Ecology of Climate Change

THE IMPORTANCE OF BIOTIC INTERACTIONS

Eric Post

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ERIC POST

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EDITED BY SIMON A. LEVIN AND HENRY S. HORN

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For Pernille

Tempus fugit, amor manet

Preface

Purpose, Perspective, and Scope

Reports of above-average annual temperatures and record-warm years are by now well familiar. The U.S. National Oceanic and Atmospheric Administration (NOAA) announced on January 12, 2011, that 2010 had equaled 2005 as the year of highest global mean temperatures on record. In the same report, NOAA listed a series of global climate highlights, including the fact that 2010 had experienced the greatest average global precipitation on record, but with substantial regional variation, and that it had also been the fourteenth year in a row with above-average temperatures in the United States. As this book moves into production in the summer of 2012, the report titled "State of the Climate National Overview—May 2012," released by NOAA's National Climatic Data Center, declared, "The average U.S. temperature during spring was . . . 5.2°F [2.9°C] above average, the warmest spring on record." This book is aimed at clarifying how and why climate change matters from an ecological perspective.

Despite the obvious focus this objective places on the importance of abiotic influences in ecological dynamics, the emphasis throughout this book is, perhaps somewhat counterintuitively, on the primacy of biotic interactions in shaping responses to climate change. Although the earliest work addressing specifically the ecological consequences of contemporary climate change was concerned with quantifying biological responses to changes in abiotic factors such as temperature, precipitation, and nutrient availability, more recent research has made increasingly clear the importance of interactions among organisms in determining responses to climate change across levels of organization (Gilman et al. 2010; Urban et al. 2012). Within a framework emphasizing the classic topics of enduring relevance in ecology, this book argues that interactions among organisms are not merely background noise that must be accounted for statistically or experimentally in the study of climate change but rather the determining factor in the responses of individuals, populations, communities, and ecosystems to climate change. Hence, the perspective advanced in this book holds that an appreciation of the importance of interactions among organisms will improve our understanding and study of individual-level life history or phenological responses to climate change, which most commonly have been studied purely as organism-environment interactions. We will also see that both competition among conspecifics, or density dependence, and interactions with aspecific competitors, resources, and predators determine the dynamical responses of populations to climate change. At the community level, the strength of exploitation and interference interactions exerts tremendous influence over the stability response of species assemblages to climate change. Finally, interactions at and among all these levels of organization come to bear on ecosystem responses to climate change, which traditionally have been studied within the conceptual framework of abiotic influences on variation in the availability and rates of turnover of nutrients.

THE TENSION AND FACILITATION HYPOTHESES OF BIOTIC RESPONSE TO CLIMATE CHANGE

As a central theme that illustrates the importance of organism-organism interactions in responses to climate change across levels of biological organization, we may consider a generalized tension or, alternatively, facilitation between the strength of climatic versus biotic influences on dynamics at the level of interest and the implications these influences pose for the stability properties of such dynamics. This tension (or facilitation) is formalized mathematically in individual chapters on phenological, population, and community dynamics; a heuristic overview is presented here as a means of establishing a viewpoint from which the rest of this book advances.

We may consider first the simple case in which the strength of interactions among organisms ranges along a spectrum from weak to strong (figure 0.1). In the perspective developed throughout this book, the strength of the climatic influence on interactions among organisms, which interactions also range along a spectrum from weak to strong, is expected to be related to the strength of the biotic interactions occurring among organisms, as depicted in figure 0.1. In general, we may think of the interaction between climatic and biotic influences in ecological dynamics as assuming one of two forms, either *tension* (the dashed line in figure 0.1) or *facilitation/promotion* (the solid line in figure 0.1). In this context, use of the term *tension* implies a trade-off between the strengths of climatic and biotic influences on ecological dynamics; in other words, these forces oppose each other. By contrast, use of the term *facilitation* or *promotion* implies an enhancement of the strength of climatic or biotic influences on ecological dynamics by an increase in the strength of the other; in other words, these forces enhance each other.

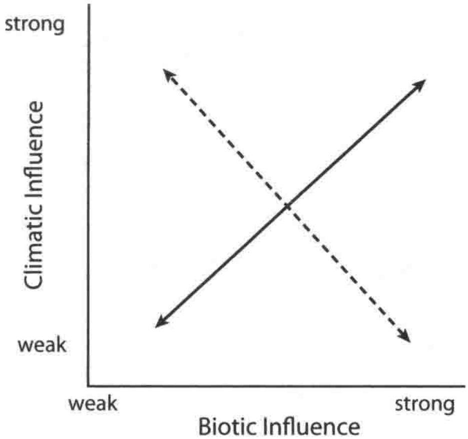

Figure 0.1. The tension (dashed line) and facilitation/promotion (solid line) hypotheses of the relationship between the strength of biotic interactions and climatic influence in ecological dynamics. According to the tension hypothesis, in general, weak biotic interactions will be associated with strong climatic influences on ecological dynamics, while strong biotic interactions will be associated with weak climatic influences on dynamics. In contrast, according to the facilitation/promotion hypothesis, as biotic interactions strengthen, so do climatic influences on ecological dynamics, while weak biotic interactions are associated with weak climatic influences on dynamics.

