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Homogenizing an urban habitat mosaic: arthropod diversity declines in New York City parks after Super Storm Sandy

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Abstract. The frequency and intensity of hurricanes are increasing globally, and anthropogenic modifications in cities have created systems that may be particularly vulnerable to their negative effects. Organisms living in cities are exposed to variable levels of chronic environmental stress. However, whether chronic stress ameliorates or exacerbates the negative effects of hurricanes remains an open question. Here, we consider two hypotheses about the simultaneous consequences of acute disturbances from hurricanes and chronic stress from urbanization for the structure of urban arthropod communities. The tipping point hypothesis posits that organisms living in high stress habitats are less resilient than those in low stress habitats because they are living near the limits of their environmental tolerances; while the disturbance tolerance hypothesis posits that high stress habitats host organisms pre-adapted for coping with disturbance, making them more resilient to the effects of storms. We used a before-after-control-impact design in the street medians and city parks of Manhattan (New York City, New York, USA) to compare arthropod communities before and after Super Storm Sandy in sites that were flooded and unflooded during the storm. Our evidence supported the disturbance tolerance hypothesis. Significant compositional differences between street medians and city parks before the storm disappeared after the storm; similarly, unflooded city parks had significantly different arthropod composition while flooded sites were indistinguishable. These differences were driven by reduced occurrences and abundances of arthropods in city parks. Finally, those arthropod groups that were most tolerant to urban stress were also the most tolerant to flooding. Our results suggest that the species that survive in high stress environments are likely to be the ones that thrive in response to acute disturbance. As storms become increasingly common and extreme, this juxtaposition in responses to storm-associated disturbance may lead to diversity loss in cities, potentially leading entire urban landscapes to mirror the reduced diversity of street medians.

Key words: biotic homogenization; disturbance adapted; diversity; extreme weather; hurricane; New York City; Super Storm Sandy; tipping point; urban ecology.

Introduction

The frequency and intensity of extreme weather events are increasing globally, likely due to anthropogenic activities (Gao et al. 2012, Lubchenco and Karl 2012, Goodess 2013, Cai et al. 2014, Holland and Bruyére 2014, Fischer and Knutti 2015, Herring et al. 2015, Easterling et al. 2016). The effects of these high-intensity, acute disturbances can be dramatic. For example, Hurricane Katrina caused ~1,500 human deaths and an economic burden of US$108 billion in Louisiana, USA (Blake and Ginbney 2011). The storm additionally caused declines ranging from 45% to 100% in resident bird populations (Yaukey 2008), a fourfold increase in tree mortality (Chapman et al. 2008), and ~40% decline in local herpetofauna populations (Schriver et al. 2009).

Consequences of the increased frequency and intensity of extreme weather events, and especially hurricanes, are likely to be particularly strong for organisms living in urban ecosystems. Cities are among the only habitats on the planet that are currently expanding (Grimm et al. 2008), and much of this expansion is concentrated along ocean coasts (Neumann et al. 2015). An added complexity of these important systems is that they rely on not only natural inputs, but also direct inputs from humans, which are often poorly measured or difficult to measure. Anthropogenic modifications to cities have created systems that may be particularly vulnerable to the effects of

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hurricanes. Cities are dominated by impervious surfaces (Rosenweig et al. 2006), blocks of tall buildings that can act as wind tunnels (Blocken and Carmeliet 2004), and relatively sparse storm-buffering vegetation (Watson and Adams 2011). Diversity and ecosystem services in cities are potentially vulnerable to hurricane-related acute disturbance, but we still have no framework for predicting which organisms are sensitive to the effects of hurricanes. This lack of knowledge is problematic, because without it we cannot make general predictions about the responses of diversity and ecosystem services to extreme weather. We do know that organisms living in different habitats in cities are exposed to variable levels of chronic environmental stress. High stress habitats, such as street medians, are smaller, hotter, drier, have less leaf litter, and have higher levels of pollutants than habitats with lower stress, such as city parks (Savage et al. 2014; A. M. Savage, *unpublished data*). It is reasonable to expect that the degree of exposure to chronic environmental stress will influence the responses of urban communities to the acute disturbances associated with hurricanes. Whether chronic stress ameliorates or exacerbates the negative effects of hurricanes remains an open question.

Here, we consider two hypotheses about the simultaneous consequences of acute disturbances from hurricanes and chronic stress from urbanization for the structure of ecological communities in cities. First, environments with high levels of chronic urban stress may be populated by organisms that are living near the edge of their environmental tolerances, making them less resilient to the effects of extreme weather events than organisms living in lower stress urban environments (hereafter, "tipping point hypothesis"). Alternatively, high levels of chronic stress may act as environmental filters, such that stressed habitats host only organisms that possess adaptations for coping with high levels of disturbance. In this case, organisms in high stress environments will be more resilient to the effects of extreme weather than those living in lower stress habitats (hereafter, "disturbance tolerance hypothesis").

In this study, we examined litter arthropod communities in Manhattan (NYC) before and after Super Storm Sandy. Manhattan is home to habitats ranging from heavily stressed street medians on Broadway, with little more than 1 m of dirt above the subway that runs below them and four lanes of traffic surrounding them, to the old forests of Inwood Hill Park. These habitats are best described as an urban habitat mosaic rather than a simple stress gradient. Our previous studies showed that variation in the richness and composition of ant species was associated with this fine-scale heterogeneity (Savage et al. 2014). Super Storm Sandy, a hurricane that coincided with a storm surge, made landfall in Manhattan on 29 October 2012. While flooding only affected the southern part of the island, high winds, heavy rainfall, and intensive clean-up efforts were common throughout Manhattan. Because we sampled not only ants, but all litter arthropods across this chronic stress gradient just before Super Storm Sandy (August 2012), we were uniquely poised to assess the interactive effects of acute disturbance (from extreme weather) and chronic stress (from urbanization) on local arthropod communities.

We tested the contrasting predictions of the tipping point and disturbance tolerance hypotheses using a before-after-control-impact design. Specifically, we identified sites with high and low levels of chronic environmental stress before the hurricane (in street medians and city parks, respectively) and sampled litter arthropod communities just before Super Storm Sandy (late August 2012) and in the late spring after Super Storm Sandy (mid-May to early June 2013). While all sites experienced the extreme weather event, the most intense aspect of the storm, flooding, only occurred in a subset of our sites. Thus, in the control-impact portion of the study, we examined litter arthropod diversity at flooded and unflooded sites.

