nature ecology & evolution

Article

https://doi.org/10.1038/s41559-023-02205-7

Spatial sorting promotes rapid (mal) adaptation in the red-shouldered soapberry bug after hurricane-driven local extinctions

Received: 5 September 2021

Accepted: 24 August 2023

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Predicting future evolutionary change is a critical challenge in the Anthropocene as geographic range shifts and local extinction emerge as hallmarks of planetary change. Hence, spatial sorting—a driver of rapid evolution in which dispersal-associated traits accumulate along expanding range edges and within recolonized habitats—might be of growing importance in ecology and conservation. We report on the results of a natural experiment that monitored recolonization of host plants by the seed-feeding, red-shouldered soapberry bug, *Jadera haematoloma*, after local extinctions from catastrophic flooding in an extreme hurricane. We tested the contribution of spatial sorting to generate rapid and persistent evolution in dispersal traits, as well as in feeding traits unrelated to dispersal. Long-winged dispersal forms accumulated in recolonized habitats and due to genetic correlation, mouthparts also became longer and this shift persisted across generations. Those longer mouthparts were probably adaptive on one host plant species but maladaptive on two others based on matching the optimum depth of seeds within their host fruits. Moreover, spatial sorting eroded recently evolved adaptive divergence in mouthpart length among all host-associated biotypes, an outcome pointing to profound practical consequences of the extreme weather event for local adaptation, population resilience and evolutionary futures.

Predicting adaptive and maladaptive evolution in a rapidly changing world is a critical challenge of the Anthropocene—the current geological epoch in which human activity is the dominant influence on climate and the environment. Effectively doing so will better inform the decisions of policy-makers, conservationists and environmental managers alike[1–3]. Climate change is a hallmark of the Anthropocene, where warming is associated with increased frequency and intensity of hurricanes[4,5]. These weather-related catastrophes can cause local extinctions and disrupt ecological interactions[6]. Such disruptions are expected to become more impactful and frequent in the near future[7] and, consequently, so will the associated regularity of localized extinction and post-disturbance recovery. Such recoveries are often dependent on a species' capacity for recolonization and thus organismal dispersal ability has the potential to assume a central role in the contemporary evolution of the Anthropocene. Here, in the spirit of understanding organismal responses to weather-related catastrophes, we test an understudied evolutionary mechanism, promoted by phenotype-dependent dispersal, for its ability to shape post-disturbance recovery and drive both adaptive and maladaptive outcomes in dispersal-associated traits and traits that are genetically correlated with them.

Recent work on the biology of invasive species has highlighted 'spatial sorting' as an underappreciated evolutionary mechanism that relies on dispersal and, thus, promotes rapid evolution across space[8–11].

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Here, phenotypes that enhance dispersal, including behavioural, physiological or morphological traits, accumulate at the leading edge of an expanding range or in newly colonized habitats. Ensuing mating among these high-dispersing pioneers can then maintain or drive a local evolutionary increase in the magnitude and (or) frequency of dispersal phenotypes and other linked traits across following generations[11–15]. This is distinct from classical Darwinian theory which predicts that adaptive traits evolve due to natural selection on the basis of differential survival and (or) reproduction among a set of genetically based phenotypes[16–19]. Under natural selection, evolution is a phenomenon that occurs between generations across time. In contrast, spatial sorting can occur rapidly across space, with allele frequency changes due to the immigration of individuals rather than fitness, per se, resulting in phenotypic shifts that may not necessarily be adaptive[20].

Further, spatial sorting is distinct from the influence of genetic drift present in small populations after random colonization events (founder's effect). Similarly, spatial sorting is distinct from gene surfing, with associated stochastic changes in allele frequencies at the leading edge of an invasion[21,22]. Spatial sorting instead relies on the probability that colonization will occur by strong dispersers, as poor dispersers are less likely to move away from the core of their range. Therein lies the distinction; unlike the stochasticity of founder's effects and gene surfing, the process of spatial sorting generates non-random shifts in genetic-based phenotypes that enhance dispersal, irrespective of how those phenotypes affect an organism's survival or reproductive success[10,19,20,23,24]. As an evolutionary mechanism, spatial sorting has been suggested as an important understudied source of speciation with the potential to drive adaptive radiations[25].

Evolution driven by spatial sorting in natural systems has been documented in interglacial plant migration[8], as well as in several cases along leading invasion fronts in amphibians[13,26–28], birds[29,30] and mammals[31–33]. Beyond observational studies, the effects of spatial sorting have been verified in laboratory-based experimental manipulations using agricultural grain pests[14,15]. However, even though the impact of spatial sorting is well tested in systems investigating changes in invasion speeds or the pace of range expansions (for example, refs. 14,15), the potential role for spatial sorting to facilitate or impede rapid adaptive divergence due to genetic correlations between dispersal and non-dispersal traits, as well as its more general role in response to the increasing frequency of localized extinction due to extreme weather events, has yet to be examined[28].

In the present study, we exploited the ecological perturbation of a 2017 flood event driven by a catastrophic hurricane in southeastern Texas, United States (Hurricane Harvey; Fig. 1a–d) to test the role of spatial sorting in evolution due to patterns of post-hurricane recolonization in the red-shouldered soapberry bug (*Jadera haematoloma;* hereinafter, soapberry bug; Fig. 2a–c). This plant-associated insect specializes on seeds of the soapberry family (Sapindaceae; Fig. 2d–f) where the length of the mouthparts is critical to reaching their primary resource inside host fruits. We measured wing length and mouthpart length in 15 soapberry bug populations in the region for 6 months before the hurricane and for 3 years of monitoring thereafter (Extended Data Fig. 1). We compared 11 flooded sites where soapberry bug populations disappeared and were subsequently recolonized to four control sites that did not flood and maintained continuous soapberry bug populations through the 3.5 year monitoring period (Supplementary Table 1).

We used field observations and laboratory-based studies of flooding survival to interpret our findings and to address three major questions regarding spatial sorting. (1) Did hurricane-associated floods extinguish local soapberry bug populations? (2) Did soapberry bug individuals with better dispersal capabilities recolonize first and consequently alter the distributions of genetically influenced phenotypes—including traits directly associated with dispersal and genetically correlated traits with different important functions? (3) Did shifts in soapberry bug phenotypes persist across generations? The answers provide a landscape-scale, real-time portrait of spatial sorting as a potent but overlooked mechanism of contemporary evolution that can be variously adaptive or maladaptive in response to environment change.

Natural history of the study system

Soapberry bugs are well-known examples of rapid adaptive evolution in response to Anthropocene environments[34], where populations on native host species have shifted and adapted to feed on introduced, non-native plants in the same family over the past ~60 years[35–37]. Feeding involves piercing the surrounding seed pods with needle-like mouthparts[38], commonly referred to as 'beaks' (Fig. 1e). The range of mouthpart lengths in nature strongly reflects fruit size of the host plant on which each population feeds[35] and these host-associated differences in beak length evolved through divergent natural selection between hosts[35]. When beak length matches the distance between outer fruit wall and the interior seeds, it increases seed access and decreases handling time, leading to higher fecundity in females[39]. Beak length is a polygenic trait influenced by epistatic and dominance interactions and is highly heritable ($h^2 = 0.51–0.87$)[37,40,41].

There are three soapberry bug host plant species in our southeastern Texas study area and these hosts differ dramatically in fruit size: (1) native balloon vine (*Cardiospermum halicacabum*; Fig. 2d), with large seed pods hosting soapberry bugs with the longest beak lengths; (2) native western soapberry (*Sapindus saponaria* var. *drummondii*; Fig. 2e), with intermediate-sized seed pods hosting soapberry bugs with intermediate-sized beak lengths; and (3) non-native goldenrain tree (*Koelreuteria elegans*; Fig. 2f), with narrow, open seed pods hosting soapberry bugs with the shortest beak lengths[35,36]. In this humid subtropical region, soapberry bugs breed continuously year-round, with overlapping generations (adult lifespan <60 days; ref. 42) and do not enter diapause at sites with host seeds available[43]. Once mated, females oviposit eggs in shallow (~1 cm) holes in the ground that they excavate beneath their host plants[38].

Soapberry bugs may develop as either flying or flightless adults (Fig. 2b). Flying adults comprise a long-winged 'macropterous' dispersal form, whereas flightless adults comprise a short-winged 'brachypterous' form. Brachypterous individuals express much less developed wing membranes and flight muscles but can begin reproducing at a younger age compared to their macropterous counterparts[44]. The frequency of these two forms differs among host-associated populations and experimental crosses between macropterous and brachypterous individuals suggest a polygenic inheritance of wing form[44,45]. Importantly, wing form and beak length are genetically correlated ($r = 0.68$ to 0.84) (ref. 41), such that a genetic change in one trait will favour change in the other[46].

The difference between the flighted and flightless forms in their capacity for natural dispersal, along with the genetic correlation between wing form and beak length expression, allows us to test the role of spatial sorting in shifting the mean beak length of populations on each host plant. Macroptery is essential for accessing spatially distant food sources yet having an appropriately matched beak length is a critical phenotype for efficient feeding, survival and reproduction on arrival[35,36,39]. Thus, long-wing dispersers are predicted to be better adapted to host species with larger seed pods and maladapted to use hosts with smaller seed pods. Here we use the terms adaptation and maladaptation to reference the matching of individual beak length to the optimum distance to the seed within the fruit for each of the three regional hosts (Fig. 2d–f) with direct consequences for fitness[35,37,39,40,47]. However, we recognize that one can consider and examine adaptation and maladaptation in many ways (for example, refs. 48,49).