In the simple case in which biotic interactions take the form of density dependence, or intraspecific competition, weak interactions are expected to be destabilizing for dynamics, while strong interactions should be stabilizing, as will be exposed quantitatively in chapter 4. According to the tension hypothesis, when biotic interactions are weak, the role of climate in dynamics may assume greater importance, moving such dynamics toward instability (figure 0.2a). Conversely, with strong, stabilizing biotic interactions, the contribution of climate to ecological dynamics would be expected to be minimized (figure 0.2a). The tension hypothesis also recognizes, however, that the direction of causality in the tension between climatic and biotic factors in determining ecological dynamics may be reversed: strong climatic effects may weaken or override biotic influences, potentially leading to destabilization of ecological dynamics. Conversely, a weakening of any climatic influence would be expected to promote a strengthening of stabilizing biotic influences.

The use of arrows in the example illustrated in figure 0.2 and the following illustrations to depict the net effect on ecological dynamics of the interaction between the strengths of climatic and biotic influences on dynamics is intended to represent the variable nature of the expected outcomes of this interaction. Hence, when I refer to a strengthening or a weakening of climatic or biotic influences on dynamics and a tendency toward stabilization or destabilization of ecological dynamics, I am describing a variability that might be observed through time in a single population, species, or system; or across space among populations, species, or systems; or across levels of biological organization, from individuals to populations to communities, in a given location.

The nature of the interaction between the strengths of abiotic and biotic influences on ecological dynamics is, of course, reversed in the facilitation/

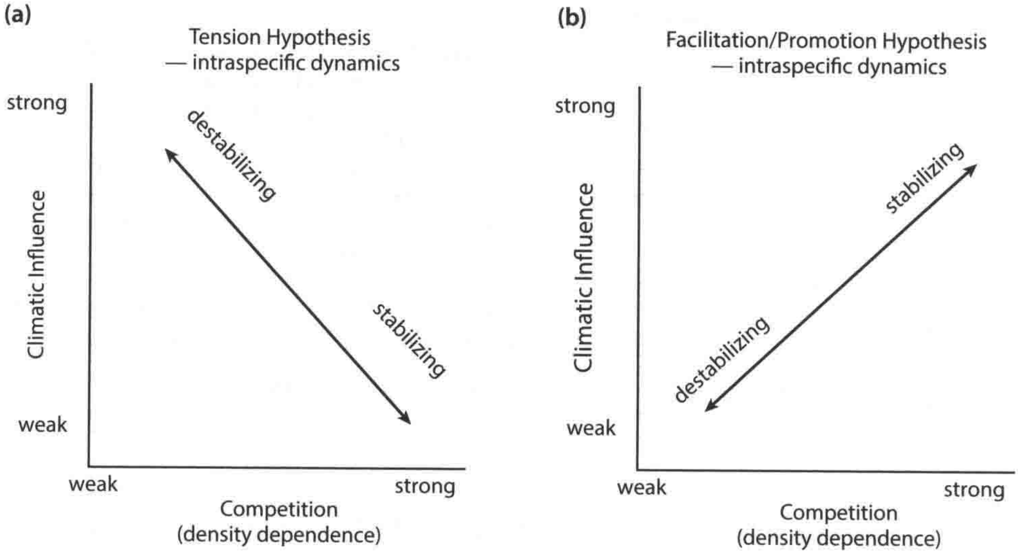

Figure 0.2. Contrasting predictions of the tension hypothesis (a) and facilitation/promotion hypothesis (b) for the stability of population dynamics. According to the tension hypothesis, strong density dependence is associated with a weak climatic influence on population dynamics, producing stable dynamics, while weak density dependence is associated with a strong climatic influence on dynamics, which leads to a destabilization of dynamics. According to the facilitation/promotion hypothesis, stable population dynamics result from the association of an increasingly strong influence of climate on dynamics with a strengthening of density dependence, while destabilization of population dynamics results from a weakening of density dependence with a weakening of the influence of climate on dynamics.

promotion hypothesis (figure 0.2b). In this case, the strengths of the biotic and abiotic influences on dynamics increase together or weaken together (figure 0.2b). Hence, in the simple example of intraspecific competition, as the strength of density dependence increases, the contribution of climatic conditions to the dynamics of that population may increase. This appears to have been the case with the population of reindeer introduced to St. Matthew Island in the U.S. state of Alaska, which, after increasing rapidly for several years, began to exhibit indications of density-dependent limitation through reduced offspring production and recruitment just before a severe winter precipitated a population crash (Klein 1968).

