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Research

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Disturbance Mediates Homogenization of Above and Belowground Invertebrate Communities

Karl A. Roeder,[1,3] Diane V. Roeder,[2] and Michael Kaspari[1]

[1]Department of Biology, Graduate Program in Ecology and Evolutionary Biology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019, [2]Department of Agriculture, Biology and Health Sciences, Cameron University, 2800 W Gore Boulevard, Lawton, OK 73505, and [3]Corresponding author, e-mail: karoeder@ou.edu

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Abstract

Natural disturbances can occur stochastically with profound impacts on fauna and flora. Here we quantified the impact of a one in 100-yr flood on terrestrial invertebrate communities in south central Oklahoma. Before the flood, we observed 4,082 individuals from 92 species weighing a total of 18.61 g that belonged to compositionally different above or belowground communities. One year after the initial sampling period and 9 mo post-flood, we measured a 93% decrease in abundance, a 60% decrease in species richness, and a 64% decrease in biomass as well as increased compositional similarity between the above and belowground communities. Of the eight insect orders that were present before the flood, only the Coleoptera and Orthoptera increased immediately after the flood. Of these, only the Orthoptera remained at an elevated level across all post-flood sampling periods, specifically due to an increase in crickets (Orthoptera: Gryllidae). As we enter an era of global change, using natural perturbation experiments will improve our knowledge about the ecological processes that shape patterns of community assembly and biodiversity.

Key words: biodiversity, community assembly, disturbance, flood, weather

As Earth's atmosphere and oceans warm, the severity of weather events is predicted to increase (Easterling et al. 2000, Dale et al. 2001, IPCC 2014). The resulting floods, hurricanes, and tornadoes perturb ecological communities, altering their physical structure and species composition (Spiller et al. 1998, Dale et al. 2001, Miriti et al. 2007, Thibault and Brown 2008). Such disturbances can blur habitat boundaries, creating hybrid communities (Chase 2007, Clavel et al. 2011) that can represent new stable or transient states (Schröder et al. 2005, Fukami and Nakajima 2011). For example, arthropod communities in different habitats of New York City were recently homogenized due to the extreme flooding of Super Storm Sandy (Savage et al. 2018). Understanding how and which species within these newly assembled communities persist in space and time is a fundamental ecological question.

The rules by which such communities are assembled—which species persist and which do not—fall along a continuum from neutral to niche (Drake 1991, Hubbell 2001, Chase 2003, Chase and Leibold 2003, Leibold and McPeek 2006). Niche-based assembly is deterministic and emphasizes the role of environmental conditions, individual requirements, and biotic interactions in filtering a predictable subset of species from the available pool (Hutchinson 1957, Vandermeer 1972). Neutral assembly ignores such differences, and predicts that species composition is a random draw of those species arriving in a habitat from the larger pool (Hubbell 2001). Severe disturbances that erase habitat boundaries and combine disparate assemblages are a unique opportunity to contrast these two forms of assembly, an often difficult task (Fukami 2010). However, such tests are rare, given the highly improbable combination of a thorough survey of adjacent distinct communities followed immediately by an extreme homogenizing disturbance.

In the spring of 2015 at the University of Oklahoma Biological Station on Lake Texoma, the highly improbable happened. Record levels of rainfall raised lake levels 10 m causing substantial flooding that persisted for weeks (Fig. 1, Oklahoma Climatological Survey). Most studies of flooding impacts on soil communities focus on floodplains and riparian habitats where the biota regularly experience flooding (Uetz 1976, Milford 1999, Ellis et al. 2001, Ballinger et al. 2007, Gerisch et al. 2010). As a result, such species pools reflect prior selection for flood adaptations. For example, in both Central Amazonia and Central Europe, flood stress decreased diversity with more predictable flooding favoring morphological, physiological, and behavioral adaptations to survive these events (Adis and Junk 2002). Such adaptations include millipedes that can live almost a year under water (Adis 1986) and bristletails that synchronize production of flood resistant eggs to annual flooding events (Adis and Strum 1987). At this locale in Oklahoma, flooding events have only

