

Global change in marine coastal habitats impacts insect populations and communities[☆]

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Salt marsh and mangrove coastal ecosystems provide critical ecosystem services, but are being lost at an alarming rate. Insect communities in these ecosystems are threatened by human impacts, including sea level rise, habitat loss, external inputs including nutrients, metals, and hydrocarbons, as well as weather events, such as hurricanes. While some disturbances are felt throughout the food web (e.g. hurricanes), others are mediated by impacts on the dominant plants (e.g. nutrient subsidies). The impacts of these disturbances on insects/spiders and their rate of recovery is dependent on trophic level, life history, and diet breadth. While we understand impacts of single disturbances relatively well, we have very little understanding of how multiple disturbances interact to affect insect communities.

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Introduction

Salt marsh and mangrove coastal ecosystems are being lost at an alarming rate yet provide valuable ecosystem services such coastal protection during storm events, waste treatment by filtering terrestrial runoff, fisheries maintenance, carbon sequestration, and recreation [1,2]. Indeed, services

provided by coastal ecosystems per unit area are greater than any other ecosystem [3]. Coastal ecosystems also serve as nursery grounds for commercially important fish and crustaceans (e.g. [4]), for which arthropods serve as important food sources [5]. However, these ecosystem services and coastal insect communities are threatened by natural and human impacts, including sea level rise, habitat loss, external inputs, and hurricanes (Figure 1; [2,6,7]). Because of the critical ecosystem services provided by coastal ecosystems, these areas are often the target of resilience and restoration efforts. Thus, an understanding of how these ecosystems function and the factors that destabilize them are critical to successful mitigation strategies.

Insect communities in coastal ecosystems are typically dominated by specialist species that feed on the foundation plant species, and these dominant insects play pivotal roles in affecting critical ecosystem processes such as productivity and decomposition [8]. Notably, specialist insects are often more affected by anthropogenic global change than are generalist species [9]. While many studies examine the impacts of a single global change factor, coastal ecosystems are simultaneously impacted by multiple factors and how these multiple disturbances interact to affect insect communities is not well understood. Thus, it becomes increasingly important to examine whether different global change factors act in a synergistic or antagonistic manner to influence insect communities.