We considered the following specific questions, for which the tipping point and disturbance tolerance hypotheses have opposite predictions. First we asked (1) How does the structure of local arthropod communities in street medians and city parks compare before and after Super Storm Sandy? The tipping point hypothesis predicts that post-storm arthropod composition would shift more dramatically in street medians than in city parks after a hurricane; the disturbance tolerance hypothesis predicts that arthropod composition would change the most in city parks. We were also interested in the effects of fine-scale variation in storm intensity on the responses of local arthropod communities to Super Storm Sandy. Consequently, we asked (2) How does the composition of arthropod communities compare in street medians and city parks that were flooded vs. those that were unflooded during Super Storm Sandy? The tipping point hypothesis predicts that the flood would have negligible effects in city parks, but strong negative effects in street medians; the disturbance tolerance hypothesis makes the opposite prediction. Finally, while they make opposite predictions, both the tipping point and disturbance tolerance hypotheses suggest that tolerance (or lack thereof) to high levels of chronic environmental stress may be used to predict which arthropod groups are likely to be most vulnerable to the effects of acute disturbance. Therefore, we asked (3) Can pre-storm tolerance to urban stress be used to predict the vulnerability of arthropod groups to flooding during extreme weather events? The tipping point hypothesis predicts that those arthropods with higher abundances in street medians relative to city parks would be the most vulnerable to flooding from hurricanes since they are already living near the limits of their environmental tolerances; while the disturbance tolerance hypothesis predicts that it is the arthropods with the highest abundances in parks relative to street medians that will be most vulnerable to flooding from hurricanes.

Methods

Study sites

The sites in this study were all located in Manhattan, New York (USA). Manhattan is the most urbanized borough of the most urban city in the United States. Manhattan is home to 39,667 people/km^2, which is more than 1,100× higher than the U.S. national average human density of 35 people/km^2 (World Population Review 2017). Manhattan is also dominated by human infrastructure, with >90% impervious surface on the ground (Rosenweig et al. 2006) and ~3× more space in the indoor biome than is covered by actual geographical land area (Martin et al. 2015). Super Storm Sandy is the second deadliest hurricane recorded in New York, and it caused 53 human deaths. Although it was downgraded from hurricane to tropical storm status when it made landfall on the northeast coast of North America, Hurricane Sandy was upgraded to "super storm" status because a storm surge occurred at the same time (Galarneau et al. 2013). The most recent models based on sedimentary evidence indicate that other extreme weather events of similar magnitude are likely to occur more frequently in NYC than original projections of return intervals (~900–1,600 yr) for storms originally suggested (Brandon et al. 2015).

Detailed descriptions of the sites sampled in 2012 and 2013 can be found in Savage et al. (2014) and Youngsteadt et al. (2015), respectively. Briefly, we sampled 14 street medians and 18 sites in city parks in 2012 (although we considered parks managed as forests and parklands separately in Savage et al. 2014, we consider them together in this study), and 29 street medians (n = 14 flooded and 15 unflooded) and 30 sites in city parks (n = 11 flooded and 19 unflooded) in 2013 (Fig. 1).

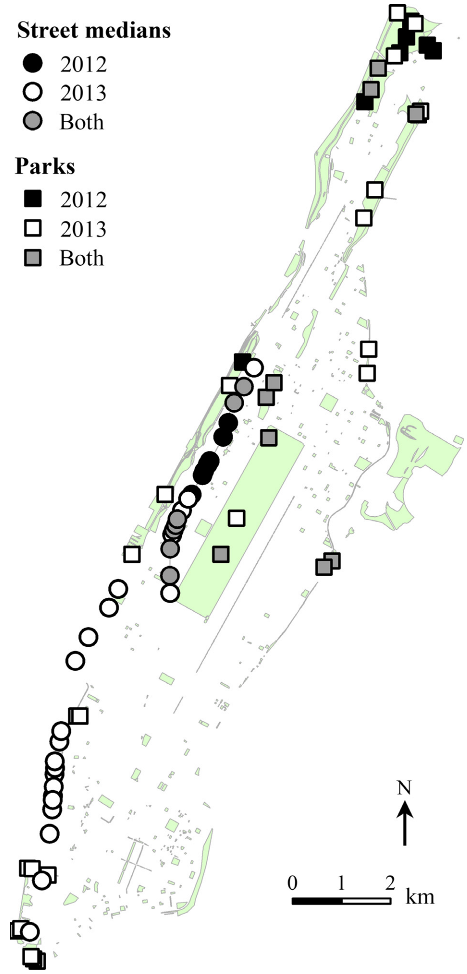

Fig. 1. Map of our study sites in Manhattan. Squares represent sites that were sampled in 2012 and circles represent sites that were sampled in 2013. Square symbols represent city parks, while circles represent street medians; black symbols represent sites that were sampled in 2012, white symbols 2013, and gray symbols both years. [Color figure can be viewed at wileyonlinelibrary.com]

Field sampling protocols

We sampled the ground-foraging arthropod community using the Winkler extraction method in August 2012 and June 2013 (Agosti and Alonso 2000). However, there were small differences in the collection methods among years. In 2012, we delineated sampling areas 5 × 50 m across parks and street medians. The size of sampling areas were determined based on the average dimensions of Broadway medians (Savage et al. 2014). We collected 1 L of sifted leaf litter and ground debris using a Winkler sifter (4 mm mesh, used in both years) across the entire sampling area. Similarly, we collected 1 L of leaf litter in 2013; however, the dimensions of the sampling areas were smaller, due to the inclusion of medians from West Street. In 2013, we collected litter every 4 m along a 20 × 5 m transect at each site. We immediately sifted the litter in the field and transferred the sifted material to a litter bag, which was securely tied. We then transferred 1 L of the sifted litter into mesh bags that were hung inside a Winkler extractor with a cup containing 95% ethanol securely tied to the base. We tied the Winkler extractors closed and left them for 48 h, when we extracted arthropods and stored them in 95% ethanol. We sorted and identified arthropods from these samples in the laboratory. We sorted all arthropods to the order level; we identified Diplura, Collembola, Diptera, Hymenoptera, Hemiptera, and Coleoptera to family level, and ants to the species level.