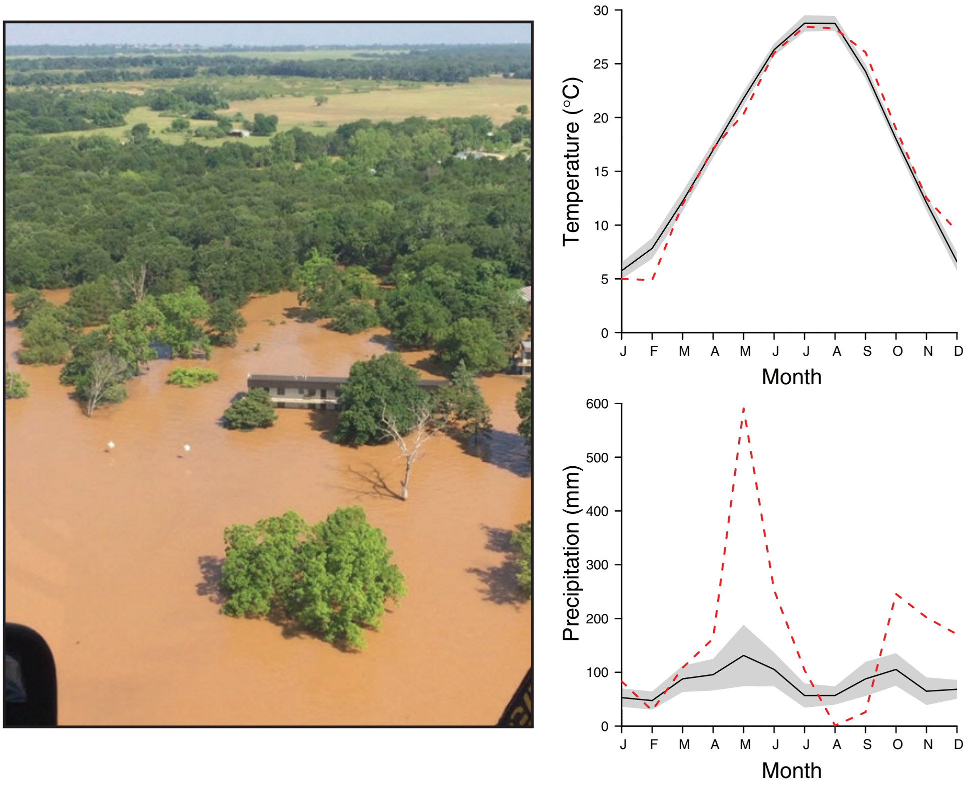

Fig. 1. Aerial photograph of flooding at the University of Oklahoma Biological Station with yearlong environmental variables from the surrounding area. For temperature and precipitation, black lines represent monthly averages from 1996 to 2015 with 95% confidence intervals represented by grey areas, red dashed lines represent values from 2015. Photograph by Jeff Thrasher.

occurred three times in the last 70 yr, thus we have no a priori reason to suspect similar adaptations occur in our community. As we had begun to survey the above and belowground invertebrate communities 3 mo prior, this rare event allowed us to quantify the effects of a severe flood on invertebrate communities and assess the relative importance of niche and neutral assembly of these communities pre- and post-flood.