Turning to a consideration of interspecific interactions, we may, for instance, examine the consequences of interspecific competition, or interference interactions, for the coexistence of two species in a laterally structured community (figure 0.3). The distinctions between interference and exploitation and between laterally and vertically structured communities are discussed in greater

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detail in chapter 6. Here, though, according to the tension hypothesis, strong interspecific competition would be accompanied by a weak climatic influence on interference interactions between members of the competing species, in which case competitive exclusion would be expected (figure 0.3a). Conversely, weak interspecific competition may result from—or result in, depending on the direction of causality—a strong climatic influence on the interacting species, in which case stable coexistence would be expected. By contrast, the facilitation/promotion hypothesis predicts that competitive exclusion results from a simultaneous increase in the strengths of the influences of climate and competition (figure 0.3b). In this case, an increasingly strong climatic effect may have tipped the balance of competition in favor of one of the interacting species, or an adverse effect of climate on the inferior of two competitors may have been promoted by intense competition between the two interacting species.

The consequences of tension or facilitation between climatic and biotic influences on interactions among species also extend to exploitative interactions

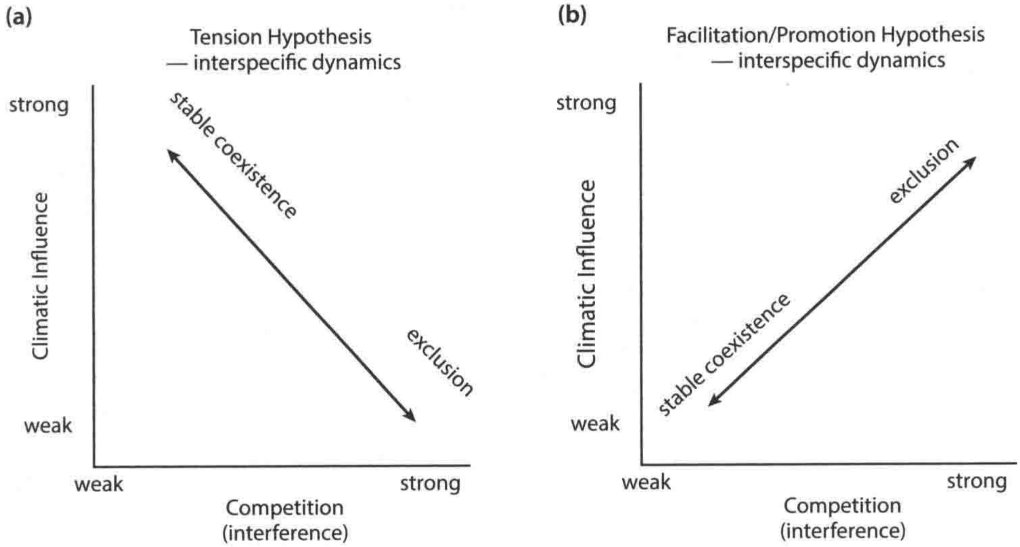

Figure 0.3. Implications of the tension hypothesis (a) and facilitation/promotion hypothesis (b) for the outcome of interspecific competition in laterally structured communities. According to the tension hypothesis, stable coexistence results from a weakening of interference in association with a strengthening of the climatic influence on one or both competitors, while competitive exclusion results from a strengthening of interference in association with a weakening of this climatic influence. In contrast, according to the facilitation/promotion hypothesis, stable coexistence should result when interference weakens in association with a weakening of the climatic influence on one or both competing species, while competitive exclusion is expected to result from a strengthening of interference with a strengthening of the climatic influence on, for example, an inferior competitor.

occurring across trophic levels in vertically structured communities (figure 0.4). In this case, however, the consequences relate to the balance between bottom-up and top-down drivers in regulating such interactions. When a tension exists between climatic and biotic influences in exploitation interactions, the dynamics across trophic levels should be regulated primarily by bottom-up interactions when the climatic influence is strong and the influence of exploitation is weak, but it should be regulated primarily by top-down interactions when climatic influences are weak and exploitation is strong (figure 0.4a). By contrast, when there is facilitation or promotion between climatic and biotic influences in exploitation interactions, bottom-up regulation should result when both the climatic influence and exploitation are weak, while top-down regulation should result when both the climatic influence and exploitation are strong (figure 0.4b). In Isle Royale National Park, for instance, wolf pack size increases with winter snowfall, leading to higher rates of moose kills, declining moose population size, and enhanced growth of balsam fir (Post, Peterson, et al. 1999).