Statistical evaluations

How does the structure of local arthropod communities in street medians and city parks compare before and after Super Storm Sandy?.—We compared within-site (α) compositional diversity of arthropod communities before and after Super Storm Sandy at the order level (with orders of millipedes and centipedes pooled). In 2012, we did not sample sites in southern Manhattan. Therefore, we excluded 2013 samples from southern Manhattan for these between-years comparisons. We created a matrix of order-level abundances per site per year. We transformed the abundances using square roots to reduce bias towards hyper-abundant orders (especially Collembola). We then constructed a Bray-Curtis dissimilarity matrix for the transformed values. To visualize the relative dissimilarity of sites across year × site type combinations, we next created a non-metric multidimensional scaling plot, with 100 restarts and a Type II Kruskal fit scheme using this dissimilarity matrix. We then conducted two pairwise PERMANOVAs. The first examined compositional differences between parks and street medians in 2012 (before Super Storm Sandy) and the second examined compositional differences between parks and street medians in 2013 (after Super Storm Sandy). We applied a sequential Bonferroni adjustment to our α for these tests, because we conducted two separate tests. Thus, of the two PERMANOVA tests we conducted, the more significant result had to have $P < 0.025$ to be considered significant, while the less significant result had to have $P < 0.05$ to be considered significant. We used SIMPER analyses to identify the orders that contributed to ~90% of differences among sites in the order abundance matrix.

How does the structure of arthropod communities vary in street medians and city parks that were flooded vs. those that were unflooded during Super Storm Sandy?—We compared within-site compositional diversity of sites flooded and unflooded during Super Storm Sandy at the family level. We removed all singletons and doubletons from the data matrix. After this filtering, we collected 14,731 arthropods, with ~98% of all individuals representing just 10 families (29% of all families). Therefore, we conducted separate analyses for the ten most numerically dominant families and for the remaining numerically subordinate families (Appendix S2, S3).

While we selected street median and park sites in both southern and northern Manhattan, flooding occurred primarily in the sites in southern Manhattan. Therefore, before conducting analyses of arthropod community structure, we first performed two-tailed Mantel tests using 9,999 iterations in PASSaGE v. 2 software (Rosenberg and Anderson 2011) to detect spatial autocorrelation in our community matrices. We conducted Mantel tests separately for numerically dominant and subordinate families. If the Mantel test indicated that spatial autocorrelation was present in the data, we performed Partial Mantel tests, with flooding held constant to determine if spatial autocorrelation was still present in the data when the effects of flooding during Super Storm Sandy were removed.

We performed analyses of compositional α-diversity as described above for our assessments of arthropod communities before and after Super Storm Sandy. Finally, we examined among-site (β) compositional diversity of arthropod communities before and after Super Storm Sandy. To do this, we transformed the density matrix into a presence-absence matrix, constructed a Bray–Curtis dissimilarity matrix, and performed PERMDISP for all combinations of year and site type (with distance to centroid as an estimate of β-diversity and 9,999 iterations). We again applied sequential Bonferroni adjustments for these tests. All analyses were conducted in Primer-E v. 7.0.9 with PERMANOVA +1 extension (Anderson et al. 2008).

Can pre-storm abundances in high vs. low stress urban environments be used to predict the vulnerability of arthropod groups to flooding?—We assessed the relationship between arthropod abundances in habitats with high vs. low levels of chronic environmental stress and arthropod abundances in flooded vs. unflooded sites at the order, family, and species levels. The orders and families were as described above. We had previously published data suggesting that ant species composition varies across urban habitat mosaics in Manhattan (Savage et al. 2014). Therefore, we used ants to assess this relationship at the species level. For each taxonomic grouping that occurred in both 2012 and 2013, we calculated the difference in abundance (1) between parks and street medians in 2012 (abundance in parks minus abundance in street medians; the lower the value, the more "median-tolerant" the organism) and (2) between flooded and unflooded sites in 2013 (abundance in all unflooded sites minus abundance in all flooded sites; the lower the value, the more "flood-tolerant" the organism). Next, we conducted Spearman rank correlations between these two tolerance measures. Because we conducted three Spearman correlations, we applied a sequential Bonferroni adjustment to our α. Thus, the most significant result had to have a $P < 0.05/3 = 0.0167$, the result with intermediate significance had to have a $P < 0.05/2 = 0.025$, and the least significant result had to have a $P < 0.05$ to be considered significant for the correlations. We used SAS v. 9.4 (SAS Institute, Cary, North Carolina, USA) to conduct the correlations.

Results

How does the structure of local arthropod communities in street medians and city parks compare before and after Super Storm Sandy in high vs. low stress sites?

Super Storm Sandy obscured the existing ecological gradients in the city in terms of the order-level composition of arthropods, with the direction of this effect supporting the predictions of the disturbance tolerance hypothesis. Specifically, significant compositional differences in arthropod communities living in city parks vs. those living in street medians before Super Storm Sandy (Fig. 2A, B; Appendix S1: Table S1, pairwise PERMANOVA: $P_{\text{Site type}} = 0.01$, $\alpha = 0.025$) were no longer apparent after the storm (Fig. 2A, C; Appendix S1: Table S1, pairwise PERMANOVA: $P_{\text{Site type}} = 0.10$, $\alpha = 0.05$).