Materials and Methods

Study Site and Sampling Design

We sampled 12 transects in March, September, and December 2015 as well as March 2016 in similar habitat within a 17.5 ha field at the University of Oklahoma Biological Station on the northern border of Lake Texoma (33.88°N, 96.84°W, 194 m elevation). This location was previously an old agricultural field that is now dominated by Indiangrass (*Sorghastrum nutans* (L.) Nash), Johnsongrass (*Sorghum halepense* (L.) Pers.), and little bluestem (*Schizachyrium scoparium* (Michx.) Nash). All 12 transects were underwater during June 2015. For each transect, we set out ten pitfall traps for 3 d arranged 10 m apart along a 100 m transect oriented in a North to South direction. Pitfall traps were comprised of 50 ml centrifuge tubes (Opening diameter: 3 cm, Length: 11.6 cm; Corning Incorporated, Corning, NY) filled with 20 ml of a solution of 80/20 propylene glycol/ 95% ethanol and a drop of fragrance free detergent (Roeder and Roeder 2016). Of the 12 transects, half were designated aboveground and had pitfall traps installed flush at ground level. The other half were designated belowground and had pitfall traps that were placed 15 cm below the surface with a thin strip of plastic covering the hole at ground level to prevent aboveground invertebrates from entering. Transects of a similar placement type (i.e., above or belowground) were spaced at least 100 m apart from each other. While pitfall traps may be limited in capturing large bodied, herbivorous taxa—specifically species that primarily occupy vegetation above the surface (e.g., Acrididae)—our sampling method was designed to standardize collection of invertebrates across habitat types.

Temporal Differences in Abundance, Species Richness, and Biomass

To determine how communities changed over time, we counted and identified individual invertebrates to major taxonomic groups and then assigned species or morphospecies names to unique identities. Morphospecies often provide reliable estimates of species richness for invertebrate community analyses (Oliver and Beattie 1996). Individuals were then dried to constant mass at 60°C for 48 h and weighed to the nearest 0.01 mg using a R 200D electronic semi-microbalance (Sartorius Research, Goettingen, Germany). We used generalized linear models (GLM) with a negative binomial distribution to compare differences in count data that was not normally distributed and overdispersed for abundance and species richness (O'Hara and Kotze 2010). Dry mass (i.e., biomass) was checked for normality using the Shapiro-Wilks test, log transformed and compared using ANOVA.

Species Composition and Null Models of Community Assembly

We used a non-parametric multivariate analysis of variance (i.e., PERMANOVA) with 1,000 permutations to test if 1) the composition of the pre-flood communities was different than post-flood communities and 2) if above and belowground communities became compositionally more similar after the flood. To account for potential seasonal variation in species occurrence, we focused on sampling periods that occurred during the month of March in 2015 and 2016, which had similar temperature (2015 = 11.94°C; 2016 = 14.17°C) and precipitation profiles (2015 = 108.46 mm; 2016 = 115.06 mm). PERMANOVA tests the null hypotheses of no difference amongst groups using random permutations of the data with a pseudo *F*-statistic (Anderson 2001). For both comparisons, we used the incidence-based Jaccard's index of dissimilarity which scales from 0 (completely similar) to 1 (completely dissimilar). Differences in above and belowground invertebrate communities during March 2015 and March 2016 were visualized using non-metric multidimensional scaling (NMDS) ordinations.

