Integrating biological invasions, climate change and phenotypic plasticity

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Invasive species frequently change the ecosystems where they are introduced, e.g., by affecting species interactions and population densities of native species. We outline the connectedness of biological invasions, climate change and the phenomenon of phenotypic plasticity. Integrating these hot topics is important for understanding the biology of many species, their information transfer and general interactions with other organisms. One example where this is particularly true is the zooplankton species *Daphnia lumholtzi*, which has successfully invaded North America. The combination of a high thermal tolerance and a phenotypically plastic defense in *D. lumholtzi* might be responsible for its invasion success. Its morphological defense consists of rigid spines and is formed after sensory detecting the presence of native fish predators. The integration of biological invasions, climate change and phenotypic plasticity is an important goal for integrative biology.

**Biological Invasions**

In the last two decades, an increasing number of studies have been published on invasive species. One reason for this great interest is the impact of invasive species on global biodiversity and ecosystem functioning. Invasive species are defined as those species that have completed the invasion process (also known as “invasion pathway” or “naturalization-invasion continuum”). Most simply, the invasion process can be divided into three stages:

1. **Introduction** (transport and release)
2. **Establishment**
3. **Spread**

A species has taken the first step of this invasion process—“introduction”—if it has been (deliberately or accidentally) transported and released beyond its native or historic range. According to most definitions of invasive species, this first step must be mediated by humans. Due to globalization, increasing numbers of organisms are being transported around the globe. Many of these organisms are intentionally introduced for a variety of reasons (e.g., horticulture, agriculture, aquaculture, sport fishing, biological control or conservation). At the same time, intentional species introductions can also lead to unintentional introductions of exotic species. For example, seeds, eggs, dormant stages, parasites or pathogens can be unintentionally introduced as contaminants of intentionally introduced species. The second step of the invasion process is termed “establishment.” If an introduced species survives and successfully reproduces beyond human care/cultivation, i.e., if it has established one or more self-sustaining populations in the wild, it is referred to as “established.” Finally, the third step of the invasion process is “spread.” If the species spreads substantially beyond its point of introduction, it is termed “invasive.” Some authors additionally ask that an invasive species has a demonstrated negative impact (e.g., ecological, economic or human-health impacts). Although there are many examples of invaders exerting devastating impacts, it is hard to actually demonstrate impacts for some species, for example because of time lags between the arrival and spread of a species and the impacts caused. Many invasive species have a range of impacts (e.g., direct, indirect, little, major, negative, positive and a mixture of all), which further complicates the assessment of impacts. Most invasion biologists therefore do not include the condition of harmfulness in the definition of an invasive species and neither do we.

In this review, we outline the connectedness of biological invasions with (1) climate change and (2) the phenomenon of phenotypic plasticity, thereby focusing on the different steps of the invasion process. Integrating these three topics—biological invasions, climate change and phenotypic plasticity—is important for understanding the biology of many species, their information transfer and general interactions with other organisms. One species example where this is particularly true is the phenotypically plastic zooplankton species *Daphnia lumholtzi* which has successfully invaded North America, one likely reason for its success being climate change.

**Invasions and Climate Change**

Climate change has already been shown and predicted to substantially alter biodiversity, causing changes in species distributions, species interactions and ecosystem processes. In the face of climate change, a redefinition of what is termed an “invasive species” seems necessary. As outlined above, current typical definitions include the condition that the introduction of a non-indigenous species was mediated by humans, e.g., the species was transported across a geographic barrier that...
previously limited the species’ dispersal. We are not questioning that the definition of an invasive species should include the condition of human mediation, as there are differences between natural and human-mediated range expansions (e.g., the latter are happening much faster, and more of them are happening simultaneously). However, human mediation can also occur at other steps of the invasion process than the introduction-step: current climate change is mediated by humans, and climate change allows species to establish in regions where they could not establish before due to previously unsuitable climatic conditions (e.g., thermal constraints). Many species are shifting their distributions poleward or upward in elevation, as a response to climate change. These species have naturally dispersed to these regions, so there was no dispersal barrier that needed to be overcome by human mediation. The species were previously absent from these regions because they could not survive and reproduce there before. If we agree to term such species “invasive,” we use another definition than the one outlined above, as their introduction was not human-mediated but based on natural dispersal. Here, human mediation affects steps two and three of the invasion process:

(1) Introduction

(2) Establishment: climate change allows some species to establish where they could not establish before

(3) Spread: climate change allows some species to spread into regions where they were absent before

We thus propose to modify the definition of an invasive species as follows: An invasive species is a species that has completed the steps of the invasion process, where at least one step was facilitated by humans. There are many invasive species where all three steps of the invasion process—introduction, establishment and spread—were facilitated by humans: introduction directly by human transport, and establishment plus spread via climate change. An example for such a species is the gypsy moth (Lymantria dispar), which is native to Europe and Asia. A European strain was introduced accidentally to North America and has subsequently invaded Canada due to suitable climate.