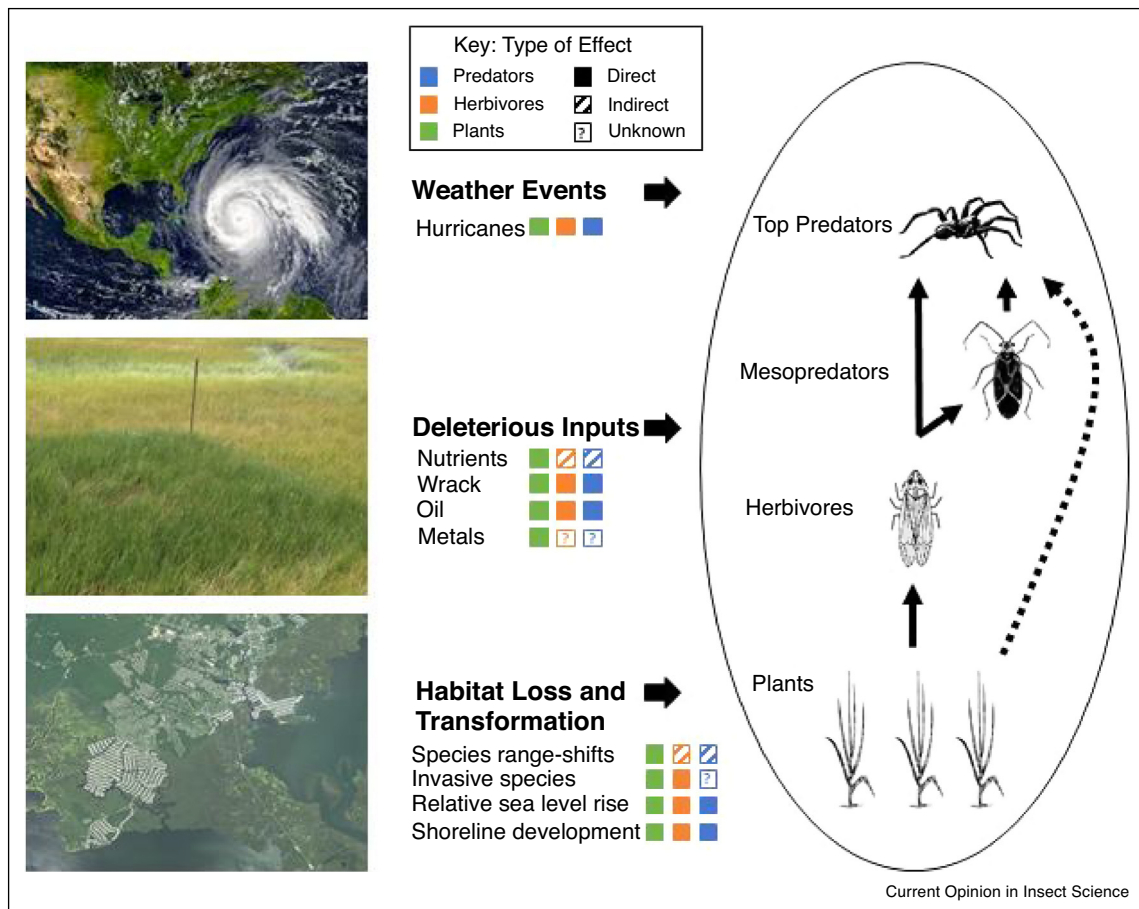
Here we provide a brief review of the recent advances in our understanding of insect responses to disturbances in marine coastal ecosystems, focusing mainly on salt marshes and mangroves. We highlight how coastal disturbances alter species interactions and how the functional roles of insects within the community may affect their recovery. We also discuss areas of the literature that are lacking and that may therefore prove fruitful for future research endeavors.

Habitat loss and transformation

Throughout the world, coastal ecosystems are being lost or transformed via sea-level rise, shoreline development, invasive species, and species range-shifts [10]. Considering marine coastal ecosystems typically have a low diversity of primary producers, the loss of native foundation plant species has dire implications for the animals that depend on them. Recent studies confirm that past disturbance and present native plant distribution are robust

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Figure 1



Schematic of how global change disturbances in marine coastal habitats impacts insect populations and communities. Weather events, deleterious inputs, and habitat loss and transformation are three main categories of human-caused global change disturbances that affect coastal plant and arthropod communities. Current knowledge on the type effects (direct, indirect, or unknown) on the trophic level (plants, herbivores, or predators) is indicated by symbols next to each subcategory. The simplified arthropod community shows basic feeding relationships.

predictors of native insect diversity in mangroves [11,12], sand dunes [13], and salt marshes [14]. Species-range shifts, such as the advancement of mangrove species into salt marsh marshes, have altered arthropod communities at transition zones [15]. Notably, when mangroves reforest, their food webs tend to restore relatively quickly if native species subsist [16]. However, in other systems where arthropod communities are dominated by invasive species, native insect species are replaced [17]. Thus, relative sea level rise, shoreline development, and invasive species are dire threats to coastal habitats and the animal biodiversity within these habitats.

As sea levels rise along the eastern coast of North America, upper-marsh plants that are incapable of surviving sustained tidal flooding, such as *Spartina patens*, are being replaced by lower marsh species, such as *Spartina*

alterniflora, a species tolerant of sustained tidal flooding. Aside from the direct losses of *S. patens*, which extirpates the specialist insects who use *S. patens*, recent research has demonstrated that when foundation species like *S. patens* become increasingly fragmented, insect abundance and composition are altered as patch sizes get smaller and degraded, or as habitat edge effects alter trophic dynamics [18,19,20]. Further, some insect species appear to be more severely impacted by sea-level rise than the plant species on which they depend, such as in the case of the red imported fire ant *Solenopsis invicta*, where coastal colonies that experience flooding have altered morphology and physiology and exhibit more aggressive behavior [21]. Similarly, reconstructions of sea-level rise and sea water intrusion over the last 7000 years in the Mediterranean showed that even halophilous beetles declined as sea levels and salinity levels rose in the area [22].