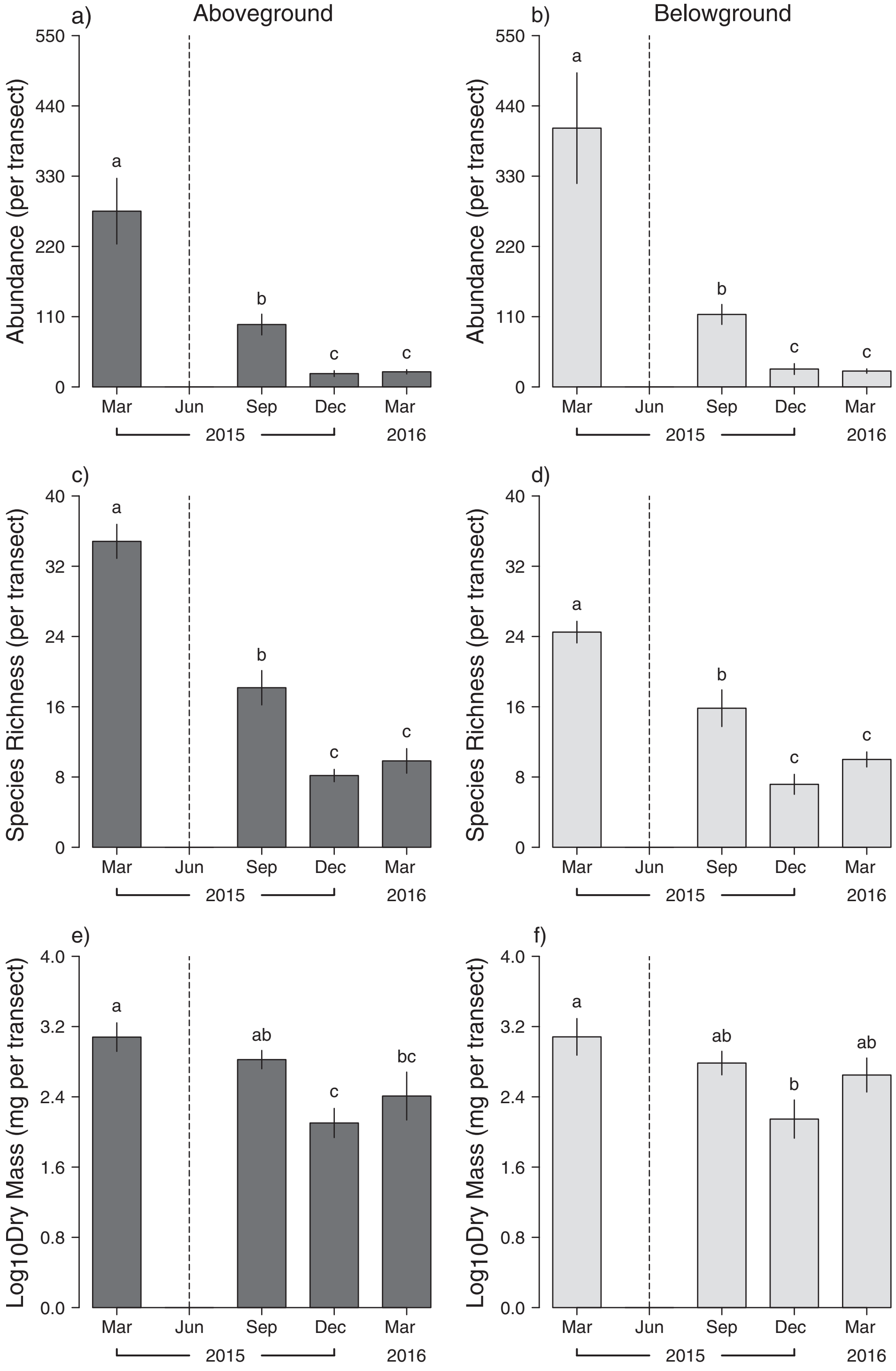

Fig. 2. Temporal changes in above and belowground invertebrate communities. Panel (a) and (b) show abundance, panel (c) and (d) show species richness, and panel (e) and (f) show dry mass (i.e., biomass) per transect. For each variable, dark grey boxes denote aboveground communities, while light grey boxes denote belowground communities. Vertical --- lines represent the period of flooding. Different letters above the bars indicate statistically significant differences between time periods ($P < 0.05$).

We next created null models to test for the signatures of niche versus neutral assembly (sensu Chase 2007). Specifically, we predicted that if deterministic niche assembly is occurring, then communities should be more similar and have lower Jaccard's dissimilarity values compared to randomly structured communities. Alternatively, if neutral, dispersal mediated assembly predominates, then Jaccard values should converge on randomly structured communities. We first used the entire regional species pool to assemble random communities, maintaining observed species richness. We then calculated a mean Jaccard's dissimilarity value amongst similar types of random communities and replicated this process 1,000 times. Next, we created 95% confidence intervals of dissimilarity for each set of random communities and compared these values to the mean Jaccard's dissimilarity from our natural communities. As we observed temporal differences in species richness, we also created null models in a similar way as above but changed the number of species in the regional pool to an equivalent number found in communities at the time of collection. Finally, we calculated effect sizes for the deviation from the null between natural and randomly structured communities using the following equation from Chase (2007): Effect Size = ln(natural dissimilarity) − ln(randomly generated dissimilarity). We replicated this method 1,000 times to create a *P* value from the proportion of effect sizes of pre-flood communities that were greater than post-flood communities. All analyses were run in R, version 3.2.2.