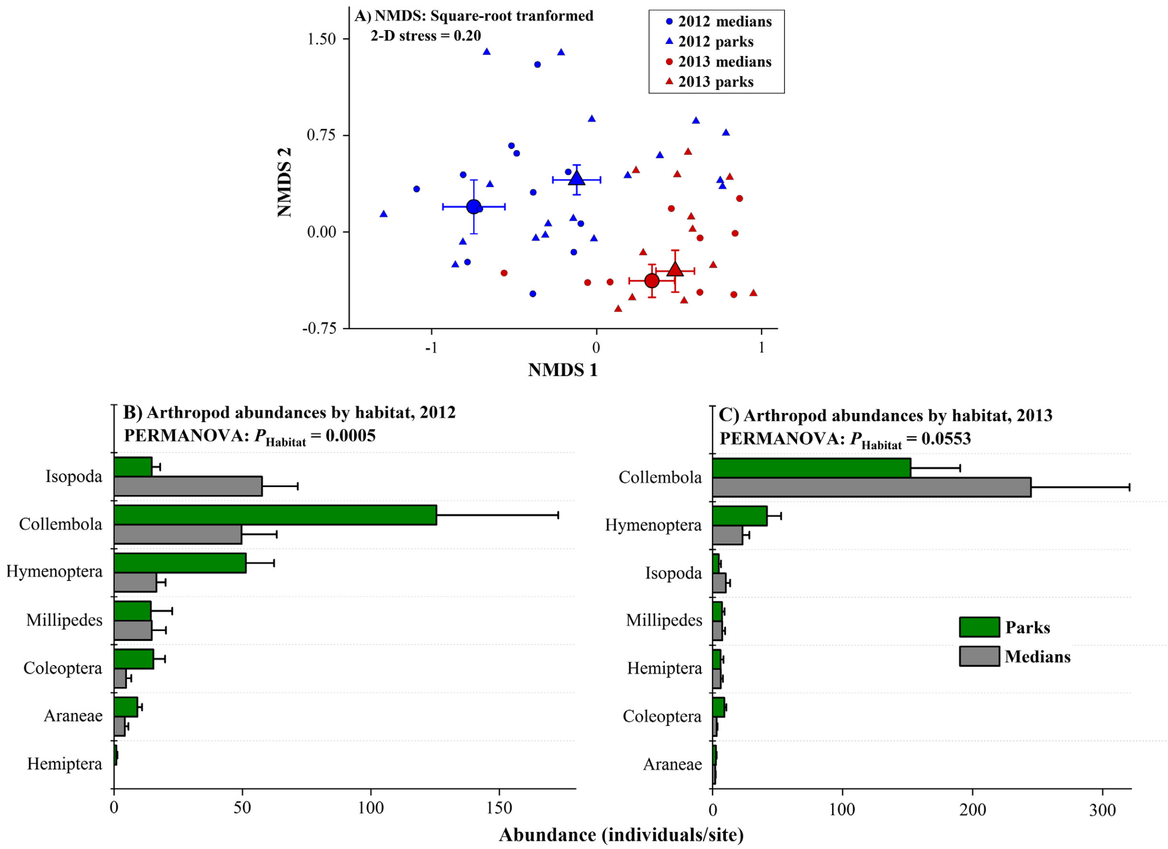

Fig. 2. Comparisons of arthropod communities at the order level before and after the storm in city parks and street medians. (A) Arthropod communities in city parks were significantly different before Super storm Sandy, but indistinguishable after the storm. (B) In 2012, arthropods living in city parks significantly differed from those in street medians. (C) In 2013, differences between city parks and street medians were no longer significant. Green bars represent average abundances of each order in city parks, gray bars represent average abundances of each order in street medians, and error bars represent SE. [Color figure can be viewed at wileyonlinelibrary.com]

Overall, arthropod groups in parks tended to have lower abundances after the storm, while those in street medians were either more abundant or relatively unaffected by the storm. Several groups that were more abundant in city parks than street medians before the storm became less abundant in parks after the storm. For example, Hymenoptera (ants, bees, and wasps) went from being 3.1× more abundant in city parks than in street medians before the storm (post hoc test: $P = 0.02$) to only 2.4× more abundant in city parks (post hoc test: $P = 0.09$) after the storm and Coleoptera (beetles) dropped from 3.3× before the storm (Post-hoc test: $P = 0.06$) to 2.1× more abundant in parks after the storm (Post-hoc test: $P = 0.09$). Super Storm Sandy actually reversed the abundance patterns for Collembola. Before the storm they were 2.5× more abundant in city parks (Post-hoc test: $P = 0.19$); after the storm, they were 1.5× more abundant in street medians than in city parks (Post-hoc test: $P = 0.31$). Before the storm, Hemiptera (true bugs) were absent from our samples of street medians, but present in our park samples (post hoc test: $P = 0.01$) However, Hemiptera were found in both street medians and city parks after the storm. While highly variable, Hemiptera were 4.3× more abundant in parks than in medians after the storm (post hoc test: $P = 0.08$). Not all arthropod groups had higher abundances in city parks than in street medians before the storm. Isopods (pill bugs) were 3.9× more abundant in street medians than in city parks before Super Storm Sandy (post hoc test: $P = 0.01$) and approximately 2 × more abundant in street medians than in city parks after the storm (post hoc test: $P = 0.14$; Fig. 2B, C; Appendix S1: Table S2).

How does the composition of arthropod communities compare in street medians and city parks that were flooded vs. those that were unflooded during Super Storm Sandy?

Before assessing arthropod communities in street medians and city parks that were flooded vs. those that were unflooded during Super Storm Sandy, we first tested for spatial autocorrelation in flooded and unflooded sites for both numerically dominant and subordinate families. Spatial autocorrelation existed for numerically subordinate families. However, once we accounted for whether or not a site was flooded, spatial autocorrelation disappeared, which is to say autocorrelation was due to our variable of interest. As a result, all analyses below do not explicitly account for space (Appendix S2).

Numerically dominant families.—While numerically dominant families exhibited an overall reduction in abundance at flooded sites relative to unflooded sites, we did not detect a strong signal of site type on their abundance or occurrence patterns with respect to flooding. In other words, numerically dominant organisms did not provide strong support for either the tipping point hypothesis or the disturbance tolerance hypothesis, each of which predicted differential effects of flooding in city parks and street medians. In unflooded sites, the within-site composition of numerically dominant families was significantly different between street medians and city parks (Fig. 3A; Appendix S3: Table S1, pairwise PERMANOVA: $P_{\text{Site type}} = 0.01$, $\alpha = 0.025$). Three families were responsible for 63% of the differences among city parks and street medians: Formicidae (ants) and two families of springtails (Entomobriidae and Isotomidae). Ants and isotomids were 2.2× and 8.3× more abundant in unflooded city parks than in unflooded street medians, respectively; while entomobriids were 9.6× more abundant in unflooded street medians than they were in unflooded city parks (Fig. 3B inset; Appendix S3: Table S2). With the exception of aphids, all other numerically dominant families had higher abundances in city parks than in street medians before the storm (Fig. 3B; Appendix S3: Table S2).

Abundance patterns for numerically dominant families in flooded city parks and street medians were mostly similar to the abundance patterns that we detected in unflooded sites (Fig. 3A, pairwise PERMANOVA $P_{\text{Site type}} = 0.006$, $\alpha = 0.0167$). Ants, entomobriids, and

