Maria Meza-Lopez

Effects of anthropogenic nutrient enrichment and climate change on invasion success and impacts on native freshwater communities

Biological invasions are one of the largest threats to global biodiversity, they alter ecosystem function, threaten human health, and are expensive to control (Pimentel *et al.* 2005). Ecosystems that are invaded by one exotic invasive species often contain abundant populations of other exotic invasive species. This may result from positive invader-invader interactions or a response to common anthropogenic factors. In addition to biological invasions, there are other major threats to ecosystems which include nutrient pollution and climate warming (Dukes 2011). Nutrient rich environments are more likely to be invaded over time and can accumulate multiple exotic invasive species (Vilà *et al.* 2007). Climate warming may enhance exotic species invasions by altering climate regimes in the introduced range to closely resemble climatic conditions experienced by exotic species in their native range (Dukes 2011). Yet, we know little about the combined effect of nutrient pollution and climate warming on exotic species success and their impact on native species at the community level. Studies on biological invasions alone provide valuable information for exotic species management but to fully understand biological invasions, biotic (invader-invader interactions) and multiple anthropogenic factors (nutrient pollution and climate warming) on invaded habitats must be evaluated.

In general, species survival and performance depends on the characteristics of environment that they encounter. Species invasion success depends on whether or not they can tolerate the environmental conditions that they encounter regardless of their invasive potential. Nutrient rich habitats are known to support more exotic invasive species compared to nutrient poor habitats (Vilà *et al.* 2007). Increases in nutrients reduce environmental stress that results in increase in exotic plant growth and competitive ability and exotic grazer performance. Climate warming, another anthropogenic factor, may influence exotic species invasion success. Climate warming could alter the physiological ability of exotic species to persist. For example, an exotic clam's fitness increased with warming in summer and decreased with warming in winter (Weitere *et al.* 2009). Climate warming could also alter competitive interactions between native and exotic species by creating climatic conditions in the introduced range similar to conditions encountered by exotic invasive species in their native range and conditions that are novel to resident species (Bradley *et al.* 2010). Studies have investigated effects of nutrient addition on exotic invasive species with fewer studies on nutrient addition effects on exotic plant-herbivore interactions. Our knowledge of climate warming effects on species primarily relies on bioclimatic models that often neglect climate warming interactions with other anthropogenic factors. The mechanisms underlying effects of climate warming on invasion success and community composition currently remain unexplored. Studies that manipulate multiple anthropogenic factors are necessary because it has been speculated that nutrient addition and climate change may enhance invasion success by creating novel environmental conditions that may alter or intensify species interactions. A study on the effect of carbon dioxide, nutrient addition, and climate warming on native species showed that interactions between multiple anthropogenic factors are important in plant-pollinator interactions therefore the effect of anthropogenic factors cannot be evaluated or predicted in isolation from one another (Hoover *et al.* 2012). Exotic invasive species are better suited to succeed in novel environments compared to native species (Bradley *et al.* 2010), therefore it is critical to evaluate exotic species invasion success considering both biotic and abiotic characteristics of invaded habitats to better predict invasions.

Study System:

In southeast Texas, exotic plants and exotic snails heavily invade local wetlands. Common local native wetland plants that were included in our studies are broadleaf cattail (*Typha latifolia)*, pennywort (*Hydrocotyle umbellata)*, frog's bit *(Limnobium spongia),* and pickerelweed *(Pontederia cordata)* together with native snails *Physa acuta* and *Planorbella trivolvis*. These native species co-occur with exotic invasive plants water hyacinth *(Eichhornia crassipes), alligator weed (Althernanthera philoxeroides),* and water lettuce (*Pistia stratiotes)* in addition to exotic apple snails (*Pomacea maculata).* These exotic plants' native range is characterized by warmer climate than the Gulf Coast but, for most native species this region already represents the warmest climate in which they occur. *Pomacea maculata* occurs in a cooler climate compared to the Gulf Coast but can tolerate water temperatures between 15-36°C.

Experiment 1: Biological invasions and multiple anthropogenic factors: Impacts on wetland communities

Questions 1:

1. Do nutrient addition and/or warming increase exotic plant invasions in the presence of exotic herbivores? Do these reflect greater herbivory on native plants and/or increased exotic plant growth?
2. Do nutrient addition and/or warming enhance exotic herbivore invasions? Do these effects depend on the presence of exotic plants?

Methods 1:

We established 40 wetland communities in late fall 2011. Each 473-liter tank received 15 cm of topsoil/sand mixture, municipal water, individuals of each native plant species, and 40 snails of each native snail species. In summer 2012, established wetland communities received 3 juvenile apple snails (*P. maculata)* and were randomly assigned to treatments in a factorial design (2 × 2 × 2 × 5 reps): **1) plant origin:** 160 g of native plants or exotic plants, **2) nutrient addition:** control (ambient – municipal water) or high (municipal water plus 6 mg/L Nitrogen & 1.7 mg/L Phosphorus), and **3) warming:** control (ambient) or +2°C (using solar water heaters). Each tank received a continuous input of 63 ml / minute (91 liters / day) and drained through an overflow pipe. We conducted weekly exotic snail egg mass surveys (eggs were removed, measured, weighed, crushed and then returned to tanks). At the end of the experiment (October 2012), we removed, sorted and weighed aboveground plant biomass and removed, measured, and weighed apple snails.

