Concepts regarding effects of recurrent natural disturbances and subsequent responses of communities are central to ecology and conservation biology. Tropical cyclones constitute major disturbances producing direct effects (damage, mortality) in many coastal communities worldwide. Subsequent reassembly involves changes in composition and abundance for which the underlying mechanisms (deterministic and stochastic processes) are still not clear, especially for mobile organisms. We examined tropical cyclone-induced changes in composition and reassembly of entire insect communities in 16 Louisiana coastal salt marshes before and after Hurricane Isaac in 2012 and 2013. We used the Shannon index and multivariate permutational ANOVA to study insect resistance and resilience, β diversity partitioning to evaluate the importance of species replacement, and null models to disentangle the relative roles of different assembly processes over time after the tropical cyclone. The α diversity and species composition, overall and for different trophic levels, decreased immediately after the tropical cyclone; nonetheless, both then increased rapidly and returned to pre-cyclone states within one year. Changes in species abundance, rather than species replacement, was the primary driver, accounting for most temporal dissimilarity among insect communities. Stochastic processes, which drove community composition immediately after the tropical cyclone, decreased in importance over time. Our study indicates that rapid reformation of insect communities involved sequential landscape-level dynamics. Cyclone-resistant life cycle stages apparently survived in some, perhaps random locations within the overall salt marsh landscape. Subsequently, stochastic patterns of immigration of mobile life cycle stages resulted in rapid reformation of local communities. Post-cyclone direct regeneration of salt marsh insect communities resulted from low resistance, coupled with high landscape-level resilience via re-immigration. Our study suggests that the extent of direct regeneration of local salt marsh insect communities might change with the size of larger marsh landscapes within which they are imbedded.

Keywords: direct regeneration, Hurricane Isaac, resistance and resilience, salt marsh cordgrass, Spartina alterniflora, stochastic and deterministic patterns of community reassembly
Introduction

Recurrent natural disturbances affect many ecological communities. Fundamental theories of ecology, such as succession, are based on understanding the effects on populations of species present at the time of disturbance and subsequent responses (Connell and Slatyer 1977, Platt and Connell 2003). Nonetheless, it can be difficult to predict general responses due to variation in disturbance regimes, the complexity of interactions among local species assemblages, past selection for life history traits associated with resistance and resilience, and changing environmental parameters (Halpern 1988, Pfisterer and Schmid 2002, Allison 2004, Klinger 2006, Loreau and de Mazancourt 2013). Elucidating individual community responses to recurrent natural disturbances is critical for understanding how species assemblages are organized, as well as for formulating appropriate conservation strategies in fragmented habitats that are undergoing rapid changes in environmental conditions as a result of climate change.

Tropical cyclones (also regionally known as hurricanes or typhoons) constitute dramatic meteorological phenomena that disrupt ecological communities. High winds and storm surges occur annually within three large cyclone belts in most subtropical and warm-temperate regions of the world (Emanuel 2005). These storms directly damage and influence survival of individuals within populations, as well as initiate post-cyclone responses, often in altered environments (Whitmore 1974, 1989, Batista and Platt 1997, Turton and Stork 2008, Lin et al. 2012, Turton 2012, Chi et al. 2015, Ibanez et al. 2019). As a result, tropical cyclones impact local species distributions, species interactions, community structure, and ecosystem functions (Vandermeer et al. 2000, Schoener et al. 2001, Turner et al. 2006, Spiller and Schoener 2007, Willig et al. 2007, Sanchez-Galvan et al. 2012, Platt et al. 2015). Further, recurrent tropical cyclones produce consistent compositional and structural patterns regionally and worldwide, despite large taxonomic and evolutionary differences among organisms in the different regions experiencing these recurrent disturbances (Quigley and Platt 2003, Keppel et al. 2010, Ibanez et al. 2019).

Studies concerning effects of tropical cyclones on natural ecosystems have produced important concepts in ecology. Such concepts include resistance and resilience of populations to disturbance (sensu Bellingham et al. 1995, Batista and Platt 2003) that results in direct regeneration of community composition and structure (sensu Boucher 1990, Boucher et al. 1990, 1994, Yih et al. 1991, Vandermeer et al. 2000, 2001, Dietze and Clark 2008, Lin et al. 2011, Imbert 2018). The direct regeneration hypothesis, that communities are likely to return to pre-disturbance conditions following disruption, emerged primarily from empirical study of sedentary organisms in forested ecosystems (Lugo 2008, Keppel et al. 2010, Xi 2015, Imbert 2018, Ibanez et al. 2019) and marine coral reef and intertidal systems (Harmelin-Vivien 1994, Connell 1997, Lugo et al. 2000, Greening et al. 2006, Gouezo et al. 2019, Mathews and Maccarone 2019, Olin et al. 2019). Development of concepts related to effects of tropical cyclones on natural systems thus should benefit from studies of different types of systems.