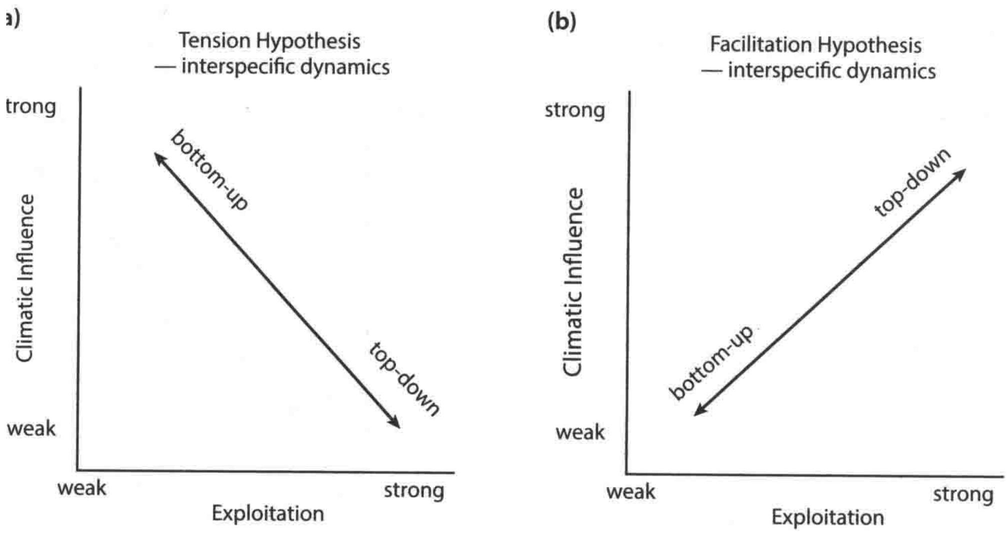

Figure 0.4. Predictions of the tension hypothesis (a) and facilitation/promotion hypothesis (b) for the directionality of regulation of trophic interactions in vertically structured communities. According to the tension hypothesis, top-down regulation is expected to occur as a result of a strengthening of exploitation interactions in association with a weakening of climatic influences on exploitation, while bottom-up regulation is expected to occur when exploitation interactions weaken with a strengthening of climatic influences. In contrast, according to the facilitation/promotion hypothesis, top-down regulation is expected to occur when a strengthening of climatic influences is accompanied by a strengthening of exploitation interactions, while bottom-up regulation should result from a weakening of exploitation interactions with a weakening of the influence of climate on exploitation.

Conceptualizing the relationships between biotic interactions and climatic influences on ecological dynamics according to the tension and facilitation/promotion hypotheses should improve our thinking about the ecological consequences of climate change and our understanding of how and why individuals, populations, species assemblages, and ecosystems respond to climate change in variously disparate or similar ways. I will note consistencies with these two hypotheses at various points throughout this book to make their distinction clearer but will not do so in every single case, to avoid tedium.

Many important studies did not make it into this book, and some readers will no doubt take exception to the absence, or in some cases the presence, of certain case studies. At the outset, I will admit that I have not taken extensive measures to present a taxonomically, geographically, or disciplinarily balanced view of the study of ecological responses to climate change. Nor have I attempted to assemble a complete review of such responses. Omissions may motivate some authors to reemphasize and draw attention to their own work in the literature, which in the end serves the objective of this book just as well because such action focuses attention on a subject that as a whole exceeds in importance the work of any individual. At the same time, some of the ideas presented in this book will undoubtedly stir disagreement and foster debate within the scientific community, but this too should be viewed positively because it forces us as scientists to scrutinize our assumptions and explore more thoroughly the foundational principles that underlie our understanding of how nature works.

I have tried to include in this book what I believe are the most salient aspects of ecological responses to climate change and, more important, to place them in the context of the foundations of ecology as a discipline and of ecological theory as a body of knowledge. In some cases, relevance to the classic studies on which contemporary ecology has been built will be more obvious than in others, but in the latter instance the broader context of ecology as a discipline should be apparent. I have also tried to incorporate, more through structure than through outright proselytizing, some sense of the utility and importance of studying the ecology of climate change across levels of organization, from individuals to populations, to species, to species assemblages, and finally to ecosystems. I have done this out of a personal conviction that understanding what one observes at the level of one's own investigation is enhanced by understanding how that level relates to all other levels of organization. Such a perspective also serves to emphasize, and through this emphasis to help develop an understanding of, the importance of biotic interactions in ecological responses to climate change. I hope readers will see the connections I have tried to draw among the related topics herein, and perhaps realize new ones that will fuel stimulating and important research on the ecology of climate change.

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