It is expected to further expand its invaded range under climate change. The Asian tiger mosquito (Aedes albopictus) is another unintentionally introduced species in many parts of the world, and climate change will likely further increase its range. This invader also acts as transmission vector for several human diseases (e.g., Dengue virus, West Nile virus). Invasive species often have broad climatic tolerances, which enables them to compete effectively with native species. Obviously, climate warming will favor exotic species from warmer regions and climates.

The zooplankton species Daphnia lumholtzi is native to tropical and subtropical Africa, Asia and Australia. In 1990, the first D. lumholtzi populations in North America were detected in Texas and Missouri. Stockings with exotic fish species (e.g., Nile perch Latex niloticus) from Lake Victoria (Africa) seem to have caused this accidental introduction. Within a few years, D. lumholtzi has rapidly and widely spread across the southeastern and mid-western US. It is now found in freshwaters from the Atlantic to the Pacific coast, and from Florida to the Great Lakes. In invaded waters, D. lumholtzi exhibits high population peaks at warm temperatures during summer, while populations of native zooplankton species decline. Due to its (sub-)tropical origin, D. lumholtzi appears to be well adapted to high temperatures. Climate warming may stress native species, thus changing species interactions between native species and exotic invaders. Lennon et al. demonstrated that D. lumholtzi has a high temperature optimum between 20 and 30°C, and concluded from their experiments that D. lumholtzi has a similar reproductive rate as native Daphnia species between 20 and 25°C, but that it may out-compete some native Daphnia above 25°C. Therefore, a high thermal tolerance may provide a competitive advantage over native North American species, and thus might have favored its establishment under current climate warming. Our recent experiments showed that a temperature-mediated shift in competitive dominance occurs when D. lumholtzi competes against a North American Daphnia species at a warm temperature. While the native Daphnia species competitively dominated over D. lumholtzi at cool and slightly elevated temperatures, the dominance was lost at warmer temperatures. This clear temperature effect suggests that a high temperature tolerance in D. lumholtzi has favored its establishment, and potentially also its spread across North America under climate change. However, this is not the only explanation: our recent study suggests that predator-induced phenotypic plasticity in D. lumholtzi might also be an important determinant for the invasion success.

Figure 1. Phenotypic plasticity in two individuals of the same Daphnia lumholtzi clone. The individual on the left, but not the one on the right, was exposed to chemical cues exuded by fish.
Invasions and Phenotypic Plasticity

Phenotypic plasticity is defined as the capacity of an individual (single genotype) to exhibit variable phenotypes in different environments, and is a widespread phenomenon among many animals, plants and other organisms (reviewed in refs. 36–40). Phenotypic plasticity can manifest as changes in morphology, physiology, life history or behavior. Many studies have shown that it affects interactions between individuals and their abiotic (e.g., climate, temperature and light) as well as biotic (e.g., predation and competition) environment in a wide range of taxa.36,38–40 Accordingly, phenotypic plasticity is likely to play an important role for the invasiveness of introduced exotic species in new habitats,6,7,37,41,42 as it may allow for rapid and adequate adaptations to these new environments.43 Phenotypic plasticity may promote invasion success, and several invasive species have been shown to have a higher phenotypic plasticity than indigenous species, both in plants and animals (reviewed in refs. 6, 41 and 42). For instance, phenotypic plasticity in defensive traits may allow an invasive species to effectively reduce the risk of consumption by resident native predators. Such inducible defenses46 are anti-predator strategies that are formed by prey species if their predators are present, and are not formed if their predators are absent. For example, individuals of

D. lumholtzi

form head spines as inducible defenses against fish predators if fish are present in their water body but not if fish are absent (Fig. 1).40 Prey species with an inducible defense frequently detect the presence of their predators by sensing predator kairomones (chemical cues released by predators). Accordingly, an invasive species with an inducible defense has to detect the presence of potential predators in its new range by their chemical cues. These information transfers between invasive and native species are not well studied. Most likely, the predators release chemicals that are structurally similar to cues released by predators in its original habitat. If native prey species are unable to form inducible defenses against certain resident predators, non-native species with an inducible defense against these predators may have a competitive advantage and may thus become invasive. In a recent paper,38 we demonstrated that the inducible defense of

D. lumholtzi

against fish predators provides an important benefit in the competition with a North American Daphnia species. The combination of this inducible defense with the high thermal tolerance mentioned in the previous section might be responsible for the invasion success of

D. lumholtzi

in North America.

Further studies on other species that integrate the three topics biological invasions, climate change and phenotypic plasticity are needed. As mentioned above, the information transfer between invasive and native species is another important but currently understudied research topic.

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