There is no clear consensus regarding effects of tropical cyclones and the responses post-cyclone on mobile organisms. Small organisms such as insects and other terrestrial invertebrates appear especially susceptible to the violent nature of tropical cyclones. Nonetheless, both decreases and increases in abundances of invertebrates post-cyclone have been observed and inferred (Willig and Camilo 1991, Torres 1992, Pascarella 1998, Schowalter and Ganio 1999, Koptur et al. 2002, Angulo-Sandoval et al. 2004, Hirao et al. 2008, Spiller et al. 2016). Further, insects in different microhabitats respond differentially to wind damage (Schowalter et al. 2017), and species interactions within/between trophic levels have been suggested to influence post-disturbance changes and resulting assemblages in different ways (Schoener and Spiller 2006, Schowalter 2012, Novais et al. 2018). Studies are needed that explore how tropical cyclones affect mobile organisms, as well as how they respond post-cyclone.

Monitoring community dynamics following a tropical cyclone disturbance also can inform ecological theory regarding post-disturbance community reorganization. For instance, replacement sequences constitute a core prediction in traditional successional models wherein ‘early’ colonizers communities are replaced by competitively-dominant ‘late’ colonizers (Connell and Slatyer 1977, Lichter 1998, Platt and Connell 2003). In contrast, community nestedness occurs when 1) early colonizers remain in the system and early communities are subsets of later ones (Nascimbene et al. 2017, Woods 2017), or 2) all species are present post-disturbance and groups of species disappear in orderly sequences over time (Initial Floristic Composition, Egler 1954, Imbert 2018). Alternatively, assemblage dynamics post-disturbance can be determined mainly by abundance differences rather than species composition changes, resulting in neither replacement nor nestedness patterns (Schowalter and Ganio 1999, Carnicer et al. 2007, Novais et al. 2018). The patterns of community reassembly post-disturbance thus are still not fully understood, and more studies are needed (Platt and Connell 2003).

Disturbance also can reset underlying mechanisms that govern post-disturbance reassembly of communities. Either deterministic (environments, species interaction) or stochastic processes (e.g. chance arrivals, historical legacy) can be the dominant force that drive community composition over time (Clements 1916, Chase 2003, Norden et al. 2009, Trowbridge 2007). The relative importance of each process can also change during community development (Walker and Chapin 1987, Kayes et al. 2010). For instance, some studies suggested that disturbance can act as a deterministic force and only allow certain species to survive (Benscoter 2006, Flinn 2007), leading to homogenization of species compositions (lower β diversity, Sarmiento et al. 2003). Subsequently, the relative importance of stochastic processes may increase...
(Jurburg et al 2017) and thus community trajectories may diverge. The alternative view states that stochastic processes prevail during the initial post-disturbance period, causing random patterns of species distributions (higher β diversity). Later, deterministic selection becomes stronger and thus communities converge on similar states (Sara et al. 2006, Wanner et al. 2008, Réjour-Méchain et al. 2014, Fukami 2015, Maren et al. 2018, Martins et al. 2018). These divergent viewpoints indicate the need for more empirical studies to assess how assembly processes change over time after disturbances (Fukami et al. 2005, Li et al. 2016).

We examined the effects of a North Atlantic hurricane on foliar insect communities in salt marshes of coastal Louisiana (USA). We asked three questions: 1) what are the effects of a tropical cyclone on resistance and resilience in salt marsh insect communities? 2) Does species replacement occur post-hurricane in salt marsh insect communities? 3) What are the post-hurricane temporal dynamics of deterministic and stochastic processes in salt marsh insect communities? To examine these questions, we sampled plots in salt marsh communities before and after a category 1 hurricane (Isaac, 130 km h\(^{-1}\), 2–4 m storm surge for 12h) made landfall in southeastern Louisiana in August 2012. Our study provided data that enabled us to explore whether concepts regarding post-cyclone responses developed primarily for plant communities might also be applicable to insect communities. In addition, our study has important implications for understanding how organisms respond to disturbance in coastal ecosystems with a simple physical structure. Throughout, we use tropical cyclone to refer to general concepts related to these wind disturbances, and we use hurricane when describing specific cyclones in the region, including the one we studied.

**Methods**

**Study site location and hurricane**

We established 16 study sites (29°25′58.01″–29°32′16.61″N, 89°36′57.03″–89°52′55.97″W) in the lower delta region of the Mississippi River prior to passage of Hurricane Isaac. All sites were adjacent to open water of the Gulf of Mexico in Plaquemines Parish, on either side of the main channel of the Mississippi River, about 60 km from the mouth of the Mississippi River (Supplementary material Appendix 1). All sites contained salt marshes strongly dominated by salt marsh smooth cordgrass, *Sporobolus alterniflorus* (Loiseleur) P.M. Peterson and Saarela (Weakley 2015). We note that nomenclature of this grass, previously *Spartina alterniflora* Loiseleur, based on molecular data (Peterson et al. 2014a, b), has remained contentious based on long use of *Spartina* to designate this group of often dominant grasses in marsh ecosystems (Bortolus et al. 2019). Within each site, we established two 20 m transects (separated by 5 m) that extended into marsh vegetation from the edge of open water (Adams et al. 2017).