Results

We collected a total of 5,933 individuals from 101 morphospecies across four time periods, one 3 mo prior to the flood, and three that were 3, 6, and 9 mo post-flood. Abundance was lower in the post-flood samples by up to one order of magnitude both above (GLM: $\chi^2 = 166.27$; df = 3; $P < 0.001$; Fig. 2a) and belowground (GLM: $\chi^2 = 151.46$; df = 3; $P < 0.001$; Fig. 2b). Species richness declined 69% aboveground (from 80 to 25; GLM: $\chi^2 = 141.09$; df = 3; $P < 0.001$; Fig. 2c) and 52% belowground (from 56 to 27; GLM: $\chi^2 = 71.70$; df = 3; $P < 0.001$; Fig. 2d). Biomass varied less (Fig. 2e and f) but mirrored the decreases in abundance and species richness ($\text{ANOVA}_{\text{Above}}$: $F = 7.48$; df = 3, 20; $P = 0.002$; $\text{ANOVA}_{\text{Below}}$: $F = 4.17$; df = 3, 20; $P = 0.019$), driven by an increase in the average size of invertebrates from pre- ($\bar{x} = 4.56$ mg) to post-flood communities ($\bar{x} = 22.93$ mg). Incidence, represented here as the proportion of the total number of pitfall traps containing a particular taxon, likewise decreased for most clades post-flood (Table 1). Specifically, when comparing March 2015 to March 2016, all arthropod classes had a lower incidence value and 87.5% of all insect orders were reduced (Table 1).

Invertebrate communities differed in taxonomic composition pre- and post-flood (PERMANOVA: pseudo $F = 9.23$; df = 1, 22; $P = 0.001$). Moreover, the distinct above and belowground communities found in March 2015 (PERMANOVA: pseudo $F = 2.17$; df = 1, 11; $P = 0.005$; Fig. 3a), were homogenized 1 yr later and 9 mo post-disturbance (PERMANOVA: pseudo $F = 1.42$; df = 1,11; $P = 0.113$; Fig. 3b). To explore how these differences came about, we tested null models using a regional species pool containing 1) the equivalent number of species found in communities at the time of collection (e.g., March 2015 = 92 species, March 2016 = 37 species), and 2) all species from the regional species pool. Regardless, each combination of above or belowground community sample and time period generated lower Jaccard's dissimilarity values than predicted by null models (all comparisons $P < 0.05$, Supplementary Table S1). In addition, the effect size of the deviation from the null was not different ($P = 0.244$) for pre-flood (mean effect size = −0.264) compared to post-flood communities (mean effect size = −0.249). In other words, post-flood communities did not differ more from the randomly structured communities than pre-flood communities.

Table 1. Incidence of invertebrate taxa across time

Taxon	2015 March	 June	 September	 December	2016 March
Arachnida	0.75	–	0.58	0.13	0.43
Acari	0.56	–	0.00	0.01	0.00
Araneae	0.53	–	**0.58***	0.12	0.43
Chilopoda	0.08	–	0.00	0.00	0.00
Entognatha	0.55	–	0.00	0.13	0.01
Diplopoda	0.78	–	0.00	0.00	0.00
Gastropoda	0.11	–	0.00	0.00	0.00
Malacostraca	0.87	–	0.00	0.00	0.00
Insecta	0.93	–	**0.96***	0.73	0.79
Blattodea	0.02	–	0.00	0.00	0.00
Coleoptera	0.69	–	**0.81***	0.27	0.30
Diptera	0.48	–	0.27	0.19	0.39
Hemiptera	0.23	–	0.08	0.07	0.04
Hymenoptera	0.82	–	0.58	0.16	0.15
Lepidoptera	0.03	–	0.01	0.00	0.00
Orthoptera	0.08	–	**0.72***	**0.42***	**0.36***
Thysanoptera	0.08	–	0.00	0.00	0.00

Values represent the proportion of the total number of pitfall traps (from *n* = 120) containing a particular taxon. During June, the study site was completely under water and values are not reported. Bold * indicates taxa that increased from the pre-flood period of March 2015.