Although the reestablishment of insect species threatened by sea-level rise has been successful where there are undisturbed ecosystems for reintroduction [23], specific studies regarding insect responses to sea-level rise are necessary for understanding and predicting biodiversity changes due to sea-level rise.

Weather events

Extreme weather events are predicted to increase with climate change, and in particular hurricanes will likely intensify more rapidly [24]. The direct effect of hurricanes on insects/spiders inhabiting coastal ecosystems is often negative, but organisms that are embedded in live or dead biomass appear to be less vulnerable to disturbance [25^{*}]. Indeed, some of the most abundant insect species in coastal salt marshes spend part of their life cycle embedded in the host plant, which allows these insects to quickly recover from hurricane disturbance [25^{*}]. For example, planthopper eggs are embedded in live *Spartina* plant tissue [26], and stem-boring insect eggs/larvae are embedded in *Spartina* stems [27,28]; thus, populations can recover quickly as long as some portion of these herbivore populations are embedded in the host plant at the time of disturbance. Additionally, recovery by insects is related to dispersal capability; more dispersive species recolonize the marsh more quickly [25^{*}].

The impacts of hurricanes on coastal insect communities can also be mediated by host plant responses. Salt marsh insect communities are often resilient to hurricane disturbance due to the transient impacts of hurricanes on coastal plants that quickly recover from the disturbance [25^{*}]. For example, while live culms can be damaged during hurricanes, the clonal nature of *Spartina* allows for rapid regrowth within weeks of the disturbance and this rapid recovery leads to herbivore and predator recovery [25^{*}]. This resilience is often decreased; however, in marshes with high nutrient input since fertilization decreases root biomass [29]. However, the rate at which predators recover from hurricanes is driven by specialization. For example, specialist predators (e.g. *Tytthus* egg predators) only recover their pre-storm population densities after their specialized herbivore prey recover [25^{*}], whereas generalist lizard predators in the Bahamas have been found to recover more quickly from hurricanes relative to specialists [30].

While *Spartina* grasses are relatively resilient to hurricane disturbance, mangroves are severely affected with at least 70% of mangrove dieback due to high-intensity weather events like hurricanes [31]. Shoot elongation and leaf area index are negatively impacted by hurricanes mainly due to the stripping of leaves from mangroves during the storm, yet these effects are long lasting and affect mangrove mortality five years after the storms made landfall [32]. Moreover, similar to *Spartina* described above, nutrient fertilization actually reduced mangrove

resilience to hurricane disturbance; the low stature of unfertilized mangrove trees makes them more resistant to defoliation during hurricanes [32]. Even when hurricanes are not the major driver of dieback in mangrove systems, they may aid insect herbivores that facilitate the spread of disease-causing dieback [33]. Furthermore, hurricane disturbance reduces the species diversity and visitation rates of mangrove pollinators, and it can take years for these pollinator communities to recover after disturbance, which impacts mangrove outcrossing rates [34].

Deleterious inputs

Salt marsh and mangrove ecosystems are impacted by multiple types of deleterious inputs, but the inputs most commonly studied for their impacts on insects are nutrients (eutrophication), wrack, oil, and metals. Eutrophication alters arthropod communities and changes the structure of the marsh itself, largely due to responses by the dominant grasses. For example, under high nitrogen conditions, *Spartina* allocates more growth to above-ground relative to root biomass [19^{*},20^{**}]; the plants become top-heavy, topple-over into creeks and thus no longer stabilize creek banks, which leads to increased erosion and dieback [35]. Further, the addition of nutrients that act as terminal electron acceptors increase respiration and organic matter decomposition by stimulating sediment microbial communities [36]. These changes to *Spartina*, both live and dead, have landscape-level effects because *Spartina* is largely responsible for the structure of the marsh. These changes to *Spartina* differentially affect arthropods at different trophic levels. Herbivores are inconsistently affected by nutrient addition, but higher trophic level predators experience the strongest effects of nutrients subsidies [19^{*},20^{**},37,38], which may be driven not only by increased plant biomass and quality with fertilization [19^{*},20^{**},37,38], but also enhanced structural complexity that reduces antagonistic interactions among predators [19^{*},20^{**}]. While herbivores as a group are intermittently affected by nutrients, stem-boring moth herbivores increase under high nutrient conditions [28] and these stem-boring moths are often associated with large dieback areas in the marsh [39].