Hurricane Isaac was a low-intensity hurricane. This tropical cyclone originated off the west coast of Africa in mid-August and crossed the Atlantic, the West Indies and Florida Keys into the Gulf of Mexico. There were two landfalls in Louisiana as a large-scale category 1 hurricane with sustained winds of 36 m s\(^{-1}\) (130 km h\(^{-1}\)) on 29 August, 2012. The initial landfall was in Plaquemines Parish along the southwest channel of the mouth of the Mississippi River. Isaac then stalled for several hours before a second landfall just west of Port Fourchon in Lafourche Parish (<www.nhc.noaa.gov/archive/2012/refresh/ISAAC.shtml>). Our study plots were located in the right front quadrant of this hurricane as it made these landfalls. For approximately 12 h all our study sites experienced tropical storm/hurricane force winds and were inundated by a storm surge of 2–4 m. The vegetation structure was not greatly altered, however, because the salt marshes along the Louisiana coast were underwater during passage of the hurricane. For example, there were no gaps along our transects where vegetation in the salt marsh was uprooted.

We placed Hurricane Isaac in the context of records of tropical cyclones affecting the northern coast of the Gulf of Mexico. We used a 530 km stretch of coastline (Louisiana and Mississippi) of the North Gulf of Mexico, which includes our study sites. We obtained NOAA records (<www.coast.noaa.gov/hurricanes/> and compiled the years, intensity (Saffir–Simpson Scale) and date that each tropical cyclone crossed the coastline during the 117-yr interval between 1901 and 2017. A total of 47 tropical cyclones (cat 1–5) and 17 major tropical cyclones (cat 3–5) were included. Mean return periods within this 530 km stretch of coastline were 2.5 yr for all tropical cyclones and 6.9 yr for major tropical cyclones. Non-major cyclones comprised 64% of all tropical cyclones; the average intensity of all cyclones on the Saffir–Simpson Scale was 2.0 ± 0.18 (SE). The mean date of landfall was August 26 ± 5 d (SE). Based on these data, we consider Hurricane Isaac as a typical lower-intensity tropical cyclone making landfall along the north Gulf coast.

The timing of Isaac relative to prior hurricanes also falls within expected return periods of tropical cyclones. The last hurricane to make landfall in this area prior to Isaac was Gustav (cat 2) in 2008. The last major hurricanes, Katrina and Rita, made landfall in 2005; both hurricanes had strong storm surges that inundated the delta region containing our study sites. Because 4–7 yr had elapsed since landfalls in close proximity to our sites, we treated our initial collections as independent of prior hurricanes. We considered pre-hurricane reference samples as likely to represent salt marsh insect communities that have recovered from prior hurricanes and post-hurricane samples as representing the direct effects of the current hurricane independent of any prior hurricane.

**Methods of sampling and collection processing**

We made eight collections of insects at each of the 16 sites. The initial samples were collected five days before hurricane landfall. Post-hurricane samples were taken 3, 14, 22, 30, 35, 51 d, and one year after the hurricane. Insects were collected from the vegetation using sweep nets along the two transects...
spaced five meters apart at each site. Data from the paired transects at each site per sampling time were pooled together for analysis; sites were considered as the experimental units. Care was taken to standardize sweep net collection among the people sampling. All collections were stored in 95% ethanol until examined.

We focused on the insect communities specifically excluding non-insect arthropods such as spiders. We compiled data for analysis based on adult insects in samples, excluding juveniles. A total of 38,028 individual adult insects were collected during the course of the study; a total of 216 genera, 69 families and 10 orders were collected during the study. Of these, 14 taxa were identified to species level. The remainder were identified to genus, except for specimens damaged during collection (14 taxa were identifiable only to family). Hymenoptera and Diptera were the most diverse (number of genera and abundance) orders throughout the survey. Insects were categorized into trophic groups: herbivore, predator, parasite, and parasitoid and detritivore.

Data analysis

We compiled data for analysis based on adult insects in samples, excluding juveniles. Most insects were identified to genus level (see above). We initially examined inherent spatial autocorrelation of insect taxa among the 16 collection sites (R package ‘adespatial’, Legendre 2014). We identified no consistent site-level differences among collection periods in these analyses (Supplementary material Appendix 2). Thus, we conducted temporal tests of differences among the insect communities, assuming negligible spatial autocorrelations among sites.