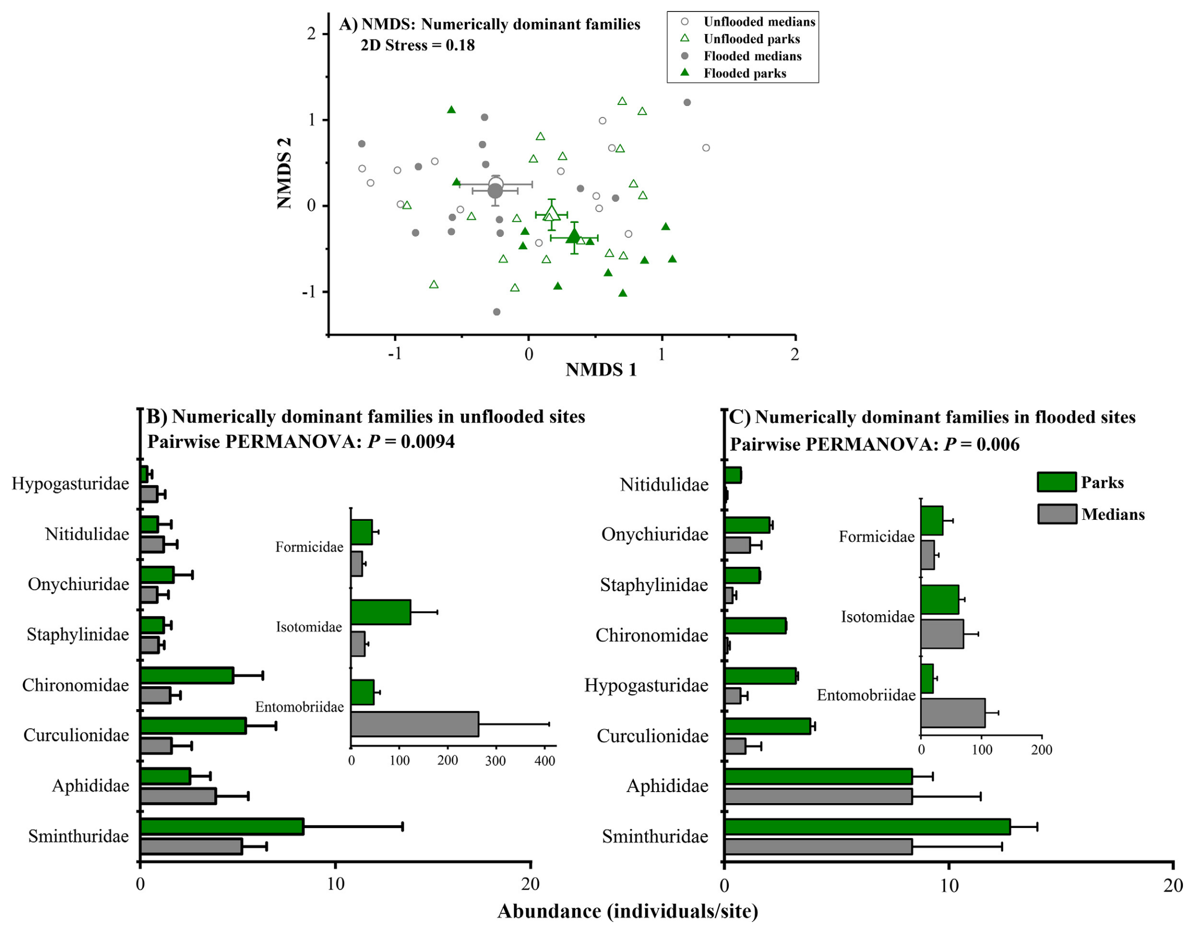

FIG. 3. Comparisons of numerically dominant arthropod families in city parks and street medians that were flooded and unflooded during Super Storm Sandy. (A) Differences in the composition of numerically dominant families in city parks compared to street medians were significant in both flooded and unflooded sites. (B) Relative abundances of numerically dominant families in sites that were not flooded during Super Storm Sandy. (C) Relative abundances of numerically dominant families in sites that were flooded during the storm. Green bars represent average abundances of each order in city parks, gray bars represent average abundances of each order in street medians, and error bars represent SE. [Color figure can be viewed at wileyonlinelibrary.com]

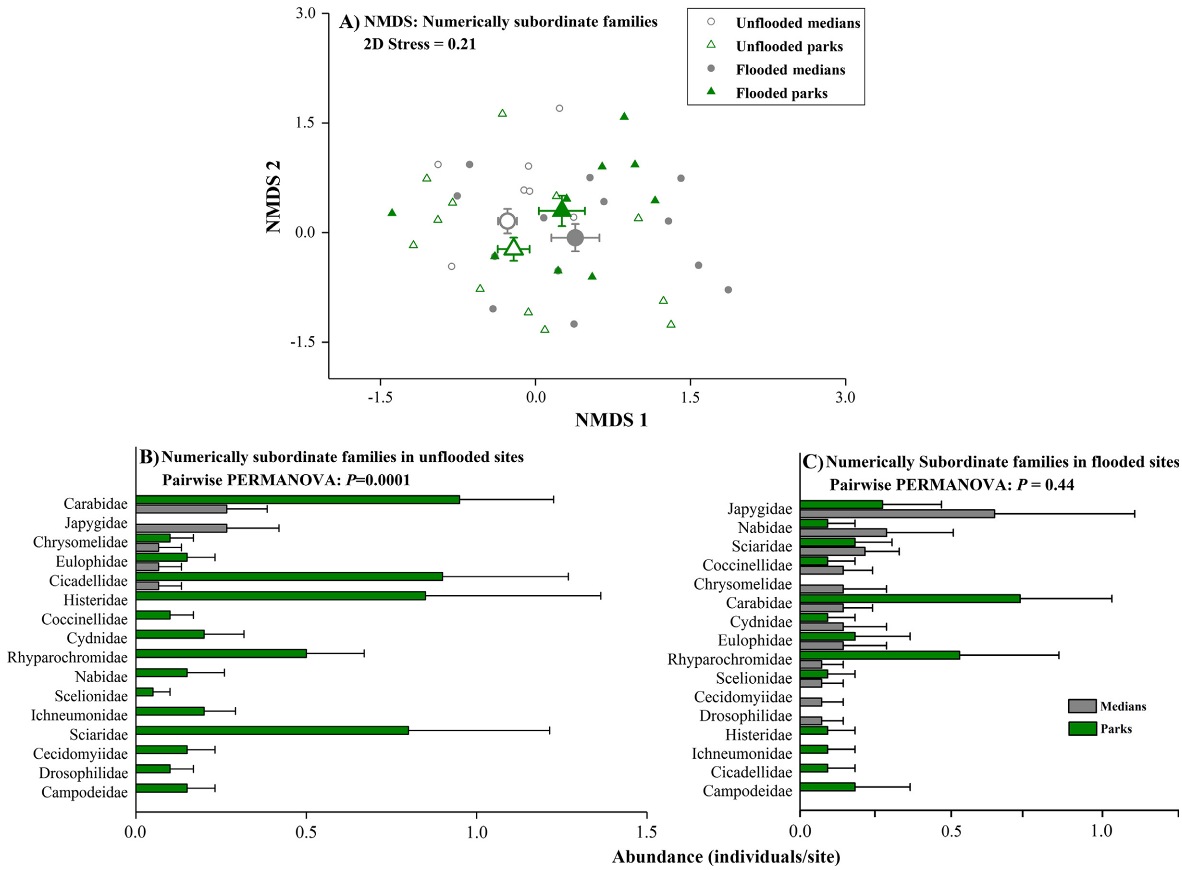

FIG. 4. Comparisons of numerically subordinate arthropod families in city parks and street medians that were flooded and unflooded during Super Storm Sandy. (A) Differences in the composition of numerically dominant families in city parks compared to street medians were significant in unflooded sites, but not in flooded sites. (B) Relative abundances of numerically subordinate families in sites that were not flooded during Super Storm Sandy. (C) Relative abundances of numerically subordinate families in sites that were flooded during the storm. Green bars represent average abundances of each order in city parks, gray bars represent average abundances of each order in street medians, and error bars represent SE. [Color figure can be viewed at wileyonlinelibrary.com]