Results and discussion

Test of local extinction: field surveys and egg mortality

In a test of question 1, we observed a significant, prolonged absence of soapberry bugs at the 11 flooded sites after the hurricane, where the

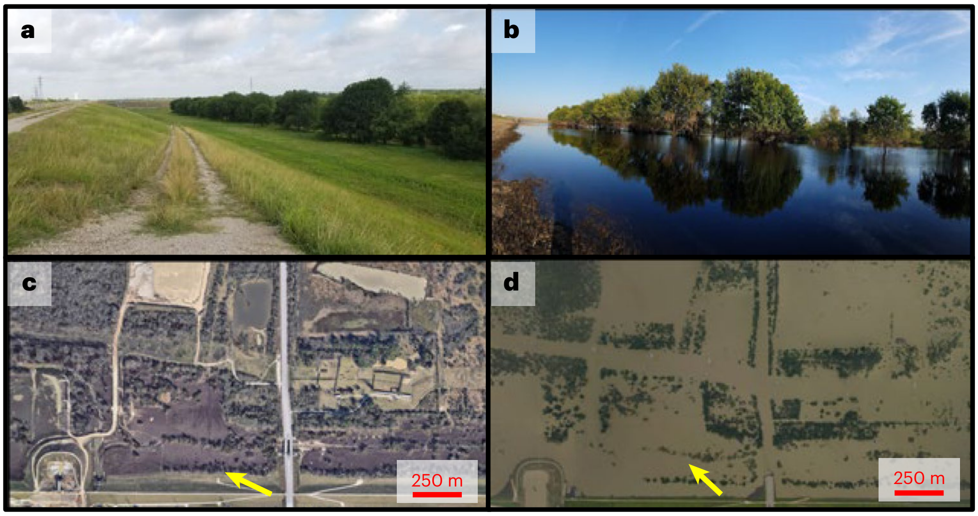

Fig. 1 | Hurricane-associated flooding. a–**d**, Images of a soapberry bug sampling site from our study. **a**, Photograph taken 1 week before Hurricane Harvey hit the Gulf coast of Texas. **b**, The same site photographed 3 months later from a similar vantage point as **a** illustrating the flooding that occurred in response to the storm. **c**,**d**, Pre- and post-hurricane satellite images of the same site. Yellow arrows indicate the vantage points of images **a** and **b**. Data for **c** and **d** are from Google © 2023, Landsat/Copernicus.

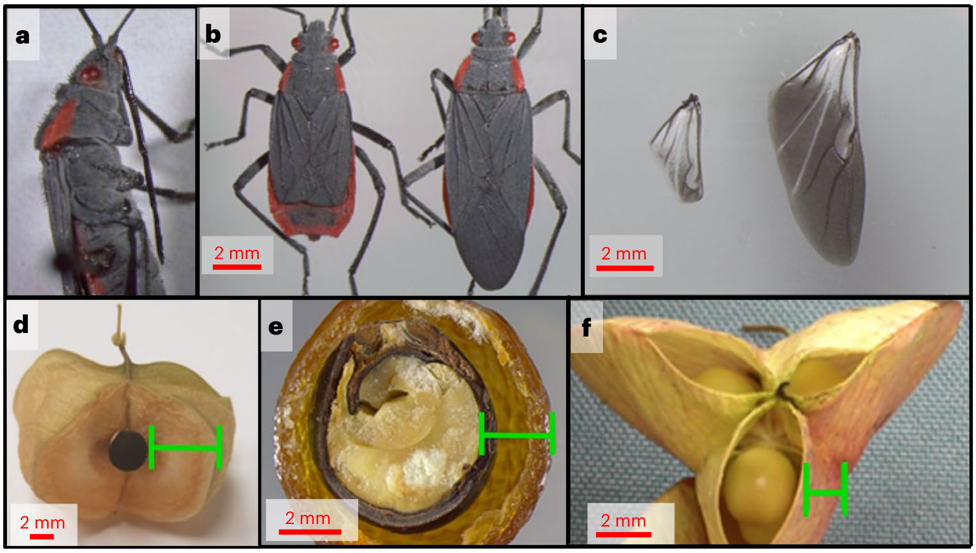

Fig. 2 | Soapberry bug morphology and host plants. a, Lateral view of soapberry bug's beak-like mouthpart used for feeding on the seeds inside the fruits of their host plants. **b**, Images illustrate the discrete wing polymorphism in soapberry bugs with the flightless, brachypterous form on the left and flighted, macropterous form on the right. The underdeveloped distal membrane of the forewing is visually apparent in the brachypterous morph. **c**, Muted development of non-volant hindwings of the brachypterous form (left) and the fully developed volant hindwing of the macropterous form (right). **d**, Air-filled seed pods of *C. halicacabum*. **e**, Fleshy drupe and seed of *S. saponaria* var. *drummondii*. **f**, Thin, open seedpod of *K. elegans*. Green lines show the distance a soapberry bug's beak must penetrate to access and feed on an enclosed seed (beak length fitness optimum).

number of individuals captured per unit of effort (CPUE) dropped from a mean ± s.e. of 9.05 ± 0.62 pre-hurricane to 0 ± 0 post-hurricane (generalized linear mixed model (GLMM): $\beta = 2.245$, s.e. = 0.202, $Z = 11.13$, $P < 0.001$; Fig. 3a and Supplementary Tables 1 and 2). The duration of this absence at flooded sites was longer than the expected maximum adult lifespan of the insect in the wild, which is ~60 days (refs. 42,50). In contrast, there was no change in soapberry bug abundance at the four control sites that did not flood (Tukey's test: pre- versus post-hurricane $t = 0.711$, $P = 0.893$; Fig. 3a and Supplementary Table 3; Supplementary Results—field surveys). Additionally, submergence assays demonstrated that soapberry bug eggs were no longer viable when submerged for periods equivalent to localized Hurricane Harvey flooding. Background hatching success was reduced from 55.2% to 15.2% when soapberry bug eggs were submerged for 2 days and we observed 0% hatching success when eggs were submerged for 10 days (Fig. 3b; Supplementary Results—egg mortality). This evidence of flood-induced egg mortality, in conjunction with the protracted absence of soapberry bugs at flooded sites, is consistent with local extinction associated with hurricane-associated flooding.

Test of spatial sorting: wing form frequency and length

We found that post-flood recolonization closely aligned with our predictions of spatial sorting, as only macropterous dispersal form individuals arrived at re-established flooded sites (Fig. 4).

Fig. 3 | The effect of hurricane-associated flooding on soapberry bug population size and egg survival. a, Box plots illustrating a GLMM designed to test for differences in the number of insects CPUE (30 min of sampling per the number of observers) during pre-hurricane (white) and post-hurricane (brown) sampling periods shows a significant decrease in soapberry bug population size at flooded sites post-hurricane ($P < 0.001$; Supplementary Table 3). The upper and lower edges of boxes indicate the first and third quartiles, the midline indicates the median value and the whiskers show the 95% confidence intervals with dots as outliers. Data included here are the four sampling periods just before and just after the hurricane. Boxes labelled with different letters are significantly different in a Tukey's test ($P < 0.05$). Grey values at the top indicate the number of sample sites included in the survey. For individual sample site locations, see Supplementary Table 1 and Extended Data Fig. 1. **b**, Dot plot illustrating the mean ± 95% confidence intervals of egg survival between the three flood submergence treatments (0, 2 and 10 days underwater). A BLLM found that egg survival was significantly reduced with increasing submergence time ($P < 0.001$; Supplementary Table 20). Grey values at the base of the plot represent the number of eggs per treatment. Values not connected by letters are significantly different ($P < 0.05$) per a post hoc Tukey's test (Supplementary Table 21). Inset image is of two soapberry bug eggs with a grain of white sand for size reference.

Before hurricane-associated flooding, the composition of the regional populations ($n = 1{,}011$ insects) that occupied the 15 monitored sites ranged from 48.7% to 76.9% macropterous individuals with a mean of 60.9% (Supplementary Table 4). The flooded sites that experienced local extinction were recolonized anywhere from 136 to 821 days after extinction resulting from complete inundation by flood waters (Supplementary Table 1). When recolonization occurred, immigration was limited by dispersal form, as the frequency of macropterous individuals increased to 100% at all re-established flooded sites over the first 8 weeks after recolonization occurred (Fig. 4). This a priori selected timespan is shorter than nymphal development and thus the observed shift represents rapid change occurring within a single generation of migrating adults.

At flooded sites, this shift in wing form frequency was not dependent on host plant association and occurred consistently at all 11 flooded sites representing a non-random reorganization of the dispersal traits during recolonization—a pattern associated with spatial sorting. Specifically, we observed a significant increase in macropterous individuals from 76.9% ($n = 290$ pre-flood insects) to 100% ($n = 36$ post-flood insects) at flooded *Koelreuteria*-associated sites ($n = 6$ sites), from 48.7% ($n = 78$ pre-flood insects) to 100% ($n = 33$ post-flood insects) at *Cardiospermum*-associated sites ($n = 2$ sites) and from 53.2% ($n = 124$ pre-flood insect) to 100% ($n = 69$ post-flood insects) at *Sapindus*-associated sites ($n = 3$ sites) (Fisher's exact tests, $P < 0.01$ for all three comparisons; Fig. 3 and Supplementary Table 4). In contrast, the control sites, where flooding did not occur, did not experience this same shift (Fig. 4). Here, the frequency of post-flood macropterous individuals was slightly lower than pre-flood measurements with a 15.5% reduction at the one *Cardiospermum*-associated control site and a 10.6% post-flood reduction in macroptery across the three *Koelreuteria*-associated control sites (Fig. 4 and Supplementary Table 4).

Beyond the increase in the frequency of macropterous individuals at flooded sites, the average soapberry bug wing length within each wing form (macropterous or brachypterous) also shifted in association with post-flooding recolonization. This shift supports our prediction as wing form is controlled by both genetic and environmental factors[39,44,51–53] and, although bimodal, there is variation in length within each wing form category[36,53]. Using just our flooded *Koelreuteria*-associated sites ($n = 6$ sites), which provided the largest sample of individuals pre- and post-flood while controlling for variation between host plants, we compared pre-hurricane forewing lengths across three post-hurricane generations of *Koelreuteria*-associated brachypterous females. Here, the use of brachypterous individuals guarantees that individuals collected post-hurricane must be the offspring of the macropterous colonizers. We found that the interaction of 'site condition' (flooded versus control; linear mixed model (LMM): $F_{(1, 4.5)} = 11.10, P = 0.024$) and 'generation' (pre-hurricane, post-hurricane, first generation, second generation and third generation; LMM: $F_{(4, 205.3)} = 11.96, P < 0.001$) was a significant predictor of forewing length (LMM: $F_{(3, 205.1)} = 10.80$, $P < 0.001$; Supplementary Table 5). At flooded sites, the brachypterous individuals observed post-flood had forewings 14.2% longer than brachypterous individuals pre-flood (Extended Data Fig. 2a). Further, this increase persisted for at least three generations post-recolonization. This is not true for control sites, where the forewing length remained unchanged throughout the five generations of the monitoring period. This shift towards longer-winged flightless brachypterous females at recolonized flooded sites provides no known adaptive advantage and it is probably the consequence of the arrival during colonization of macropterous parents with longer wings (Supplementary Results—wing length).