Changes of α diversity and community composition

We examined α diversity of the entire insect community using the Shannon index, $H' = -\sum_{i=1}^{S} p_i \ln p_i$, where $S$ is the number of taxa recorded and $p_i$ represents the proportion of abundance for taxon $i$. This index incorporates both richness and evenness (Magurran 2004). Repeated-measures ANOVA was performed to compare the $H'$ across time periods. We also used additional repeated measures ANOVAs to assess the changes of abundance of the four most common species over time. Raw values for each time period were used instead of values rarefied to the lowest recorded abundance values as two sites had only a single insect present three days after Hurricane Isaac.

We also divided the insect community based on life history strategy to examine if the effects of Hurricane Isaac were consistent among four broad trophic groups (herbivores, predators, detritivores, and parasites/parasitoids). We explored changes in $H'$ using repeated-measures ANOVAs for each trophic group independently.

We explored how insect composition changed and/or recovered over time in the salt marsh following Hurricane Isaac. We used multivariate permutational ANOVA to examine changes in insect composition (PERMANOVA; 9999 permutations; Anderson et al. 2008, 2013). First, we created a Bray–Curtis distance matrix using the square-root transformed abundance values of individual taxon per collection. We treated the eight sample time periods as a fixed effect in the model and location (the east versus the west side of the Mississippi River) and sites within a location as random grouping factors to account for repeated measures (Anderson et al. 2008). If global differences were detected among sampling periods, we used post-hoc pairwise PERMANOVA to examine differences in community composition between individual time periods.

Replacements versus abundance differences

β diversity partitioning was used to determine if taxon replacement is the dominant pattern of insect temporal changes after the hurricane (Baselga 2010). β diversity, measurement of differences in community composition among sites and/or time periods (Anderson et al. 2011), can be partitioned into components of relative replacement and relative richness difference (Carvalho et al. 2012, Legendre 2014). These two components of β diversity can explain how communities are organized along spatial and temporal gradients. Methods proposed in Podani and Schmera (2011) and Podani et al. (2013) enable decomposing the compositional differences among communities into three complementary components: replacement (R), abundance difference (A), and similarity (S). Replacement is a measure of how frequently species are substituted along an ecological gradient. In contrast, abundance difference is a measure of how differences in species richness and/or abundance contributes to differences in β diversity. Similarity is a measure of the lack of β diversity between two sites (e.g., the degree of shared species between two sites). As we are specifically interested in how β diversity changes and sites recover following a tropical cyclone, these three indices were calculated between consecutive time periods (e.g., surveys between pre-Isaac and the third day after it landed, between the third and 14th day after the hurricane, and so on). We used a Bray–Curtis distance measure to calculate a dissimilarity index for each site (Corte et al. 2017, Vokurkova et al. 2018), and ternary plots to visualize the relative contribution of the three components of β diversity to overall differences between consecutive time periods. In the ternary plots, values of replacement, abundance difference, and similarity decide the position of each dot (representing the difference in community structure measured between consecutive time periods) in the plot. For example, dots closer to the A corner in a ternary plot indicates that differences in β diversity are mainly a product of abundance difference. Dots closer to the bottom line (A + S) suggest communities are characterized by high nestedness which occurs when species in lower richness assemblages are a subset of that in species-rich ones (see more details in Podani et al. 2013).

Temporal beta-diversity indices (TBI) were used to further explore the gain and loss of taxon. We followed the procedure in Legendre and Salvat (2015). B and C, the coefficients for calculating β diversity indices (e.g., Jaccard and Sørensen index), were computed for two consecutive time periods as
above. \( B \) is the sum of the \( b_i \) (the abundance of species \( i \) that is higher in time \( T \) than in time \( T + 1 \)) for all species, \( C \) is the sum of the \( c_i \) (the abundance of species \( i \) that is higher in time \( T + 1 \) than in time \( T \)) for all species. \( B \) and \( C \) represents the unscaled sum of species loss and gain between two consecutive periods, respectively. \( B \) and \( C \) were then divided by \((2A + B + C)\) where \( A \) is the sum of \( a_i \) (the abundance of species \( i \) that is common at both times) for all species (see more details in Legendre and Salvat 2015, Winegardner et al. 2017, Legendre 2019).

**Underlying mechanisms**

\( \beta \) diversity can also be used to infer how assembly processes change. However, changes in ‘raw’ \( \beta \) diversity can result from complex mechanisms such as changes in local (\( \alpha \)) and regional (\( \gamma \)) diversity that are not associated with underlying structuring mechanisms (Chase 2007, 2010, Kraft et al. 2011). To control for differences in \( \alpha \) diversity among habitats, we used the modified Raup–Crick metric to quantify insect community dissimilarity among sites. Species from the species pool were assigned to each site randomly and community similarity was calculated based on presence/absence data. This was repeated 9999 times to generate the null distribution. The differences between empirical and randomly generated communities estimate the degree to which observed \( \beta \) diversity deviates from the stochastic assembly. Raup–Crick dissimilarity values \( (\beta_{RC}) \) close to zero suggest that community assembly is highly stochastic, while larger absolute deviations (i.e. those close to 1 or \(-1\)) suggest that deterministic processes play stronger roles (Chase et al. 2011). Changes in community composition over time were visualized using non-metric multidimensional scaling (NMDS).