isotomids were responsible for 58% of the significant differences that we detected between flooded parks and medians. Ants were 2× more abundant in flooded city parks than they were in flooded street medians; meanwhile, entomobriids were 3.7× were abundant in flooded street medians than in flooded city parks. However, isotomids actually had dramatically different patterns of relative abundances in flooded and unflooded sites; in flooded sites, they were 2.7× more abundant in street medians than in city parks: the opposite trend from that in unflooded sites (Fig. 3C inset; Appendix S3: Table S2). Finally, while other groups had smaller absolute abundances than Formicidae, Isotomidae, and Entomobriidae, the differences in their relative abundances was consistently larger in flooded than in unflooded sites (again, with the exception of Aphids; Fig. 3C; Appendix S3: Table S2).

For numerically dominant families, the β-diversity (measured as the differences in composition among sites) among street medians did not differ from that among city parks, regardless of whether they were flooded or unflooded (Fig. 5A, PERMDISP: $P_{\text{Site type}\times\text{flooding}} = 0.31$, $\alpha = 0.05$).

Numerically subordinate families.—Abundance and occurrence patterns for numerically subordinate families were much more striking than those of numerically dominant families. Composition of these families differed between parks and street medians only in unflooded areas. As predicted by the disturbance tolerance hypothesis, flooding reduced park diversity to median-like levels. In unflooded sites, numerically subordinate family composition within street medians strongly differed from that in city parks (Fig. 4B, pairwise PERMANOVA: $P_{\text{Site type}} = 0.0001$, $\alpha = 0.0125$, Appendix S3: Table S3). Overall, ~70% of all numerically subordinate families were absent from unflooded street medians but present in unflooded city parks, and only one numerically subordinate family was present in unflooded street medians but absent in unflooded city parks (Japigidae [diplurans], Fig. 4B). Five families contributed to 62% of differences in composition of numerically subordinate families in unflooded city parks compared to unflooded street medians: Carabidae (ground beetles) and Cicadellidae (leaf hoppers) were ~2.6× and 5.5× more abundant in unflooded city parks than in unflooded street medians, respectively; while Rhyparochromidae (seed bugs), Sciaridae (dark-winged fungus gnats), and Histeridae (clown beetles) were absent from street medians, but were relatively abundant in city parks (Fig. 4B; Appendix S3: Table S4).

In contrast, there were no significant differences in the within-site composition of numerically subordinate families in flooded street medians and city parks (Fig. 4C, pairwise PERMANOVA: $P_{\text{Site type}} = 0.44$, $\alpha = 0.05$). Both reduced abundance of numerically subordinate families in city parks and increased abundance of these families in street medians drove this pattern. Overall, only 25% of all numerically subordinate families were present in city parks, but absent in street medians (compared with 70% in unflooded sites); while 19% of all numerically subordinate families were absent from city parks, but present in street medians (compared with 6.25% in unflooded sites). Additionally, 67% of the numerically subordinate families that were present in flooded city parks had higher abundances in unflooded city parks (range: 1.1–9.9× higher in unflooded parks than in flooded parks, mean: 4.7 ± 1.6).

β-diversity (measured as the differences in composition among sites) of numerically subordinate families differed significantly across all flooding × site type designations (Fig. 5B, PERMDISP: $P_{\text{Site type} \times \text{flooding}} = 0.01$, $\alpha = 0.05$). Significant differences in β-diversity among unflooded city parks and that of unflooded or flooded street medians (Post-hoc pairwise comparison: $P = 0.0001$ and $P = 0.03$, respectively) drove this difference in β-diversity. However, there were no significant differences between the β-diversity of flooded city parks and unflooded city parks or street medians, regardless of flooding status. Additionally, the β-diversity in street medians did not significantly differ between flooded and unflooded sites (Post-hoc pairwise comparisons $P > 0.05$ for all). The lack of differences between flooded city parks and street medians in terms of species turnover was largely driven by the changing patterns of family occurrences in these habitats described above. Thus, flooding in city parks made them as depauperate as street medians.