Test of correlated changes in a non-dispersal trait

We found that spatial sorting at recolonized flooded sites spurred an increase in soapberry bug beak length. Before the hurricane, 'wing form' (macropterous versus brachypterous; LMM: $F_{(1, 1{,}082.7)} = 317.38, P < 0.001$) and 'sex' (male versus female; LMM: $F_{(1, 1{,}079.2)} = 1{,}754.19, P < 0.001$) were important predictors of beak length where macropterous individuals exhibited longer beaks than brachypterous individuals and females had longer beaks than males in each host-associated group (Extended Data

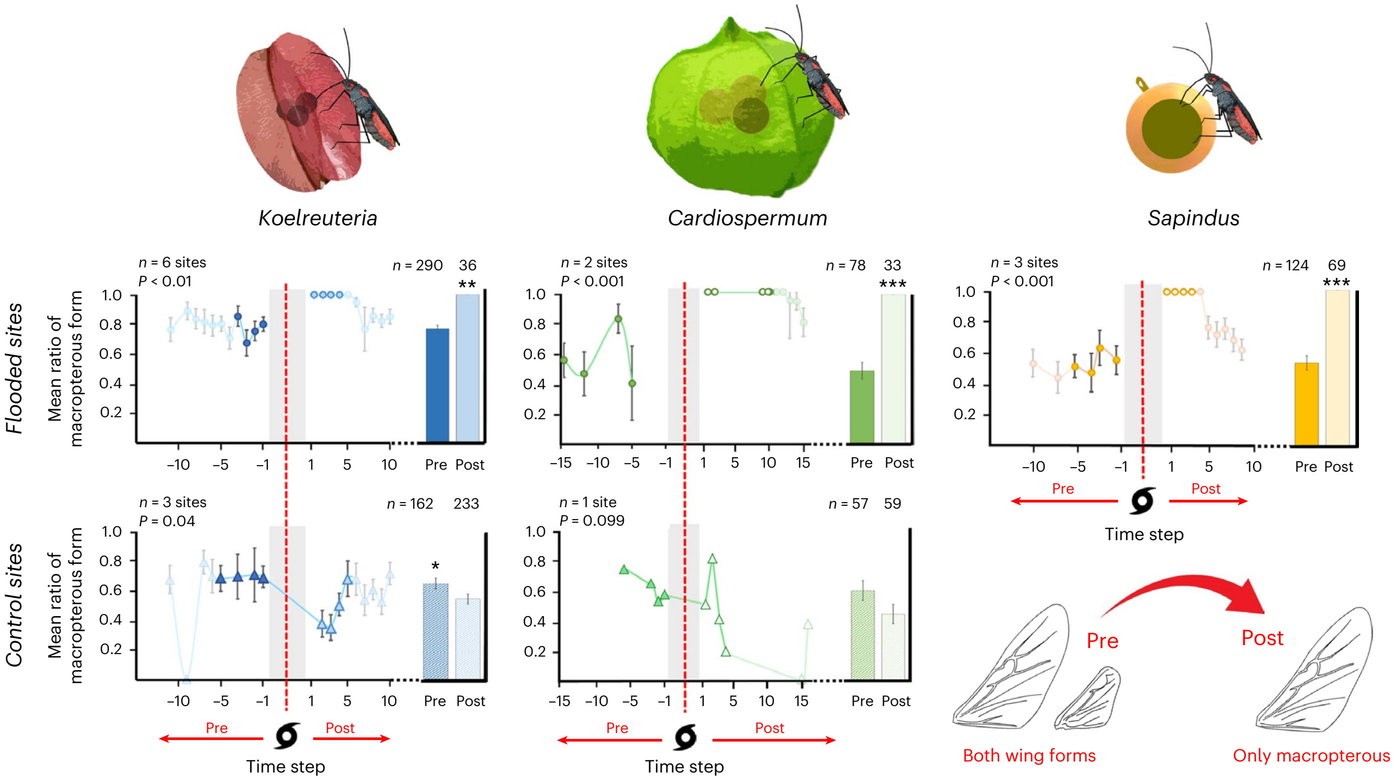

Fig. 4 | Spatial sorting shifts the frequency of macropterous soapberry bugs. Mean ± s.e. of the ratio of macropterous to brachypterous soapberry bugs at flooded (circles) and control (triangles) sites at each sampling point separated by host plant association: *Koelreuteria* (blue), *Cardiospermum* (green) and *Sapindus* (gold). Each sampling point is in relation to the hurricane depicted by the red dashed line (at $t = 0$) and represents a 2 week window of time between sampling efforts. Because insects recolonized flooded sites at different points in time, post-hurricane sampling points are standardized in relation to recolonization after the hurricane. The four emboldened points pre- and post-hurricane were used for statistical analysis, while faded points represent sampling efforts outside the period of analysis. The bar graph on the right of each plot summarizes the mean ± s.e. of the four pre- and post-hurricane samples included in the analysis. Sample sizes at the top of each plot provide the number of sites and the number of individuals included in the analysis. Asterisks indicate levels of significance per two-sided Fisher's exact test with $^{*}P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

Fig. 3, Supplementary Table 6 and Supplementary Results—association between wing form and beak).

To test the correlated effects of spatial sorting on an ecologically relevant trait genetically linked to dispersal phenotypes, we compared shifts in beak length due to the post-hurricane accumulation of macropterous individuals at recolonized flooded sites. In doing so, we compared the macropterous individuals, as they were the only wing form to recolonize flooded sites. Here, we find that the effect of spatial sorting on having limited recolonization to only macropterous individuals corresponds with a rapid phenotypic shift in beak length resulting in longer beaks at flooded sites post-recolonization (Fig. 4a,b). In a comparison of female soapberry bug beak lengths, the interaction of site condition (flooded versus control; LMM: $F_{(1, 12.9)} = 2.998$, $P = 0.107$) and 'time period' (pre- versus post-hurricane; LMM: $F_{(1, 514.1)} = 124.511$, $P < 0.001$) was highly significant (LMM: $F_{(1, 514.1)} = 127.63$, $P < 0.001$; Supplementary Table 7). Beak lengths compared to pre-flood conditions underwent an immediate 11.6% increase in the generation of macropterous females that colonized flooded sites (Fig. 5a). Moreover, mean beak length regardless of morph for the total population before, during and after recolonization on each host, as well as the mean beak length within morphs before and after recolonization are illustrated in Supplementary Table 8.

Similarly, the interaction of site condition (LMM: $F_{(1, 12.5)} = 2.96$, $P = 0.110$) and time period (LMM: $F_{(1, 641.3)} = 66.70$, $P < 0.001$) was highly significant for macropterous males (LMM: $F_{(1, 610.3)} = 128.48$, $P < 0.001$; Supplementary Table 7). Here, we find that original colonization of flooded sites by macropterous males resulted in an 8.6% increase in beak length post-flood (Fig. 5b). At control sites, beak lengths for both males and females remained unchanged post-flood (Fig. 5a,b). Moreover, males and females at flooded sites were significantly different than their control counterparts in post-colonization beak lengths (Tukey's test: all $P < 0.01$; Supplementary Tables 9 and 10).

Test of correlated changes that persist across generations

Are the effects of spatial sorting maintained across generations? To test the persistence of changes to beak length across generations, we compared brachypterous individuals between control and flooded sites. Since brachypterous soapberry bugs are flightless and incapable of moving between habitats, those at post-flood sites must have descended from the macropterous colonizers. We found that longer beak lengths persisted in brachypterous individuals at post-colonized flooded sites (Fig. 5c,d). In a comparison of brachypterous females, we found that the interaction of site condition (LMM: $F_{(1, 12.9)} = 4.30$, $P = 0.059$) and time period (LMM: $F_{(1, 508.4)} = 76.72$, $P < 0.001$) was highly significant at predicting beak lengths (LMM: $F_{(1, 508.4)} = 68.92$, $P < 0.001$; Supplementary Table 11). At flooded sites, a 7.7% increase of beak length persisted in the subsequent two to three generations of brachypterous females descending from the initial longer beaked macropterous colonizers (Fig. 5c). Similarly, there was a persistence for the two to three generations measured of longer beak lengths in the brachypterous male descendants of colonizers at flooded sites, as post-flood beaks were 6.2% longer than brachypterous males collected at the same flooded sites before the hurricane (Fig. 5d). Here, the interaction between site condition (LMM: $F_{(1, 12.5)} = 8.23$, $P = 0.014$) and time period (LMM: $F_{(1, 621.8)} = 68.30$, $P < 0.001$) was also found to be a highly significant predictors of beak length (LMM: $F_{(1, 621.8)} = 60.689$, $P < 0.001$; Supplementary