Wrack is a common natural disturbance composed of dead marsh plant material that is deposited onto the marsh by waves and tides. Wrack physically disturbs the marsh by damaging live vegetation, but it also can increase nutrient, organic matter content and create new microhabitat conditions in the marsh [40]. Montemayor *et al.* [40] suggest that the nutrient quality of the wrack affects how wrack affects the arthropod community and that high-quality wrack can actually increase abundance of some taxa (e.g. Diptera, Hymenoptera, and Hemiptera) with creation of new microclimates. However, the timing of wrack disturbance is also important in determining its impact on salt marsh insect populations and communities.

Li and Pennings [41] determined that wrack disturbance late in the growing season led to reduction of stem-boring insect larvae compared to early season wrack disturbance because plants recovered from early season wrack before stem-boring flies began ovipositing. Current work has not explicitly connected wrack to global change, and it would be interesting to evaluate how the impacts of wrack are amplified by or interact with other global change drivers.

Research about the impacts of oil spills on insects is more recently developing. How oil spills affect coastal environments was most recently and thoroughly studied in response to the April 2010 Deepwater Horizon oil spill in the Gulf of Mexico. McCall and Pennings [42] showed that all salt marsh invertebrates had populations suppressed by 50% within the first year, but that the populations showed signs of recovery within the first year. Husseneder *et al.* [43,44**] studied greenhead flies and found that initially in oiled areas there was a severe drop in numbers of larvae and adults, which led to a genetic bottleneck; however, with increased immigration of flies from non-oiled areas to oiled areas the bottleneck disappeared after six years. Notably, multiple disturbance events can interact to affect insect communities and alter recovery trajectories as shown by Bam *et al.* [45**] who found that Hurricane Isaac in 2012 remobilized oil from the Deepwater Horizon oil spill, and negatively affected arthropod taxonomic richness. Finally, Roe *et al.* [46] is one of the first to correlate metal concentrations in mangroves with arthropod community composition; they found that 71% of macroinvertebrate assemblage composition could be explained by bioavailable manganese, zinc, and selenium along with mangrove biomass. Members of the fly family Psychodidae were lower in abundance at higher bioavailable concentrations of zinc and lead, but higher in abundance at higher bioavailable selenium and manganese. Notably, how these various deleterious inputs (metals, oil, wrack, and nutrients) interact to affect arthropod communities remains unstudied.

Conclusions and future directions

Coastal ecosystems and their associated organisms are threatened by complex global change factors, mainly driven by anthropogenic climate change and human expansion. Most research focuses on individual impacts of each global change factor, yet these disturbances often interact in complex and unpredictable ways and these multiplicative effects should be better investigated [47]. The insect species most at risk from these global changes are likely to be species that are specialists, associated with threatened plant species, poor dispersers, or that face competition with invasive species. Therefore, for conservation of these species, it may be useful to focus on functional traits or aspects of organisms that will make them susceptible to the dominant global change factors of coastal ecosystems. Future research should focus on

conservation planning for these species. Further, studies in coastal systems should examine cross-ecosystem exchanges between marine and terrestrial habitats; factors that impact estuaries (e.g. ocean acidification, saltwater intrusion, light pollution, human debris and plastics, or increasing sea surface temperature) may also affect salt marshes and mangroves or *vice versa*.

Conflict of interest statement

Nothing declared.

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