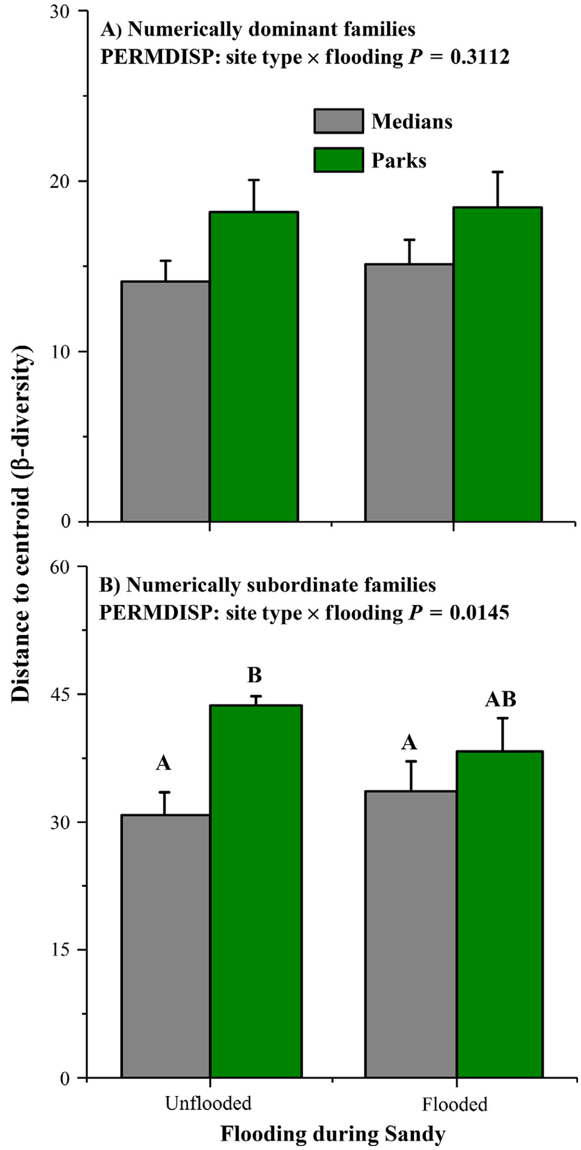

FIG. 5. (A) Among-site β-diversity of arthropod communities in flooded and unflooded city parks and street medians. There were no significant differences in the β-diversity of numerically dominant families. (B) Unflooded city parks had higher β-diversity of numerically subordinate families than both flooded and unflooded street medians, but flooded city parks did not. Error bars represent ± 1SE of the mean. Different letters denote statistically significant differences among groups (α=0.05).[Color figure can be viewed at wileyonlinelibrary.com]

Can pre-storm tolerance to urban stress be used to predict the vulnerability of arthropod groups to flooding during extreme weather events?

Arthropod orders and families that were the most median-tolerant in 2012 were also the most flood-tolerant in 2013. For ant species, the same pattern was evident as a non-significant trend. There was a strong, positive association between the differences in the abundances of orders measured in 2012 and 2013 ($n = 10$, Spearman rank correlation: $r = 0.78$, $P = 0.007$, $\alpha = 0.0167$; Fig. 6A, Appendix S4: Table S1). Those orders that were more abundant in city parks than in street medians in 2012 were the same orders that were more abundant in unflooded sites than in flooded sites in 2013 (Appendix S4: Table S1). The most abundant groups had the strongest patterns. Of the three most abundant groups, Collembola and Hymenoptera were ranked as highly median and flood intolerant, while isopods were ranked among the most median- and flood-tolerant orders. However, Coleoptera and Araneae were also ranked as both median and flood intolerant and their abundances were relatively low. Similarly,

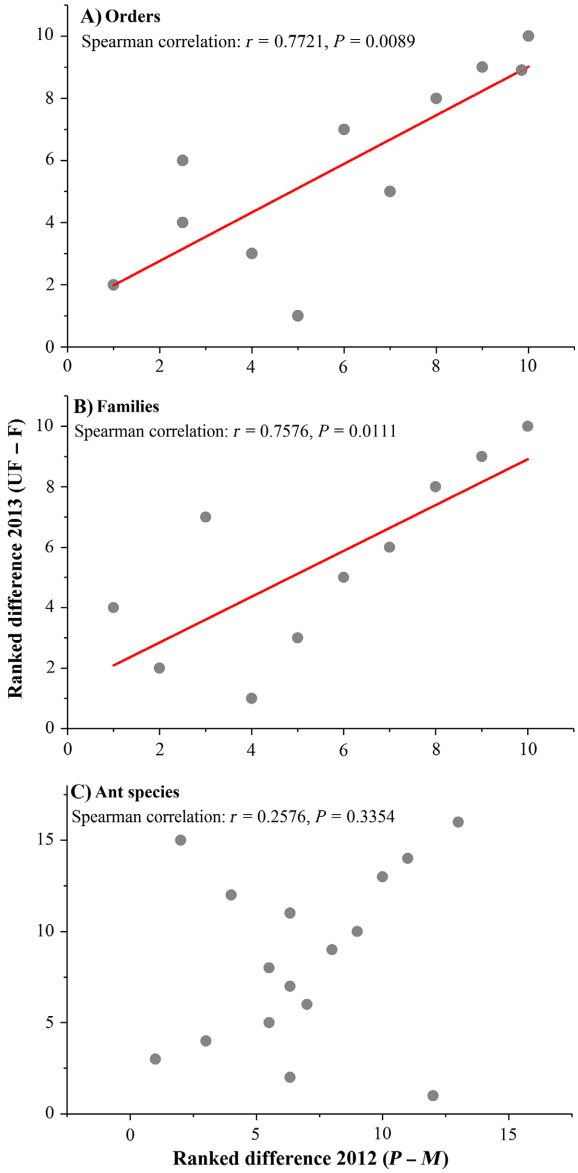

FIG. 6. Ranked correlations between "median tolerance" and "flood tolerance" at the (A) order, (B) family, and (C) ant species level. There was a positive relationship between median tolerance and flood tolerance at both the order and family levels, and a non-significant, but positive trend for ant species. UF, unflooded; *F*, flooded; *P*, parks; *M*, Medians. [Color figure can be viewed at wileyonlinelibrary.com]

Thysanoptera and Lepidoptera had relatively low abundances, but were ranked as both median and flood tolerant (Table 1). There was a significant, but weaker, positive association between the differences in family abundances measured between city parks and street medians in 2012 and those measured between unflooded and flooded sites in 2013 ($n = 10$, Spearman rank correlation: $r = 0.72$, $P = 0.02$, $\alpha = 0.0250$; Fig. 6B, Table 1). Patterns at the family level were similar to those at the order level. There was not a significant correlation between the differences in ant species abundances measured between city parks and street medians in 2012 and those measured in unflooded and flooded sites in 2013 ($n = 15$, Spearman rank correlation: $r = 0.34$, $P = 0.22$, $\alpha = 0.05$; Fig. 6C, Appendix S4: Table S2). However, those ant species that had much higher abundances in city parks than in street medians in 2012 also had much higher abundances in unflooded sites than in flooded sites in 2013 (Fig. 6C, Appendix S4: Table S3). The exception to this pattern is *Tapinoma sessile*, which was absent from all street medians in our 2012 samples. This species is a tramp ant, which is often found in association with humans (Salyer et al. 2014). In general, ant species varied more with respect to flood tolerance than for median tolerance (Fig. 6C, Appendix S4: Table S3).

DISCUSSION

In this study, we examined the relationship between the chronic environmental stress associated with urbanization and the acute disturbances associated with hurricanes for arthropod communities in Manhattan. We evaluated two hypotheses: (1) the tipping point hypothesis, which posits that arthropods living in high stress street medians would be less resilient to the effects of acute disturbance than arthropods living in lower stress city parks, because they are living near the limits of their environmental tolerances, and (2) the disturbance tolerance hypothesis, which posits that high stress street medians host only organisms pre-adapted for coping with high levels of disturbance, making them more resilient to the effects of acute disturbance than those living in lower stress city parks. Overall, our evidence consistently supported the disturbance tolerance hypothesis, with no support for the tipping point hypothesis.