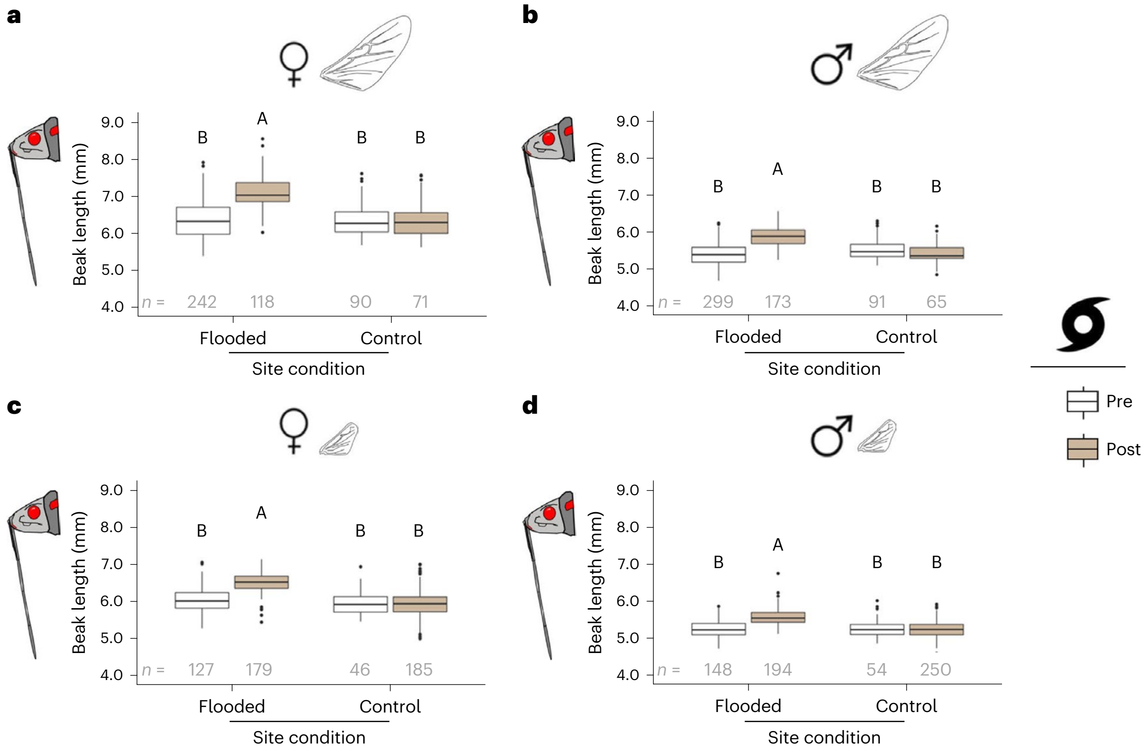

Fig. 5 | Spatial sorting promotes shifts in soapberry bug beak lengths. **a**–**d**, Box plots illustrating insect beak length at flooded and control sites before (white) and after (brown) the hurricane for macropterous females (LMM: $F_{(1,514.1)} = 127.63$, $P < 0.001$; Supplementary Table 7) (**a**), macropterous males (LMM: $F_{(1,610.3)} = 128.48$, $P < 0.001$; Supplementary Table 7) (**b**), brachypterous females LMM: $F_{(1,508.4)} = 68.92$, $P < 0.001$; Supplementary Table 11) (**c**) and brachypterous males (LMM: $F_{(1,621.8)} = 60.689$, $P < 0.001$; Supplementary Table 11) (**d**). The upper and lower edges of box plots indicate the first and third quartiles, the midline indicates the median value and the whiskers show the 95% confidence intervals with dots as outliers. Boxes labelled with different letters are significantly different (Tukey's test: $P < 0.05$; Supplementary Tables 9 and 10). Sample sizes (grey) located within panels are the number of individuals sampled per site condition and time period.

Table 11). In contrast, neither female nor male brachypterous insects at control sites exhibited a change of beak length (Fig. 5c,d). Further, the beak lengths of both female and male soapberry bugs were significantly different at post-flood sites from those of control sites, regardless of time period in relation to the hurricane (Tukey's test: all $P < 0.01$; Supplementary Tables 12 and 13).

In a more focused analysis using our largest host plant-associated dataset, which was on *Koelreuteria*, we found that longer beaks persisted for, at the very least, three generations of brachypterous females (Extended Data Fig. 2b). An LMM found the interaction between site condition (LMM: $F_{(1,3.4)} = 25.257$, $P = 0.011$) and generation (LMM: $F_{(4,202.7)} = 26.78$, $P < 0.001$) was significant (LMM: $F_{(3,202.6)} = 27.44$, $P < 0.001$; Supplementary Table 14). Beak lengths of the first generation of brachypterous females (mean ± s.e.: 6.44 ± 0.10 mm, $n = 8$) born at flooded *Koelreuteria* sites were 9.8% longer than pre-hurricane populations (5.81 ± 0.06 mm, $n = 39$). This longer beak phenotype persisted across all three generations at flooded sites post-hurricane (mean ± s.e.—second generation = 6.46 ± 0.07 mm, $n = 33$; third generation = 6.50 ± 0.08 mm, $n = 18$; Extended Data Fig. 2b). In contrast, there was no significant difference between pre-hurricane individuals (5.80 ± 0.08 mm, $n = 34$), the post-hurricane survivors (5.75 ± 0.12 mm, $n = 8$), first-generation post-hurricane (5.94 ± 0.08 mm, $n = 29$), second-generation post-hurricane (5.91 ± 0.08 mm, $n = 23$) and third-generation post-hurricane (5.73 ± 0.07 mm, $n = 26$) at control sites (Extended Data Fig. 2b). A post hoc Tukey's test found that although the three post-flood generations at recolonized flooded sites were not significantly different from each other, they were always significantly different from both the period before the flood and all generations of the control sites (Tukey's test: all $P < 0.05$; Supplementary Table 15).

Spatial sorting erodes divergence and promotes maladaptation

Spatial sorting has profoundly affected regional patterns of host-associated adaptations in beak length (Extended Data Fig. 4). Consistent with historical studies of soapberry bug phenotypes[35,54], the pre-flood variation in beak length could be explained by the three predictor variables sex, wing form and 'host association' (Extended Data Fig. 5 and Supplementary Table 16). Mean beak lengths of soapberry bug associated with *Cardiospermum* (6.23 mm, $n = 161$) were longer than *Sapindus*-associated bugs (5.85 mm, $n = 289$), both of which were longer than *Koelreuteria*-associated bugs (5.64 mm, $n = 646$; Extended Data Fig. 5). These host-associated differences were most pronounced in macropterous females (Tukey's test: all relevant comparisons $P < 0.01$; Supplementary Table 17 and Extended Data Fig. 5).

Spatial sorting eroded this recently evolved divergence among all host-associated biotypes, indicative of profound practical consequences for local adaptation (Supplementary Results—erosion of phenotypic divergence). Phenotypic variance in the beak length among macropterous females pooled across the region was reduced by >30% (pre-hurricane: $s^2 = 0.2439$; post-hurricane: $s^2 = 0.1660$). Unexpectedly, this collapse did not occur by settling on the regional average but, due to the effects of spatial sorting, all populations converged on a phenotype closer to the 90th percentile of the regional population before the hurricane (Fig. 6). Consequently, there evolved a long-lasting elimination of host-associated beak length differentiation (Tukey's test: all pairwise comparisons $P > 0.20$; Supplementary Tables 18 and 19). On one host plant, *Cardiospermum*, spatial sorting led to rapid adaptive change in beak length but, on the other two hosts, *Koelreuteria* and *Sapindus*, the outcome of spatial sorting led to rapid maladaptive

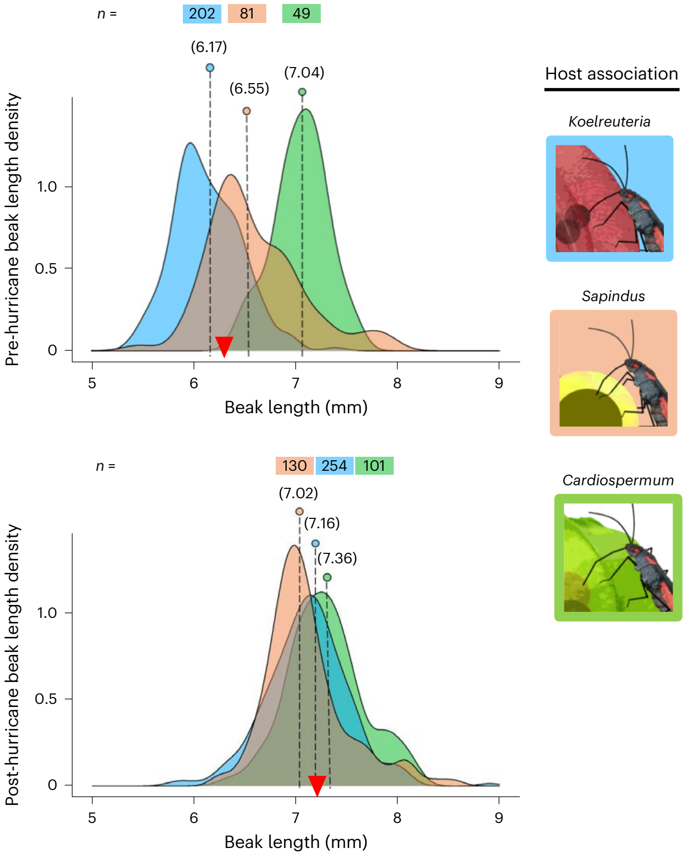

Fig. 6 | Spatial sorting erodes the history of host-associated natural selection. Density plots illustrating phenotypic variance of soapberry bug beak lengths before ($s^2 = 0.244$; top panel) and after the hurricane ($s^2 = 0.166$; bottom panel). Density plots are separated by host association: *Koelreuteria* (blue, $n = 9$ sites), *Sapindus* (orange, $n = 3$ sites) and *Cardiospermum* (green, $n = 2$). Data are limited to only include macropterous female beak lengths. Dashed lines topped with coloured circles denote the means of each host association (value in mm in parentheses) while the red triangle denotes the overall mean. Sample size reflecting the number of macropterous female insects measured is provided above each density plot coloured to correspond with host association.

change, where we define adaptation and maladaptation in reference to the matching of beak length to the fitness optimum per host plant, which is the mean distance to the seed within the fruit (Fig. 2d–f) with direct consequences for insect fitness[35,37,39,40,47].

Discussion

Spatial sorting is a process of dispersing organisms that generates non-random shifts in local phenotype frequencies, such that good dispersers are the first to arrive at the leading edge of invasions or in recolonized habitats. This leads to assortative mating, as only other strong dispersers are present during the time of colonization[10,25]. For instance, in the current study, mate options at recolonized flooded sites were initially limited to macropterous individuals as wing form during colonization was 100% biased by the ability to fly (Fig. 4). Spatial sorting could then be self-reinforcing, as offspring of colonizing individuals are expected to show similar or stronger dispersal phenotypes, along with a higher frequency of genetically correlated traits not associated with dispersal.

Prior studies of spatial sorting as a mechanism of evolutionary change have revealed its importance in migrations or invasions across a variety of diverse taxa[9,13,26–33] and its mechanisms have been verified through laboratory-based experiments[14,15]. Our study tests the potential for spatial sorting to facilitate or impede adaptive divergence due to genetic correlations between dispersal traits and important non-dispersal traits[28]. It also measures the effects of spatial sorting during recolonization of habitats after a natural disaster caused local extinctions at the regional scale. Given our rapidly changing world, the importance of evolution through spatial sorting could increase as local extinction and range shifts emerge as hallmarks of the Anthropocene.

One of the key results of our study is that spatial sorting can generate sudden and persistent directional shifts in traits with important functions beyond dispersal ability—in this case, the length of the insect's mouthparts. As suggested, spatial sorting driven by recolonizing flying individuals increased beak length at all flooded sites (Fig. 5a-d). We found a unilateral shift towards longer beak lengths arising at every recolonized site, regardless of environmental factors such as host association (Extended Data Fig. 4). Further, this change occurred in the opposite direction of previously documented phenotypic shifts on two of the three host plants due to natural selection on standing genetic variation within the regional population[35,36]. Thus, hurricane-driven spatial sorting instantaneously eroded an ~60+ year history of host-associated beak length evolution on the much smaller, non-native *Koelreuteria* seed pods (Extended Data Figs. 6 and 7).