Discussion

Floods are an obvious challenge to terrestrial invertebrates (Molles Jr. et al. 1998, Ellis et al. 2001, Ballinger et al. 2007). Of the seven different taxonomic classes that we collected before the flood, most decreased or were completely absent after a June spent underwater (Table 1). One year later, populations of isopods and millipedes—with large roles in decomposition and nutrient cycling (Wallwork 1970, Wardle 2002, Bardgett and van der Putten 2014)—had not recovered, perhaps due to low dispersal ability (Golovatch and Kime 2009, Gongalsky and Persson 2013) or a host of environmental drivers like temperature, pH, and biogeochemistry (Chase and Leibold 2003, Wu et al. 2011, Kaspari and Powers 2016). Moreover, before the flood, above and belowground communities of invertebrates were compositionally distinct. However, as species richness decreased, these once distinct above and belowground invertebrate communities were homogenized.

Flooding as an Environmental Filter to Soil Communities

Within the class Insecta, incidence decreased by 14% from pre- (March 2015) to post-flood (March 2016) periods. Moreover, for all but one insect order, incidence decreased from 19 to 100% (Table 1). Only three of 14 ant species (Hymenoptera: Formicidae), important soil cyclers and ecosystem engineers (Hölldobler and Wilson 1990, Del Toro et al. 2012), remained after the flood. They may have done so in a number of ways. The arboreal acrobat ant, *Crematogaster laeviuscula* Mayr regularly nests in trees that were above the water line; the red imported fire ant, *Solenopsis invicta* Buren often escapes floods by forming live flotillas. Only the odorous house ant, *Tapinoma sessile* Say, a mobile polygynous species, likely re-colonized from outside the flood area. Though ant occurrence decreased from 2015 to 2016 by 83%, the resilient and invasive *S. invicta* were