Results 1:

Native plant biomass was higher in absence of exotic plants. Native plant biomass (and exotic plant biomass increased with nutrient addition but were independent of warming. However, there was an interactive effect of exotic plants and nutrient addition with nutrients only increasing native plant biomass when exotics were absent. Warming decreased native plant biomass when exotics were absent but native plant biomass was low independent of warming when exotic plants were also present.

Apple snail operculum size was independent of plant origin (presence or absence of exotic plants), nutrient addition, and warming. Apple snail mass increased with nutrient addition only with warming. Apple snail egg mass was independent of plant origin and nutrient addition. Warming increased apple snail egg mass.

Conclusions 1:

Exotic plant biomass increased with nutrients while native plant biomass increased with nutrients only in the absence of exotic plants. This suggests that nutrient enrichment will accelerate exotic plant invasions. Exotic plants were unaffected by warming while warming tended to reduce native plant biomass, suggesting that warming may enhance plant invasions in these wetland ecosystems. Apple snail mass was higher with nutrient addition only with warming, suggesting that nutrient addition with warming will enhance snail invasion success but that such increases with nutrient addition would be limited in current climate conditions. Apple snail reproductive output increased 4 fold with 2°C of warming and was independent of other factors, suggesting that warming alone will increase apple snail population growth rate and may contribute to range expansion. This study indicated that these multiple invasions do not reflect positive invader-invader interactions. Rather, these habitats invaded by multiple invasive species reflect common responses to environmental factors. Significant interactions among factors emphasized that investigating multiple anthropogenic factors in invaded habitats is critical for making accurate predictions; therefore we cannot rely on bioclimatic models that neglect to consider other anthropogenic factors to predict invasion success, community composition patterns, and impacts on native species.

Experiment 2: Effects of nutrient addition, warming, and seasonal variation on native and exotic plant communities

Questions 2:

1. Do nutrient addition and/or warming reduce native plant performance and enhance exotic plant performance? Do they alter the outcome of native-exotic plant competition?
2. Does warming reduce stress of low winter temperatures on exotic plants? Does it alter the outcome of native-exotic plant competition?

Methods 2:

We conducted a mesocosm experiment manipulating plant origin, nutrient addition, and warming in a 3 × 2 × 3 factorial experiment with 4 replicates. In late spring 2012, we added 15 cm topsoil/sand mixture, municipal water, and 10 individuals of each native snail species to seventy-two 454 L tanks at Rice University South Campus Field Station. We randomly assigned mesocosms to treatments: **1) plant origin:** np (160 g native plants), 2) ep (160 g exotic plants 160g), or np+ep (160 g native and 160 g exotic plants], **2) nutrient addition:** control (ambient-no added nutrients) or high (6 mg/L Nitrogen & 1.7 mg/L Phosphorus), and **3) warming:** ambient, +1°C, or +2°C using solar water heaters. Each tank received a continuous input of 63 ml / minute (91 liters / day) and drained through an overflow pipe. We conducted monthly plant and water quality (temperature, dissolve oxygen, and pH) surveys. We collected, sorted, and weighed aboveground plant biomass in April 2013.

Results 2:

Native plant biomass was independent of the presence of exotic plants. Native plant biomass increased with nutrient addition and this increase was greater when exotic plants were absent. Native plant biomass was higher in the +2°C treatment but did not vary between controls and the +1°C treatment. Native plant diversity increased with nutrient addition in the absence of exotic plants.

Exotic plant biomass was higher in ep treatments versus np+ep treatments. Nutrient addition increased exotic plant biomass, especially in the absence of native plants. Exotic plant performance was independent of warming treatments. Exotic plant diversity was higher with nutrient addition. Exotic plant % cover increased with nutrient addition throughout the experiment.

Conclusions 2:

Both exotic plant and native plant performance increased with nutrient addition but exotic plants outcompeted native plants when both were present. Low nutrient levels reduced exotic plant diversity. This suggests that exotic plant survival and performance depends on nutrient levels and that increased nutrient enrichment will enhance exotic plant invasion success and increase exotic plant diversity. Warming benefits native plants while exotic plant performance did not depend on warming, suggesting that climate warming will have a greater effect on native plants compared to exotic plants possibly enhancing invasion success. Exotic plant % coverage continued to increase from late spring through fall and peaked around winter, suggesting that winter lows are critical and important for invasive species management because it reduces plant invasion success and can alter the outcome of native- exotic plant competition.

These experiments increase our knowledge of how exotic species invasions and anthropogenic factors such as nutrient enrichment, climate warming, and their interaction can alter native and exotic species biotic interactions and how these anthropogenic factors alter the impact of exotic species invasion on native wetland communities in SE Texas. The Shell Center for Sustainability Research Grant allowed us to purchase supplies necessary and allowed us to hire an undergraduate research assistant during summer 2012 to conduct these mesocosm experiments.

References:

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