Humans tend to create environments in which many- but not all- organisms suffer from chronic stress, be it from toxins, drought, variable conditions, reduced space, or extreme temperatures. In addition, global climate change increases the odds that many of these same, chronically stressed habitats are likely to be affected by the acute effects of storms. As urbanization and other anthropogenic changes to ecosystems continue to contribute to global climate change, these consequences are likely to increase. Our results suggest that the species that have survived in high stress environments are likely to be the ones that thrive in response to acute disturbance. So little is known about the arthropods of the world, even in places such as Manhattan, where millions live, that it is unclear what consequences the increasing abundance of stress tolerant species might have. A key question is whether these species are the ones that we would intentionally favor were we managing ecosystems wisely.

Strong evidence in support of the disturbance tolerance hypothesis

We considered the hypothesis that the organisms living in high stress street medians possess adaptations to disturbance, making them more resilient to the effects of extreme weather events than organisms living in relatively low stress city parks. Our evidence largely supported the predictions of this hypothesis. City parks and street medians had significantly different order-level arthropod composition before Super Storm Sandy, but did not differ after the storm. Similarly, while the family-level arthropod composition of street medians changed little in response to flooding, that of city parks was significantly altered. These changes resulted in post-storm arthropod communities in city parks becoming indistinguishable from those in street medians.

The change in composition in parks in response to floods appeared to be driven by the responses of numerically subordinate families. These families had both reduced abundances and lower occurrences in flooded sites than in unflooded sites after Super Storm Sandy. While numerically dominant families were less abundant in flooded sites than they were in unflooded sites, differences in their composition between street medians and city parks did not differ with flooding. Interestingly, a few numerically subordinate families were more common in flooded street medians than in unflooded street medians; these families tended to be the same families that were less common in flooded city parks than in unflooded city parks. We hypothesize that flooding created conditions that temporarily made street medians more suitable for numerically subordinate families by increasing debris, reducing predators, increasing moisture, and reducing competition from numerically dominant families. Flooding may also facilitate the dispersal of some arthropods into new areas. We further hypothesize that this response is likely to be short lived, since debris will likely decline (Xu et al. 2004, Beard et al. 2005) and the abundant families are likely to rebound over time (Schowalter and Ganio 1999, McCall and Pennings 2012). Another possibility is that some groups (e.g., Hemiptera) are more abundant earlier in the summer, so their increase in abundance was unrelated to storm damage. However, we think it is unlikely that differences in phenology were strong enough to drive the patterns that we detected across arthropods with very different life histories.

Finally, there were positive correlations between tolerance to high stress medians and tolerance to storm-associated flooding at both the family and order levels. In other words, the same orders and families that thrived in response to chronic stress also did well in response to acute hurricane disturbance. The strongest patterns were for the most abundant groups: Collembola, Hymeoptera, and Isopoda. While the first two orders were the most median and flood intolerant, isopods had the opposite response, being among the most median and flood tolerant arthropod orders. However, high abundance alone did not explain the responses of all arthropod groups. Spiders and beetles had relatively low abundances and were among the most median and flood intolerant orders; while thrips and lepidopterans also had relatively low abundances, but were among the most median and flood tolerant orders. Adis and Junk (2002) reviewed the diversity and composition of terrestrial invertebrates in floodplains and concluded that high tolerance to stress may be necessary in order to persist in environments where floods are common. They also showed that the ability to escape flooding, whether through flight or behavioral adaptations to move into trees, was a common characteristic of invertebrates who thrived in floodplains. High dispersal and reproductive rates were particularly important traits of species that survived catastrophic flooding, as compared to seasonal flooding. Indeed, many of these characteristics may explain the patterns that we detected. Most of the median and flood intolerant groups are either exclusively ground dwelling (Collembola), constrained by ground nests (ants, which were responsible for the Hymenoptera responses), or are relatively poor dispersers (beetles). Spiders should have been better able to escape, but may have been responding to reduced prey availability in medians and heavily flooded sites. In contrast, both thrips and lepidopterans are very mobile and have high dispersal rates, potentially explaining their tolerance to flooding and chronic environmental stress. Isopods do not fit this pattern, and other studies have shown that they can both increase and decrease in abundance after flooding events (Plum 2005). Further research into isopod stress responses could help us better understand their tolerances to both median and flooding stress.

The disturbance tolerance hypothesis has received less study in the ecological literature than the tipping point hypothesis. However, multiple studies have shown that success in habitats with high levels of urban stress are associated with particular physiological or behavioral traits (McKinney and Lockwood 1999, Møller 2009, Sattler et al. 2010). For example, Hawkes and Keitt (2015) found that microbes from more constant environments were more sensitive to negative effects of rapid environmental change than microbial communities from habitats with higher levels of chronic environmental variability (one form of stress). Moreover, similar to our results, Walter et al. (2013) demonstrated that exposure to environmental stress can increase resilience to future acute disturbances. They focused on multiple acute disturbances, but chronic stressors are likely to provide similar "ecological stress memory."

No evidence for the tipping point hypothesis

We also considered the hypothesis that arthropods living in high stress street medians were vulnerable to the negative influences of extreme weather because they were already living near the limits of their environmental tolerances. Unlike the disturbance tolerance hypothesis, we did not detect any evidence that supported this hypothesis. However, previous research suggests that responses to extreme weather can sometimes follow the predictions of the tipping point hypothesis. Experimental evaluation of the tipping point hypothesis has come primarily from studies of plant and aquatic invertebrate communities. For example, multiple studies have demonstrated that aquatic organisms previously exposed to anthropogenic stressors were more vulnerable to extreme weather than those living in habitats with lower levels of chronic environmental stress (Parkyn and Collier 2004, Cardoso et al. 2008, Morin et al. 2015). Sorte et al. (2011) compared marine invertebrates living in high stress coasts of the Atlantic Ocean to those living in the relatively lower stress coasts of the Pacific Ocean. They found that marine invertebrates from higher stress environments were living closer to their thermal maxima, but also had better ability to acclimate to thermal stress. Similar dynamics may be occurring for arthropod communities living in high stress street medians vs. lower stress city parks in our sites in Manhattan. That is, even if arthropods in street medians are living near their environmental limits, they may still be better able to acclimate to or tolerate further disturbance. Alternatively, detecting effects of extreme weather events on tipping point dynamics for urban arthropod communities may require longer time spans (years instead of months).

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1643/full