C-score, the average number of checkerboard units for all species pairs, was used to study insect distribution patterns in each time period. C-score compares patterns of co- occurrence in a focal study system against a null model produced with a random distribution (Gotelli 2000). We used a fixed row – equiprobable column algorithm because we assumed that all sites had an equiprobable chance of being occupied. A significantly higher C-score than the generated null suggests segregated distributions. In contrast, significantly smaller C-score indicate aggregated distribution (Gotelli 2000). A C-score value that is not different from the generated C-score indicates that species co-occur randomly. Rare taxa were excluded from the analysis because only presence/absence data can be used in the analysis.

PRIMER and R were used to perform all statistical analyses. Specifically, we carried out permutational multivariate analysis of variance (PERMANOVA) using the software PRIMER (ver. 6.1.18) including PERMANOVA+ (ver. 1.0.8; PRIMER-E). We used the R statistical packages (ver. 3.3.2; R Core Team) for other analyses: package ‘BiodiversityR’ for calculating Shannon index; package ‘adespatial’ for \( \beta \) diversity partitioning; R function ‘TBI’ (https://adn.biol.umontreal.ca/~numericalecology/Rcode/) for calculating temporal beta-diversity indices; R function ‘raup_crick’ (Chase et al. 2011) for calculating \( \beta_{RC} \); and package ‘EcoSimR’ for co-occurrence analysis.

**Results**

**Insect diversity and composition**

Insect diversity changed dramatically following Hurricane Isaac. The Shannon index prior to landfall was almost twice that recorded three days after the hurricane (Fig. 1, Supplementary material Appendix 3). The index then increased rapidly over time and returned to levels similar to the pre-hurricane state in just over a month after the hurricane. Richness showed a similar trend: 15.3 ± 6.3 (mean ± SE) taxa were collected at each site before Isaac landfall, and only 4.5 ± 3.4 were collected three days after the hurricane.

Substantial changes in insect abundance also occurred after the hurricane. Total abundance decreased from 200 ± 28.9 to 33 ± 12.7 individuals per site between before and three days after the hurricane. By the fourth post-hurricane sampling period, 30 d following the passage of Isaac, total abundance had increased to 198.1 ± 51.3 individuals per site, a level

![Figure 1. Diversity of marsh insects, as measured using the Shannon index, over time before and after Hurricane Isaac. Closed circles: mean Shannon index across all sites. Vertical bars: standard errors of the means. Hurricane Isaac occurred on day 0.](image)
similar to that prior to the hurricane. Patterns of changes in abundance were somewhat similar for the most common insects. As indicated in Fig. 2 and Supplementary material Appendix 4, abundance of all four most common species, two Hemiptera and two Diptera, decreased markedly post-hurricane, then increased rapidly and reached abundances similar to those present pre-hurricane by 51 d following Isaac. More details on abundances of species are present in the dataset (doi: 10.7266/N75T3J2W).

Changes in $\alpha$ diversity for herbivores and predators following Hurricane Isaac were similar to that of the entire community. Drastic decreases occurred right after the hurricane, followed by a gradual recovery (Supplementary material Appendix 5 Fig. A2, A3, Table A7, A8). However, the recovery patterns were not the same for detritovores and parasite/parasitoid groups (Supplementary material Appendix 5 Fig. A4, A5, Table A9, A10). Specifically, Shannon diversity of detritovores did not decrease after the hurricane but peaked 51 d after the hurricane, returning to pre-hurricane levels after one year. Shannon diversity of parasites/parasitoids remained constant for all collection periods, except for the last collection one year after Hurricane Isaac where diversity was higher than any previous collection.

PERMANOVA results revealed that insect community composition differed across the eight time periods of sampling (Pseudo-$F_{7,122} = 2.33$, $p = 0.002$, Supplementary material Appendix 6). Pairwise tests of adjacent time periods revealed that insect composition was dramatically different in samples taken three and fourteen days after Hurricane Isaac compared to the pre-hurricane samples ($t > 2.1$, $p < 0.04$). Insect composition returned to the pre-hurricane state in all samples from 22 d to one year after the hurricane ($t < 2.0$, $p > 0.06$).

**Replacements versus abundance differences**

Changes in insect communities throughout the study were driven mainly by abundance differences. As illustrated using ternary plots (Fig. 3), dots representing pairwise differences between samples taken before and three days after Hurricane Isaac tended to be concentrated at the A corner of the triangle, which indicate differences in insect communities over time is mainly driven by large decreases in insect abundance. Over time following the hurricane, the centroids of the dots moved away from the A corner and somewhat toward the S corner, indicating that the proportion of shared taxa between consecutive time periods increased. There was little evidence that replacement contributed to changes in composition over time. TBI analysis showed that mean gains were greater than mean losses in taxon numbers in most time periods (Fig. 4, Supplementary material Appendix 7), which further suggested taxon gain was important to the changes in insect community composition over time post-hurricane.