The likelihood and rate at which non-dispersing, brachypterous phenotypes may appear in flooded sites is uncertain. Flight wing development in soapberry bugs may respond plastically to environmental conditions to a modest degree, including intraspecific density and food level during development but the probability that long-winged mothers will have long-winged offspring is relatively resilient to environmental conditions and mating with short-winged fathers[41,44,55]. Thus, inferring partial genetic-based changes in response to episodic disturbance linked to climate change is most likely. However, it can be particularly challenging to isolate the exact proportion of change due to genetics and plasticity given the limitations of our non-destructive study design[37,56]. Combining the known high heritability of beak length and the strong genetic correlation between beak length and wing form established over decades of work in this system, we expect the observed phenotypic shifts to be partially genetic. Nonetheless, catastrophic weather events like hurricanes, which lead to high-amplitude temporal variation in the habitat quality for niche specialists such as soapberry bug, have been suggested to facilitate population structuring in which the effects of spatial sorting can persist or cycle indefinitely[57–60].

Another aspect of partitioning change in beak length and, thus, the degree of adaptation and maladaptation due to spatial sorting, involves breaking it down to those attributable to changes in morph frequency versus changes in mean beak length per morph[61]. In Supplementary Table 8, we report the mean beak length (±s.e.) of females for the total population associated with each host plant and the combined mean across the region at three points: (1) before the flood, (2) at initial colonization after the flood and (3) in the generations after initial colonization. We also report mean beak length (±s.e.) for each morph within each host before the flood and then in generations after initial colonization when both macropterous and brachypterous individuals are present. Collectively, we find that the largest effects are changes in the frequency of the morphs with additional changes in the mean beak size per morph.

Hurricane Harvey was locally catastrophic for the flooded soapberry bug study populations, with populations at 11 of the 15 monitored sites going locally extinct and remaining so for at least 4.5 months (Supplementary Table 1) and seven additional populations never returning over the 3 years post-hurricane. Beyond the assumed initial mortality inflicted by the wind and rain of this category 4 storm, the prolonged flooding exceeded both the life expectancy of the adult insects[42] and the time for which submerged insect eggs remain viable (Fig. 3b). These effects led to complete eradication of the insect population at those sites for an average of 14.3 months (Supplementary Table 1). Understanding the immediate and lasting impacts of episodic weather events is progressively more important with the frequency and intensity of hurricanes increasing[4,5] and more so in light of insect populations declining globally[62–64].

Appreciating spatial sorting as an evolutionary mechanism is key to understanding how it differs from other dispersal-associated ecological outcomes, including habitat matching and phenotype-dependent habitat preference[65,66], where different phenotypes disperse into habitats to which they are specifically adapted (for example, refs. 55,62). Rather than habitat matching, we found a unidirectional shift towards longer beaks in all 11 flooded sites (Extended Data Fig. 4), which is distinct from phenotype-dependent habitat preference. This evolved outcome has manifested not at range edges, which cannot expand indefinitely[67–69], but rather among metapopulations within a habitat mosaic[70], in which spatial sorting may persist unbounded by the same ephemeral limitations as range expansions[60]. What signatures of spatial sorting as a process persisted through the study? First, the decline in macropterorous frequencies across the three subsequent generations post-colonization towards pre-flood frequencies (Fig. 4) could suggest a short-lived bout of spatial sorting but could also have resulted from unmeasured elevated emigration in stronger dispersing offspring. Notable in this regard, wing lengths of the flightless brachypterous descendants of flooded site colonists were greater than those of both their pre-flood predecessors or their control-site counterparts (Extended Data Fig. 2a). The shift of this dispersal-related phenotype transpired and persisted despite their inability to fly, suggesting an enduring, maladaptive imprint of spatial sorting in the population.

The influence of spatial sorting on beak length likewise persisted, regardless of wing form. We attribute this persistence to mating between longer beaked, better dispersing macropterous forms after recolonization of flooded sites (Extended Data Fig. 6). Most notably, the unilateral shift towards longer beaks in the brachypterous offspring of the macropterous founder individuals was maintained (Extended Data Fig. 7). This shift across generations reveals not only the classical spatial effect of sorting[10] but also a temporal component. The persistence of the longer beaks in habitats where it is maladaptive also raises another question—how are new populations successful when maladapted? First, the fitness advantage of beak length in soapberry bugs arises when it matches the distance between outer fruit wall and the interior seeds. This increases seed access and decreases handling time, leading to higher relative fecundity in females over time[39]. Combined with the observation that beak length is a polygenic trait[37,40,41], this type of sublethal fitness effect is expected to have more long-term evolutionary consequences. In addition, our study only followed populations for a handful of generations after the flood; thus, it is likely that low densities of the soapberry bugs led to low levels of competition and weak selection against maladapted individuals early during recolonization.

Others[71] predicted an extremely long-lived genetic signature from spatial sorting during range expansion when directional climate change is sufficiently prolonged to eradicate low-dispersal alleles from a population. Under a twentieth-century climate analysis, Hurricane Harvey has simply erased 60 years of adaptation since *Koelreuteria* was widely introduced in the region. However, a more contemporary climate assessment points to a more tumultuous dynamic where spatial sorting acts as a periodic 'reset button' generating longer mouthparts better suited to a subset of the host species spaced by intervening divergent host use selection that tunes the adaptive differentiation in beak (and other traits) among them. The Houston region has already experienced seven major floods in this millennium, including three categorized as '500-year' floods within a span of 4 years alone[72]. Unlike the closely related soapberry bug host associations in Florida, where the ancestral, long-beaked phenotypes on native *Cardiospermum* have recently disappeared due to apparent gene flow from derived, short-beaked *Koelreuteria*-associated bugs[73], beak lengths around Houston are seen to increase following catastrophes, thus shifting back towards the optimum on one of their ancestral hosts, *Cardiospermum*. In this view, spatial sorting is creating repeated opportunities for adaptive differences to re-evolve among the host-associate populations. How well the alleles needed for that repeating resilience will persist in the new climate regimen dominated by catastrophe remains unanswered.

In summary, we provide an important case study that highlights how the climate-driven increase in the magnitude and frequency of extreme weather events demands greater knowledge of spatial sorting as an important driver of contemporary evolution. Our findings provide compelling evidence that spatial sorting can have direct and indirect effects resulting in rapid local evolution in fitness-associated traits via a process not directly related to selection, gene flow or drift.

Methods

Hurricane Harvey

Hurricane Harvey made landfall 25 August 2017, as a category 4 hurricane along the Texas coast ~50 km northeast of Corpus Christi, Texas, United States[74]. As the storm moved northward, it stalled over Houston, Texas, for a protracted period. Over the next 5 days, at an average rate of 65 mm of rain per hour, this storm event produced 1,500 mm of rain on the Greater Houston area in what was regarded as a once in a 10,000-year event[75,76]. This immense rainfall resulted in flooding across the region, exacerbated by the high degree of urbanization[77,78]. Although the entire city was overwhelmed, not all locations flooded equally. Lack of ground permeability and subsidence resulted in pockets of prolonged inundation outside of the normal floodplain, which in some locations lasted for nearly 3 months[79,80].

Field sampling soapberry bug populations

Our study was conducted as a long-term natural experiment in a 1,200 km^2 region in the Houston area that spanned the year before and the 3 years after the 2017 flooding event caused by Hurricane Harvey. In doing so, we monitored soapberry bug populations that inhabit three locally available host plant species, balloon vine (*C. halicacabum*), western soapberry (*S.* var. *drummondii*) and goldenrain tree (*K. elegans*) (Fig. 2d–f). Our study included 15 sites (three *C. halicacabum*, three *S. drummondii* and nine *K. elegans*; Extended Data Fig. 1) sampled 72 times over the 3-year period after the hurricane (September 2017 to September 2020). Sampling was performed on days without precipitation and was conducted between the hours of 10:00 and 15:00. Each site was sampled once every 14 days. Of the 15 monitored sites, 11 sites flooded (three *S. drummondii*, six *K. elegans* and two *C. halicacabum*), while four sites did not flood and serve as our controls (three *K. elegans* and one *C. halicacabum*; Supplementary Table 1). Flooded sites in this study were inundated with standing water from 7 to 90+ days. No *S. drummondii* sites were included in our control as this natural experiment relied on the serendipitous overlap of flood patterns with our previous history of insect sampling. Taking advantage of haphazard flooding also created discrepancies in host plant abundance, which varied between sampling sites, with *Koelreuteria*- and *Sapindus*-associated sites consisting of anywhere from one to seven trees and *Cardiospermum*-associated sites consisting of 5–20 herbaceous plants.

For each sampling effort, insects were collected by hand over a period of 30 min from a 50 m^2 region around the base of the host plant. Captured insects were temporarily stored in a plastic container lined with Insect-a-Slip (polytetrafluoroethylene coating, Bio Quip Products). For each individual soapberry bug, insect beak length was measured in the field using a digital caliper (Stainless Steel iGaging ABSOLUTE ORIGIN 0–6″ Digital LCD Electronic Caliper-IP54; iGaging) and wing morphology (macropterous, full flight wings; brachypterous, reduced wings) was visually assessed by the presence of developed corium of the distal membrane of the insect's forewing (Fig. 2b). Captured insects were immediately returned to their habitat after morphological measurements to avoid artificial selection on any population. Given that some flooded sites were colonized earlier than others, we limited our data analysis to individuals collected in the first year (26 sampling periods) after colonization at flooded sites and after the hurricane at control sites to avoid over-representation of any one individual site.

Field measurements of soapberry bug morphology

The morphological measurements of the focal insect traits included beak length, wing form and insect forewing length. We measured beak length as the distance from the clypeus margin of the lower sclerites to the most distal point of the labium in insects[47]. The categorical variable wing form was determined to be either brachypterous or macropterous on the basis of visual inspection. An individual was classified as brachypterous when the mediocubital and apical folding fields of the hindwing were underdeveloped and a developed distal membrane on forewing was absent; an individual was classified to be macropterous if the mediocubital and apical folding fields of the hindwing were fully developed and the distal membrane of the forewing was present (Fig. 2b,c). Forewing length was measured as the distance from the proximal margin of the scutellum to the distal edge of the forewing membrane. Individuals where trait measurements were obscured by damage were excluded.

