverse subdisciplines, including ecophysiology, community ecology, evolutionary ecology, and ecosystem ecology, are poised to contribute answers to these questions, but it will require coordinated efforts to develop new models, data streams, and research strategies. The articles contained within this special issue highlight many exciting avenues forward. Such advances in basic science will be critical for understanding, and hopefully mitigating, the negative effects of climate change on biota and the ecosystem services they provide.

Conflicts of interest

The authors declare no conflicts of interest.

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