**Underlying mechanisms**

The relative importance of deterministic and stochastic processes controlling insect assemblages changed over time. The relative importance of stochastic processes increased immediately post-hurricane. Specifically, $\beta_{RC}$ was closer to zero ($-0.03 \pm 0.05$, mean $\pm$ SE) on the third-day post-hurricane, suggesting that stochastic processes structured insect assemblages at that time. $\beta_{RC}$ deviated from zero over subsequent periods of time (Fig. 5). This result indicated that insect communities became more similar than expected by chance, which suggested that deterministic processes became important to community assembly over time after the hurricane. The patterns of dispersion indicated by NMDS (Fig. 6a) indicated insect communities were similar prior to the hurricane, were most divergent right after the hurricane (day 3), but then re-converged within 51 d. By one year, all 16 sites had re-converged into a tight cluster resembling that prior to the hurricane (Fig. 6a). Insect communities at individual sites followed different pathways of change, however, as indicated by the different directions of change, yet ended up similar to pre-hurricane communities (Fig. 6b).
The hurricane also produced short-term differences in patterns of insect co-occurrence. Prior to the hurricane, insects tended to aggregate as indicated by an observed C-score that was lower than the generated C-score. Three days after the hurricane, the insect distribution did not differ from a random pattern. Fourteen days after the hurricane, insects again began to show patterns of aggregation (Table 1).

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Discussion

Marsh insect community dynamics in relation to hurricanes

Our study indicated that foliar insect communities in local salt marshes of coastal Louisiana had low resistance, but high resilience to a low-intensity tropical cyclone. Following landfall of Hurricane Isaac, a category 1 tropical cyclone, insect diversity declined greatly, and community composition changed markedly. During the weeks after the hurricane, populations of resident insects rapidly recolonized depopulated sites. Both $\alpha$ diversity and community composition increased over the 1–2 months after the hurricane and approached pre-hurricane states within one year. Similar changes occurred at all sites, indicating a landscape-wide pattern of low local resistance, but high resilience. Although local extirpation of some populations occurred at all sites studied, these populations survived at different places within the expansive salt marshes in southern Louisiana. Thus, regional species pools were similar pre- and post-hurricane.

High resilience of insect communities appears linked to high resistance of the salt marsh plant communities. Hurricane Isaac only transiently modified the salt marsh cordgrass that dominates coastal salt marshes in southern Louisiana. The most noticeable effect was abrasion damage of live culms, which produced new leaves within weeks after the hurricane. Also, most dead attached culms were not removed.
during the storm (Platt unpubl.). As a result, suitable habitat for dispersing insects was present at all sites within weeks.

Rapid releases by grasses may have facilitated recolonization by herbivores, and thus the reformation of trophic structure. All trophic groups showed low resistance and high resilience to Hurricane Isaac. Nonetheless, post-cyclone diversity followed distinct patterns for different trophic groups. Species at higher trophic levels likely recolonized local sites after populations in lower trophic levels recovered at those sites. For example, *Tytthus* sp. (Hemiptera, Miridae) was not detected until after its prey, planthoppers, (e.g. *Prokelisia* sp.; Hemiptera, Delphacidae) were first collected one month after the hurricane. Trophic network and stable isotope analyses might facilitate understanding how species with different diets respond to the tropical cyclones.

Persistence of hurricane disturbance by plants and insects in coastal marshes appeared to involve different combinations of resistance and resilience. The plants, with high resistance, survived storm surge inundation with limited damage and produced new leaves post-hurricane. In contrast, foliar insect diversity decreased dramatically, but Hurricane Isaac did not generate unique environmental conditions that might be more suitable for pioneer species that colonize soon after disturbances, but are replaced over time, as in succession models (cf. Platt and Connell 2003). Instead, most insects detected post-hurricane were species present in the salt marsh before the hurricane. Different populations, however, survived in different sites. At all sites, local populations quickly re-established, likely from randomly located, surviving populations or from life cycle stages (eggs, larvae, pupae) that survived the hurricane. Thus, taxon replacement was not the dominant driver of dissimilarity over time among coastal salt marsh insect communities affected by Hurricane Isaac. Similar patterns have been noted after disturbances in other ecosystems (Li et al. 2007, Robinson 2012, Feckler et al. 2018).