Test of local extinction: field surveys and egg mortality

We tested for hurricane-associated local extinction of soapberry bugs across an original 22 monitored host-associated sites. Of these 22 monitored locations, 7 of the 18 flooded sites failed to undergo recolonization in the 3 years that followed hurricane flood-associated localized extinction and, thus, offer an additional cautionary tale of the impacts of extreme weather on local insect populations. Simply put, 32% of soapberry bug populations remained extirpated from previously occupied sites 3 years after the hurricane. We excluded these 7 sites from our continuing analysis of the 15 sites that were either recolonized or remained intact (Extended Data Fig. 1 and Supplementary Table 1). In doing so, population densities were assessed as the number of insects that were CPUE per sampler (30 min per number of observers). We characterized population extinction as a period of 2+ months (four sampling periods) where we failed to detect a single adult or juvenile nymph at a sampling location—a period that matches the 2 month upper limits of a reproductive adult insect's lifespan[42]. Through this methodology, we are confident that surviving adults were not missed during our sampling as we were consistently able to detect very low densities of insects. For instance, individual insect arrival was often observed post-extinction; however, their presence did not always result in established populations due to lack of mate options as male colonizers were often the only individuals present at the time. Thus, we defined successful recolonization by the arrival of both male and female adults and the detection of juvenile nymphs at a site, which is an indication that local reproduction had occurred post-hurricane. Although mated females could potentially arrive at sites, there is a tendency for females to begin histolysis of flight muscles during oogenesis[53] and sperm competition and prolonged mate guarding behaviour by males[38] is likely to greatly reduce potential for movement between sites after mating.

To assess for local extinction, we tested for the hurricane's effect on the population size of each study site using a GLMM with a Poisson distribution where our response variable was population (number of insects CPUE rounded up to the closest integer and an $X + 1$ transformation) and our predictor variables were time period (pre- versus post-hurricane) and site condition (flooded versus control). We allowed random intercepts by study site ($n = 15$).

Even when both adults and nymphs have been eradicated from a site, there remains the potential that a bank of previously oviposited eggs could be lying dormant in the soil and leaf litter ready to repopulate a site. To test if soapberry bug eggs, which are oviposited in the soil at the base of host plants, survived long-term flooding, we conducted a laboratory-based egg survival experiment where we compared eggs reared under normal laboratory conditions to eggs that were submerged in water to replicate flooding. Five independent F_2 crosses were created from locally captured insects. The eggs from each cross were collected within 48 h of being oviposited into a sand-lined 10 cm Petri dish. Eggs from each of the five families were evenly distributed between an unmanipulated control ($n = 116$ eggs) and 2 days ($n = 116$ eggs) or 10 days ($n = 116$ eggs) of being submerged in water. Each replicate ($n = 6$ replicates) was conducted in a 1.5 ml microcentrifuge tube ($n = 18$–20 eggs per tube) in which controls only included eggs, while the two manipulated submergence treatments contained both eggs and 1 ml of water. All were kept at 23.8 °C under a 13:11 h light:dark schedule. At the end of the experimental period, the eggs were removed and placed on a sterile sand substrate and allowed to hatch. Post-natal nymphs were removed within 24 h of hatching to avoid egg cannibalism. The proportion of egg survival of each submergence treatment was calculated as the number of eggs hatched divided by the total number of eggs included in the treatment. To assess how flooding influenced egg survival we used a binomially distributed Bayesian LMM to account for Hauck–Donner effect of quasicomplete separation in which the covariate completely predicts a subset of the responses[81,82]. In doing so, we use the a priori estimation of three standard deviations in our Bayesian inference that complements our LMM. The response variable for this model was egg 'survival' and the predictor variable was submergence period. We included 'maternal line' as random effect.

Test of spatial sorting: wing form frequency and length

To test for spatial sorting, we compared shifts in the proportion of macropterous individuals that were observed in the adult insects surveyed pre- and post-hurricane across each site to compare flooded versus controls. We included the last four sampling periods pre-hurricane and the first four sampling periods post-hurricane once 'recolonization' had been observed. The timing of recolonization differed by site but we defined recolonization at each site with the observation of a juvenile nymph after the arrival of the first colonizing adult pair (male and female), which signified that the habitat had been recolonized by both sexes and local reproduction had restarted.

We then standardized sampling time steps after the hurricane to align flooded populations and control populations with variable arrival times. To do so, we set time-step one of flooded populations as the arrival of colonizing individuals. The eight sampling time steps per site were then pooled together as pre- or post-hurricane samples and grouped by host assocation and site condition (flooded versus control). The analysis included 4 control sites and 11 flooded sites. Of the control sites, three were *Koelreuteria*-associated (146 individuals pre-hurricane versus 118 post-hurricane) and one was *Cardiospermum*-associated (34 individuals pre-hurricane versus 26 post-hurricane). The flooded sites consisted of six *Koelreuteria*-associated sites (333 individuals pre-hurricane versus 128 post-hurricane), two *Cardiospermum*-associated sites (51 individuals pre-hurricane versus 33 post-hurricane) and three *Sapindus*-associated sites (154 individuals pre-hurricane versus 130 post-hurricane). A two-sided Fisher's exact test was conducted to test for differences in the mean frequency of macroptery between the insect populations before and after the hurricane-associated flooding. Each analysis was conducted independently by host association and site conditions.

In addition to testing shifts in the frequency of the discrete variable of macroptery, we also tested for changes in the continuous phenotype of brachypterous wing length. In doing so, we test the ability of spatial sorting to reorganize and ultimately shift phenotypic variation by dispersal. As brachypterous individuals are unable to fly, there is no selective pressure for increased wing lengths as there is an energetic trade-off between wing development and fecundity[53]. Here, we assess the forewing length of brachypterous females collected on *Koelreuteria*-associated sites. We selected this specific group of insects for this analysis for two reasons: (1) of our host-associated sites, *Koelreuteria* was the most abundant in our experiment and therefore provide us with more adequate sample sizes; (2) we selected to use females because they experience the strongest dispersal/fecundity trade-off as brachypterous females mature faster and produce both more and larger eggs than their macropterous counterparts[53]. To test for changes in 'wing length' we constructed an LMM to compare traits between generations assessed as 60-day blocks of time starting with individuals collected pre-hurricane and ending after four generations post-hurricane for control sites. In contrast, we include only three generations post-colonization for flooded sites as there is a missing generation post-hurricane due to no brachypterous individuals being present immediately after the recolonization events. Each block is equivalent to the approximate lifespan of an adult soapberry bug[42,50]. We use wing length as our response variable and generation (pre-hurricane, post-hurricane, first generation, second generation, third generation) as an ordered fixed effect using orthogonal polynomial contrasts. To account for variation between each sampling location we included site as a random effect ($n = 11$).

Test of correlated changes in a non-dispersal trait

Having assessed the ability of spatial sorting to shift both wing form frequencies and wing lengths, we next test if shifts in dispersal traits have the capacity to also affect non-dispersal traits that are genetically correlated. One of the more important correlated traits in the evolutionary history of soapberry bugs is insect beak length, which provides no dispersal benefit but is ecologically important for feeding on their host plants. However, before we can establish the potential of spatial sorting for creating correlated phenotypic change, we first test for dimorphic beak length differences that could obscure any shift created by differential dispersal. To accomplish this, we use insects collected pre-hurricane ($n = 1{,}096$) as these individuals have not yet experienced the effects of spatial sorting. In doing so, we created an LMM that included beak length as the response variable and the two predictor variables of sex (male versus female) and wing form (macropterous versus brachypterous). The interaction of these two variables was also included. To account for potential site differences, we included 'sample site' ($n = 15$) as a random intercept. A post hoc Tukey's test was conducted to compare differences between levels.

After establishing sex and wing form dependent dimorphic differences of beak length, we tested the immediate effects of spatial sorting on beak length—a correlated yet non-dispersal-related trait. To accomplish this, we compared macropterous insects ($n = 1{,}157$) recorded in the immediate five sampling periods pre-hurricane (females, 332; males, 390), five sampling periods post-hurricane for flooded sites (females, 118; males, 173) and control sites (females, 79; males, 65). These individuals represent the instantaneous effects on phenotype due to spatial sorting, as the insects that are included in this analysis embody only the colonizing individuals at post-flooded sites, although individuals at control sites exemplify the surviving population at locations that did not flood. To test for shifts related to spatial sorting we construct two independent Gaussian distributed LLMs for each sex due to the previously assessed sexually dimorphic differences in beak length (Extended Data Fig. 3). Here, beak length was included as the response variable in each of the two models. Site condition (flooded versus control) and time period (pre- versus post-hurricane), as well as their interaction, were included as fixed effects. To account for variation between each sampling location we included site as a random effect. We also considered a weighted offset parameter to account for differences between sample sizes per site; however, this did not improve the model's predictive power, nor did it change our results. Thus, using the most parsimonious model selection, we did not include this parameter in our final model. A post hoc Tukey's test was conducted within each model to assess pairwise comparisons between each level of interaction.

Next, we tested for the consistency of spatial sorting in its ability to pattern directional shifts in non-dispersal-related phenotypes by comparing the redistribution of beak lengths among individual host plant-associated population. In doing so, we conducted two-tailed binomial tests that compare the slope of beak length for each flooded and control site pre- and post-hurricane. This analysis was conducted separately by sex and wing morphology to account for known dimorphic differences in beak lengths. A Welch's two-sample t-test was conducted of the mean shift in beak length per comparison.

Test of correlated changes that persist across generations

We test for the persistence of beak length shifts across generations in response to spatial sorting by comparing pre- (5 months of sampling before the hurricane) and post-hurricane (10 months of sampling after recolonization) beak lengths of brachypterous adult individuals at flooded ($n = 648$ insects) and control sites ($n = 535$ insects). Using brachypterous individuals that are flightless and unable to disperse between sites ensures that the insects included in the analysis were the offspring of colonizing individuals that hatched at the site in which they were collected. Thus, in recolonized sites, each brachypterous insect observed (female, 179; male, 194) is a descendant of a colonizing macropterous individual. In contrast, brachypterous insects from control sites (female, 185; male, 250) represent the offspring of the original pre-hurricane insect population. Using the brachypterous individuals, we constructed a Gaussian distributed LLM with beak length as our response variable. We included time period and site condition as fixed effects along with the interaction term. To account for variation between each sampling location we included site as a random effect. Consistent with the previous model, a weighted offset parameter to account for differences between sample sizes per site did not improve the model's predictive power and was therefore not included as a parameter in our final model. A post hoc Tukey's test was conducted within each model to assess pairwise comparisons between each level of interaction.

Next, to further test the persistence of these effects, we compare the beak lengths of five (control) to four (flooded) generations of *Koelreuteria*-associated brachypterous females in relation to flooded versus control sites. Similar to our test of wing length outlined above, we divide generations into 60-day blocks of time with our control sites consisting of a pre-hurricane generation and four generations post-hurricane for a total of five generations. In contrast, flooded sites have only four generations, as they lack a recolonized post-hurricane generation due to only macropterous individuals present at the point of colonization. An LMM was constructed using beak length as the response variable and generation as an ordered fixed effect using orthogonal polynomial contrasts. To account for variation between each sampling location we included site as a random effect. A weighted offset parameter to account for differences between sample sizes per site neither improved the model nor changed model results and was excluded.