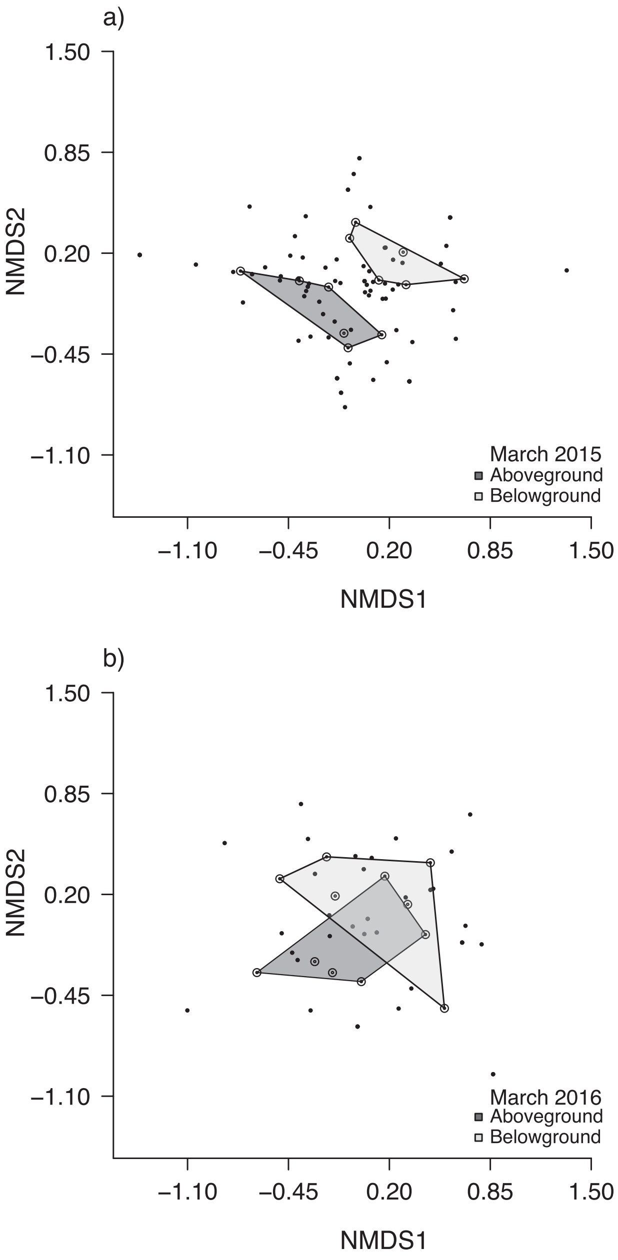

Fig. 3. Non-metric multidimensional scaling (NMDS) ordination of invertebrate communities. Panel (a) shows pre-flood communities, while panel (b) shows post-flood communities. For each, dark grey polygons denote aboveground and light grey polygons denote belowground invertebrate communities. Species are indicated by black dots.

still found 1.4 times more often in traps than native ants 9 mo after the flood. The interaction of *S. invicta* and the recolonizing native species should be of considerable interest as red imported fire ants can persist on a variety of dietary items (Vogt et al. 2001, Roeder and Kaspari 2017), excel at surviving in disturbed floodplains (Tscinkel 2006, LeBrun et al. 2007), and disrupt invertebrate communities (Porter and Savignano 1990, Resasco et al. 2014).

In contrast, one insect order—the Orthoptera—increased and remained at a high incidence. Before the flood, crickets were found in 17% of pitfall traps aboveground and 0% belowground. However, 9 mo after the flood, orthopteran incidence had more than quadrupled with a substantial increase belowground (i.e., they were present in 40% of traps). This change was primarily driven by an increase in field crickets, which are well known colonizers of not only disturbed habitats but also previously flooded environments (Beck 1972, Uetz et al. 1979, Cartron et al. 2003, Smith et al. 2006). Detritus, a primary resource for these crickets, perhaps increased post-flood as this waterlogged field now contained dead and decaying vegetation that previously would have been broken down by detritivores such as isopods and millipedes. Consequently, the biomass that was apportioned among a diversity of taxa pre-flood was concentrated in a handful of taxa that were 5-times larger on average, post-flood.

Despite these observed changes to above and belowground soil communities, there was no signal of neutral assembly pre- or post-flood—a result suggesting niche based assembly may be occurring. We would predict a neutral signature to appear when dispersal alone results in differences of community structure (i.e., species composition being a random draw from the larger pool of arriving species in a habitat; Hubbell 2001, Chase 2007). One hypothesis for a lack of neutral, dispersal mediated assembly is that this flood affected large portions of south central Oklahoma (Oklahoma Climatological Survey). Perhaps the species pool from the surrounding area, from which our communities were constructed, was likewise reduced and filtered by the flood, resulting in a more deterministically assembled subset of the previously occurring invertebrates. A second hypothesis is that dispersal structured communities may be less apparent in environments that are not bounded by borders. Previous studies have successfully shown the importance of arrival order for community dynamics (Drake 1991, Chase 2003, Fukami 2004), yet many are based in systems that are isolated such as microcosms or ponds. Relaxing the harshness of these boundaries and allowing the flow of species from other source pools may reduce priority effects in open, compared to closed, systems. These hypotheses are not mutually exclusive, nor do they represent every possibility. Instead they highlight just a portion of the complexity that occurs in the assembly of terrestrial communities.

Conclusions

Since its creation, water has reached the spillway of Lake Texamoa five times in 70 yr—two of those five times occurring during this flood (National Weather Service). The three flooding events prior to the 2015 flood, we posit, are too infrequent to select for taxa that are flood adapted. However, as global change models predict more frequent flooding disturbances driven by large rainfall events (National Assessment Synthesis Team 2000), this study gives a glimpse as to how soil invertebrate communities will be simplified and homogenized.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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