Low resistance and high resilience might characterize foliar insect communities in coastal marshes that experience frequent low-intensity tropical cyclones. Hurricanes and tropical storms cross Louisiana frequently; over the last century, coastal marshes in this region have experienced strong winds and storm surges on average every three years (Keim and Muller 2007, Doyle 2009, Platt et al. 2015). Thus, plants and insects indigenous to coastal marshes likely have become adapted for recurrent cyclones, but in different ways (Connell 1997, Platt and Connell 2003). We propose that high resilience of marsh insect communities might be dependent on the landscape context. Resilience resulting from random survival of local populations that serve as sources for surrounding depopulated sites should likely increase as the expansiveness of salt marshes increases. We further anticipate that salt marsh insect populations might be resilient even following more intense hurricanes, if there are broad contiguous expanses of salt marsh habitat in which local populations and/or resistant life cycle stages of resident insect species survive the disturbance. We expect that recovery times after more intense hurricanes also might be lengthened as a result of lowered densities of surviving populations, as well as reduced survival of resistant life cycle stages.

The effects of differential disturbance of salt marsh plant communities by tropical cyclones on persistence of indigenous insect communities needs study. To explore the generality of our low resistance/high resilience hypothesis, information is needed on insect populations in salt marshes of different sizes exposed to cyclones that differ in intensity and degree of damage to the vegetation. Along exposed coastlines or in estuaries, as well as inland less-saline marshes, especially during intense cyclones, vegetation may be more disrupted due to substrate deposition and erosion (Turner et al. 2006), damage and uprooting of exposed vegetation in high winds (Howes et al. 2010), and removal of dead culms that are subsequently deposited as large patches of wrack (Platt et al. 2015), especially during more intense cyclones. Such large-scale, intense disruptions of the vegetation might be expected to produce larger effects on the resident insect communities than those we observed. More intense effects might facilitate species replacements, as predicted in classical succession
Figure 6. Non-metric multidimensional scaling (NMDS) for marsh insect communities (a) in each time period, and (b) in each site. Lines and arrow in (b) indicate the direction of change over time.
Table 1. Checkerboard score (C-score) is used to measure insect co-occurrence patterns. Here shows C-score (observed, mean of simulated and variance of simulated), the probability of observed C-score smaller (o<s) and larger (o>s) than expected C-score based on fixed-equiprobable null model, and standardized effect size [SES=(observed C-score− simulated mean C-score)/standard deviation of simulated C-score] for different time periods of marsh insect communities after Hurricane Isaac.

| Period | Observed C-score | Mean of simulated C-score | Variance of simulated C-score | p (o<s) | p (o>s) | SES |
|--------|------------------|---------------------------|-------------------------------|---------|---------|-----|
| −5     | 3.946            | 4.772                     | 0.017                         | < 0.001 | 0.999   | −6.363 |
| 3      | 4.8              | 5.338                     | 0.123                         | 0.076   | 0.927   | −1.532 |
| 14     | 1.943            | 5.238                     | 0.021                         | < 0.001 | 0.999   | −9.005 |
| 22     | 3.415            | 5.691                     | 0.081                         | < 0.001 | 0.999   | −7.977 |
| 30     | 4.212            | 5.364                     | 0.096                         | 0.001   | 0.999   | −3.719 |
| 35     | 4.011            | 5.839                     | 0.12                          | < 0.001 | 0.999   | −5.275 |
| 51     | 4.147            | 4.736                     | 0.026                         | 0.002   | 0.998   | −3.629 |
| 365    | 4.494            | 6.544                     | 0.024                         | < 0.001 | 0.999   | −13.164 |

* Numbers in the first column indicate the days after Isaac.

Dispersal as a life history characteristic of insect communities exposed to hurricanes

Dispersal ability appears to be a shared life history characteristic of insects in hurricane-frequented ecosystems. Most insects cannot survive the strong winds and storm surges during a hurricane without refugia (Schowalter 2012). The physical structure of salt marsh vegetation does not provide such refuges, although insects with life cycle stages inside living or dead culms might be able to persist through storm surges. As a result, low resistance appears to characterize salt marsh foliar insect communities. Increases in diversity and abundance of foliar insects in all trophic levels occurred rapidly post-hurricane in our study, most likely a result of immigration by survivors in surrounding locations, coupled with local survival of immature life cycle stages of some species. Similar patterns have been noted in other studies (Spiller et al. 1998, Vanschoenwinkel et al. 2010).

Metapopulation, metacommunity, and island biogeography theory should provide insights into the dynamics of salt marsh insect communities in hurricane-frequented environments. Indeed, the effects of Isaac on salt marsh insects appear analogous to the defaunation treatments in experiments conducted using small mangrove islands in Florida Keys (Simberloff and Wilson 1969). In both situations, the habitat was not substantially affected by the ‘disturbance’; thus dispersal ability and distance to sources likely were the most important variables determining insect richness. A similar importance of dispersal and distance from source populations in post-disturbance colonization has been noted in other habitats as well (Platt 1975). We further suggest that unoccupied areas constitute temporal ‘sink’ patches after cyclones (sensu Leibold et al. 2004). Selection for dispersal ability thus could result in rapid regeneration of salt marsh insect communities present before the cyclone due to the resilience of regional populations.