Lastly, a linear model was constructed to compare the correlation between beak length and wing length regardless of site condition or time period. In doing so, we again use all the *Koelreuteria*-associated brachypterous females ($n = 218$) for this regression.

Spatial sorting erodes divergence and promotes maladaptation

With the establishment of the potential of spatial sorting to shift dispersal phenotypes and, in turn, increase beak lengths across all populations, we assessed whether changes were adaptive or maladaptive. Although host-associated selection on soapberry bug beak length is well established (see refs. 35,39,54), a comprehensive assessment of host-associated beak lengths in southeast Texas, the region encompassing this study, has overall been lacking. Before testing the role of spatial sorting in beak length evolution, we first describe the pattern of host-associated divergence before the hurricane. To accomplish this, we build off our previous LMM designed to test dimorphic differences in soapberry bug beak length by including the additional fixed effect of host association (*Cardiospermum*, *Koelreuteria* and *Sapindus*) to the interaction between sex and wing form. In doing so, beak length remained as the response variable. All interactions between the three fixed effects and the random effect of sample site ($n = 15$) were included in the model. A post hoc Tukey's test was conducted to compare interacting levels.

With local host-associated divergence of beak lengths confirmed, we test for conflict between spatial sorting and the effects of natural selection. In doing so, we assessed macropterous and brachypterous individuals independently by sex through the construction of four Gaussian distributed LLMs with beak length as our response variable. A three-way interaction between site condition, time period and host association was included as our fixed effect. Once again, to account for variation between locations, sample site was included as a random effect. A post hoc Tukey's test was conducted within each model to assess pairwise comparisons between each level of interaction.

As three-way interactions are difficult to interpret, we further subset the data by host assocation and repeated the LMMs across each subset line of data using only the two-way interaction of site condition and time period, with sample site as a random effect. The results of these reduced models corroborated the findings of our more complex three-way interaction while also resolving concerns of any possible type I errors.

Next, in our assessment of the interaction of spatial sorting with selection, we compare the distribution of the mean beak length of macropterous female insects pre- ($n = 332$) and post-hurricane ($n = 485$) at all flooded sites. We specifically chose to use females for this analysis because they are probably under the strongest host-associated selective pressure, as matching beak length to host seedpod size facilitates the ability to access still developing seed early in the season, providing a reproductive advantage[53]. Unlike previous comparisons of macropterous individuals which limited analysis to the immediate recolonization period (4 sampling periods), we now expand this comparison to include 25 sampling periods post-hurricane recolonization (~1 year) and 10 pre-hurricane sampling periods (~5 months). We delineated this sampling window to ensure each sampling site had equal representation in an effort to not bias our findings by over-representing sites that had been recolonized early on in the study. If spatial sorting is at least temporarily overwhelming natural selection, we should observe the erosion of diversification between host plant association. Here, we use two LLMs to assess the combined effect of spatial sorting and natural selection on ecological adaptation. The first model tested pre-hurricane host-associated differences in beak length under natural selection, while the second tested post-hurricane host-associated differences under both natural selection and spatial sorting. The response variable was beak length and host association was included as the fixed effect. A post hoc Tukey's test was used to test for differences between levels.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data collected for this project are freely available in the digital repository Dryad: https://doi.org/10.5061/dryad.tht76hf4t.

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Acknowledgements

We acknowledge funding by the American Museum of Natural History's Teddy Roosevelt grant to M.S.C., the American Philosophical Society's Lewis and Clark Explorer grant and the Society for the Study of Evolution's Small Grants for Local and Regional Outreach and funding to S.P.E. and S.P.C. from the National Science Foundation (award no. 1802715). We thank NSF programme officer G. Gilchrist for his critical feedback during the planning stages of this RAPID funded project. We thank J. Pawell for her integral role in insect field collections along with M. Comerford, R. LaRoche, L. Zhang and K. Gonzalez. In addition, we thank C. Boschert, K. Zhu, B. Ma and L. Ivanov for their contribution in measuring insect morphology. We would also like to extend a special thank you to C. Klein and her autumn 2018 Environmental Science class at Westside High School in Houston ISD for granting us access to Wolf Prairie and for their participation in this research. Artwork of insects interacting with host seed pods was done by T. M. Fowels.

Author contributions

The focus of this paper was conceived by M.S.C., S.C. and S.P.E. Data collection was performed by M.S.C. and T.M.L. with analysis by M.S.C. Writing was shared by M.S.C. and S.P.E. with feedback from S.C. and T.M.L.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-023-02205-7.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-023-02205-7.

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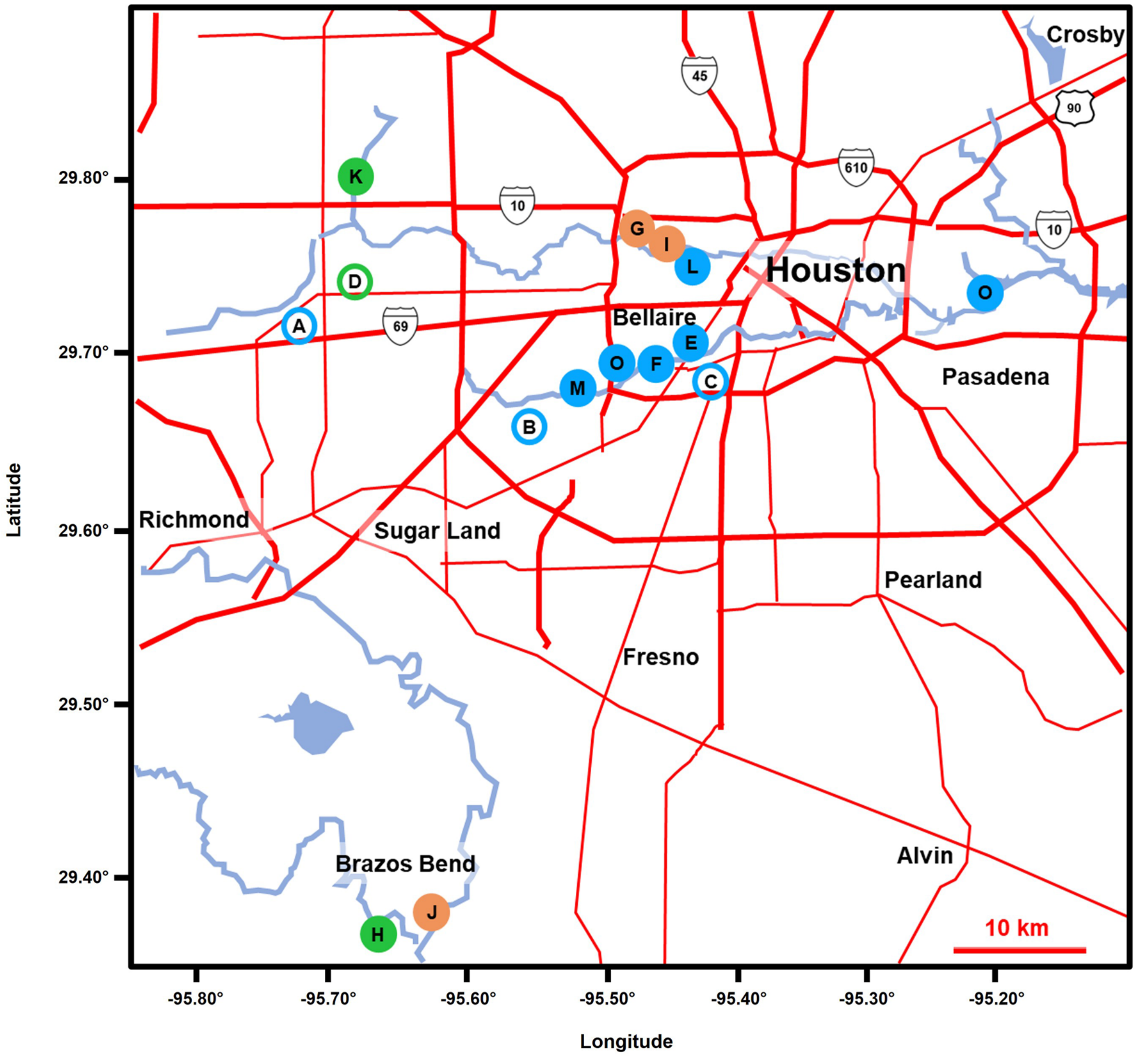
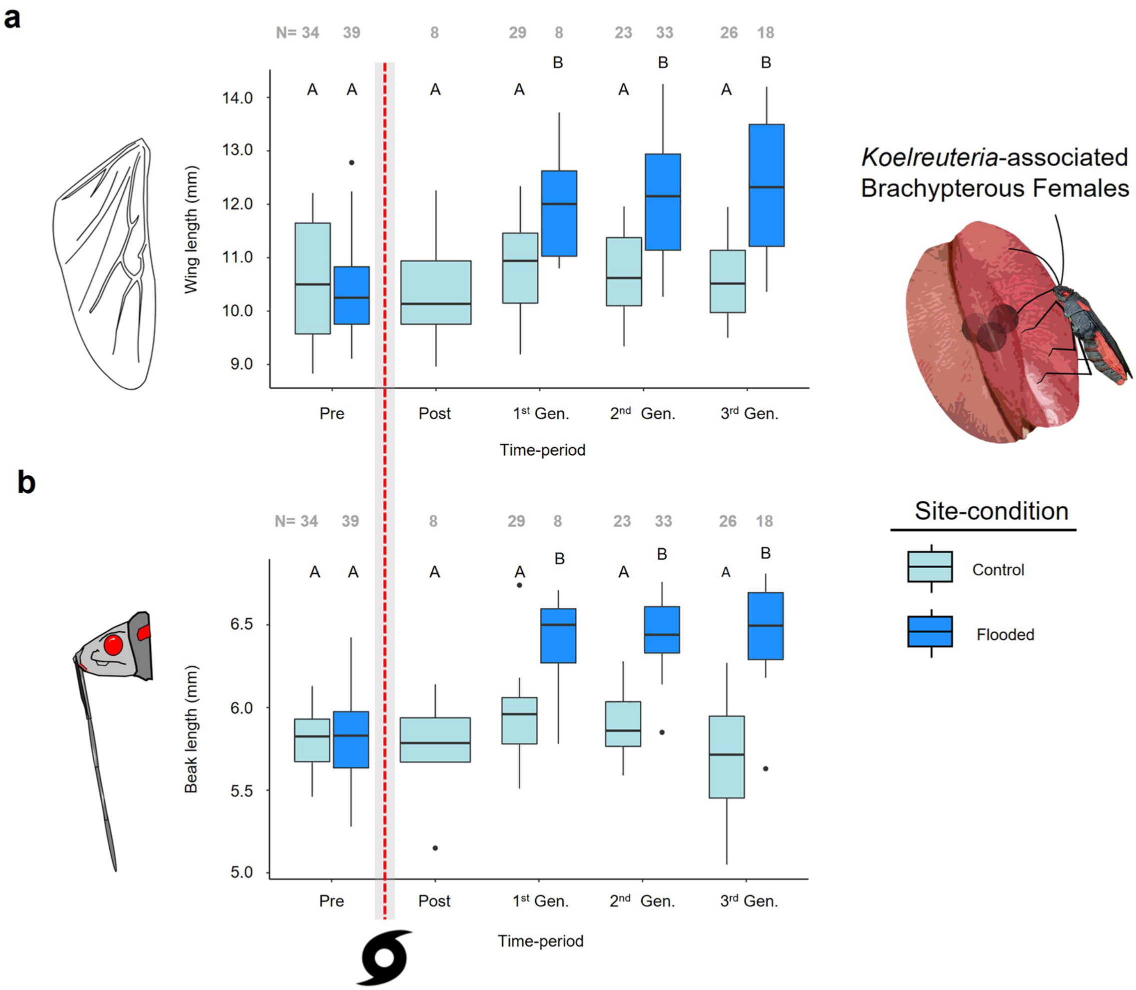
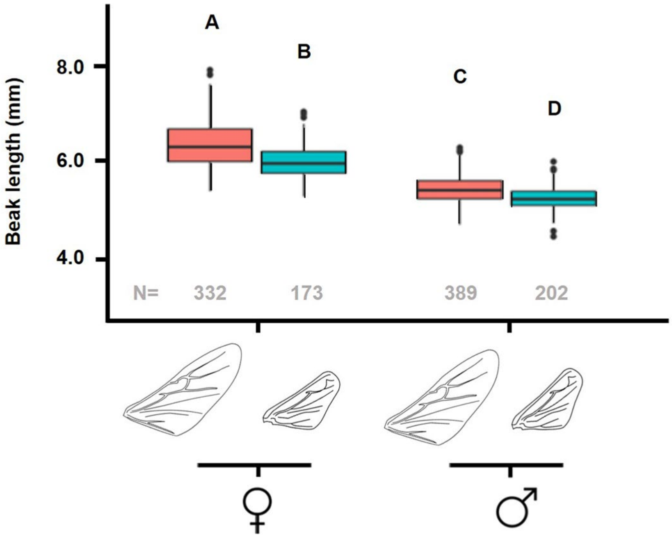
Peer review information *Nature Ecology & Evolution* thanks Meredith Cenzer and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.