Change of underlying mechanisms influencing community assembly

Some studies have suggested that deterministic and stochastic processes can occur in sequence after disturbances (Dent et al. 2013, Craven et al. 2015). Here, higher β diversity immediately post-hurricane accompanied random local species occurrences. These patterns indicated a stochastic structuring of insect assemblages at this time, which likely resulted from random active and haphazard passive dispersal, as also suggested by Martins et al. (2018). For instance, Incertella sp. (Diptera, Chloropidae) is one of the most numerous insects in Louisiana salt marshes (Adams et al. 2017). As indicated in Fig. 2, populations of this species decreased greatly after the hurricane, but recovery to pre-hurricane levels occurred within weeks. The re-colonization of any specific site by this species after Isaac was highly stochastic, in part due to Incertella’s broad habitat width and strong dispersal ability (E. Narchuk pers. comm.). Passive dispersal by the hurricane also might increase the randomness of species composition. For example, insects not normally found in salt marshes, such green lacewings (Chrysopidae) and coffee borer beetles (Hypothenemus sp.) were detected only right after the hurricane. These species were likely blown in from adjacent inland habitats, and they quickly disappeared (died or migrated back) by the next sampling period. Moreover, the unsaturated insect community immediately after the hurricane likely resulted in only marginally important biotic interactions (Fattorini and Halle 2004, Kreyling et al. 2011), and this may have increased the relative contribution of chance events (dispersal and random extinction) during initial colonization (Baasch et al. 2009, Maren et al. 2018).

The importance of stochastic processes on salt marsh insect communities decreased quickly over time. Although some studies have indicated that hurricanes could have long-term effects (Tanner et al. 1991) and even lead to distinct differences in community development among different locations (e.g. a nonequilibrium model, Vandermeer et al. 2004, Imbert 2018), we found that insect composition became increasingly similar among sites as insect communities reassembled during the year after the hurricane. We propose that
this observed similarity most likely was a result of the highly homogeneous environment of salt marshes, which results from the overwhelming dominance of salt marsh cordgrass. The similar plant species composition and architecture among sites appeared to act as a strong deterministic force affecting insect communities, driving convergence of assemblages and aggregation of distribution patterns. In addition, as more insect species recolonized the salt marsh vegetation, species interactions and co-occurrence networks likely were reconstructed and increased in importance over time (Spiller et al. 1998, Chang et al. 2015).

Concepts of direct regeneration

In summation, salt marsh insects showed low resistance, but high resilience to Hurricane Isaac. Post-cyclone changes in composition of the salt marsh insect communities immediately after Hurricane Isaac were consistent with a conceptual model in which hurricane-induced reductions in abundances caused substantial local loss of species and resulted in essentially stochastically driven assemblages post-hurricane (Turner et al. 1998). Community recovery appeared driven by rapid species recolonization, followed by increases in abundances of populations over the year after the hurricane. We did not detect patterns of taxon replacement, but instead observed patterns analogous to direct regeneration in plant communities, namely reformation of insect communities similar to those present before the hurricane. Unlike the salt marsh plant community, however, reformation of insect communities appeared to depend on colonization from a regional pool of species that survived the hurricane in various life cycle stages at locations scattered across the overall region. In this sense, we expand the concepts that underlie direct regeneration, as developed for forests (Boucher 1990, Boucher et al. 1990, 1994, Yih et al. 1991, Vandermeer et al. 2000, 2001, Dietze and Clark 2008). We propose that direct regeneration of assemblages of species similar to those present before hurricane can result either from high resistance of species present or high resilience of species that survive at different locations within dispersal range. In this context, direct regeneration of foliar insect communities might be more likely within larger than smaller marsh landscapes. We note that such direct regeneration via immigration from the regional species pool does not involve invasion (sensu Davis et al. 2005) or species replacement (sensu Platt and Connell 2003).

We expect similar community dynamics in other systems that experience relatively frequent, non-destructive disturbances and that host large regional populations of organisms with high dispersal ability. We caution that our results represent insect community responses after a low-intensity Category 1 hurricane that crossed a broad expanse of coastal marshes. It would be interesting to examine the responses of insects (and other mobile organisms) to stronger tropical cyclones, which are predicted to happen more frequently in the future as a result of global climate change (Webster et al. 2005, Elsner et al. 2008, Bender et al. 2010). In addition, it would be interesting to explore the responses of insect communities in different habitats. For example, responses of insects post-hurricane in more diverse coastal savannas, especially those whose plant communities are differentially damaged (Howes et al. 2010) or affected by hurricane wrack (Platt et al. 2015), might be more complex than the responses we observed in the less diverse and more uniform salt marshes.

Data availability statement

Data available from Gulf of Mexico Research Initiative Information and Data Cooperative (GRIIDC), Harte Research Inst., Texas A&M University-Corpus Christi: doi: 10.7266/N75T3J2W (Bui 2018).

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Supplementary material (available online as Appendix ecog-04923 at <www.ecography.org/appendix/ecog-04932>). Appendix 1–7.