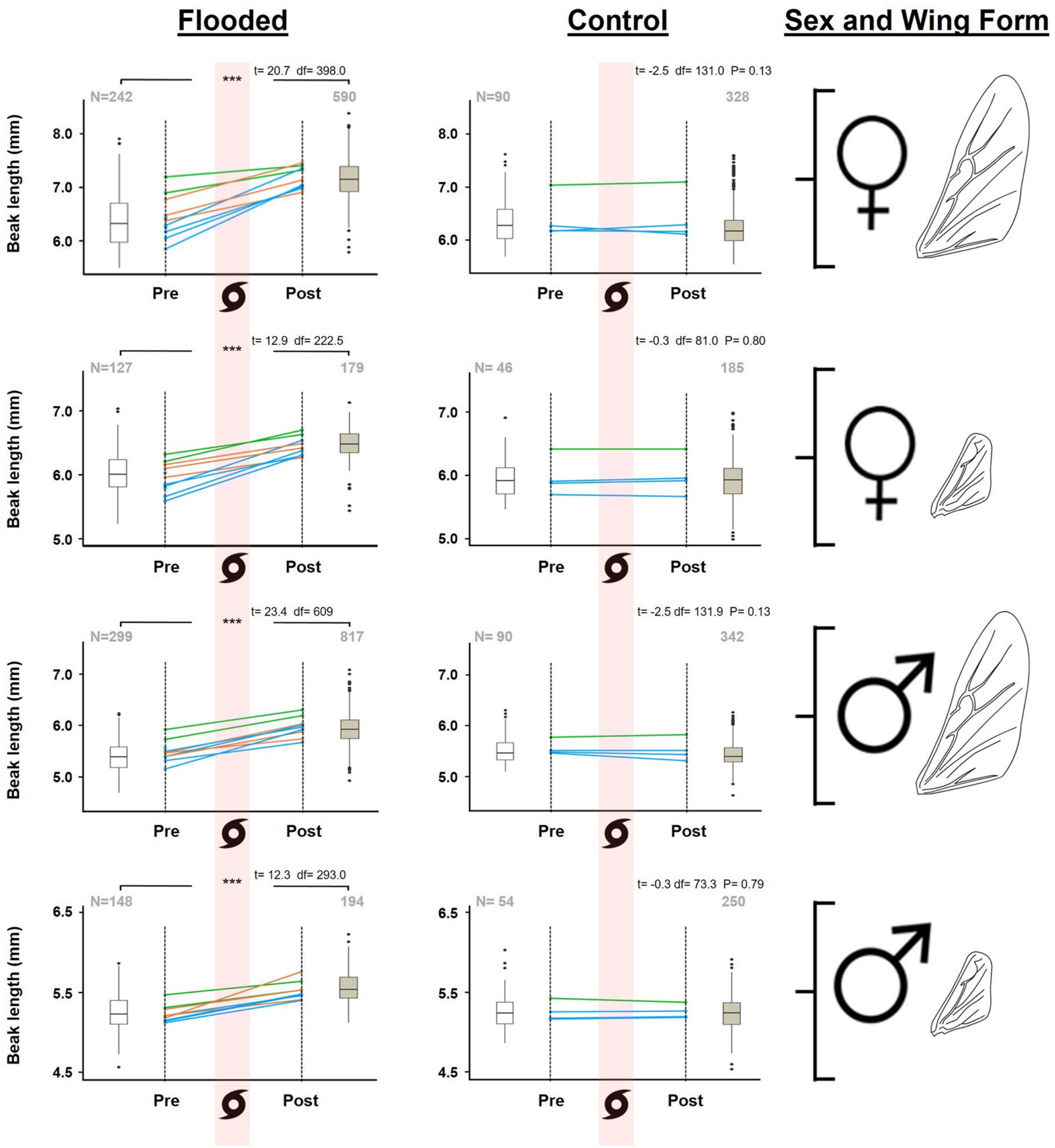
Extended Data Fig. 1 | Map of sample sites in this study. Map of soapberry bug sample sites by host association across Houston, Texas, U.S.A., from 2017 to 2020. Open circles denote unflooded control sites and filled circles denote flooded site locations. Host association is depicted by colour: *Koelreuteria* (blue), *Sapindus* (orange) and *Cardiospermum* (green). For corresponding latitude and longitude of each sample site location see Supplementary Table 1.



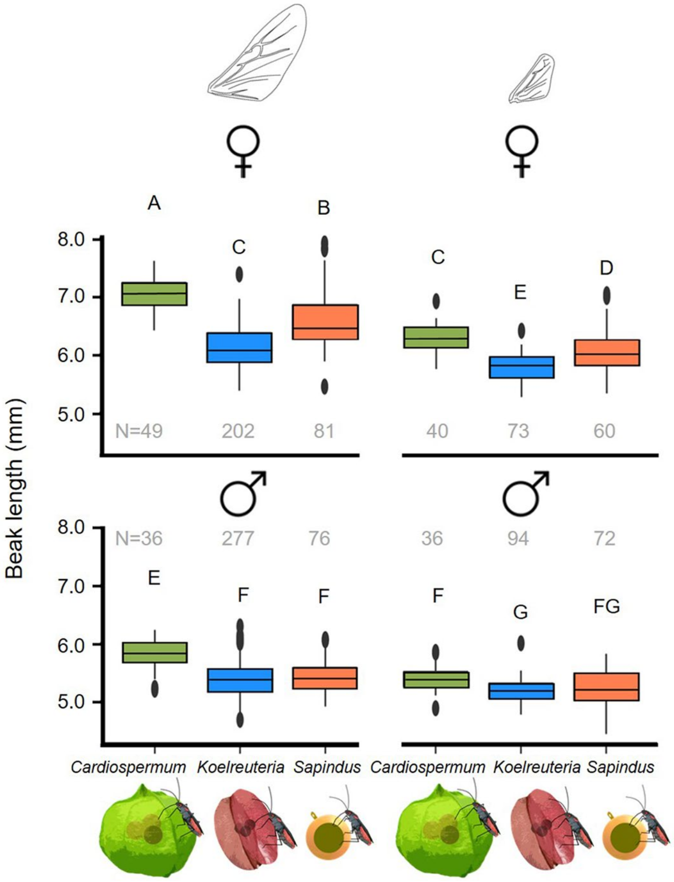
Extended Data Fig. 2 | Wing and beak lengths across multiple generations. Boxplot showing soapberry bug wing and beak lengths across multiple generations of *Koelreuteria*-associated brachypterous females. Panel (**a**) is a generational comparison of insect wing length between flooded (dark blue) and unflooded control sites (light blue). Model selection using linear mixed models (LMM) suggests that forewing lengths were longer at flooded sites in the three generations that followed recolonization (LMM: $F_{(3, 205.1)} = 10.80$, $P < 0.001$; Supplementary Table 5). Panel (**b**) is a generational comparison of insect beak length between flooded (dark blue) and unflooded control sites (light blue). Model selection using LMM suggests that beak lengths were longer at flooded sites in the three generations that followed recolonization (LMM: $F_{(3, 202.6)} = 27.44$, $P < 0.001$; Supplementary Table 14). In both panels, the red dashed line corresponds to Hurricane Harvey. Each 'generation' represents a 60-day block of time, which is equivalent to the maximum adult lifespan of a soapberry bug[50]. The upper and lower edges of the box indicate the first and third quartile, the midline indicates the median value and the whiskers show the 95% confidence intervals with dots as outliers. Sample sizes in grey within panels. Boxes capped with different letters are significantly different (Tukey's test: $P < 0.05$, see Supplementary Tables 15, 22). There were no brachypterous insects present during initial colonization, so a boxplot for flooded post-hurricane insects was not included in either panel.



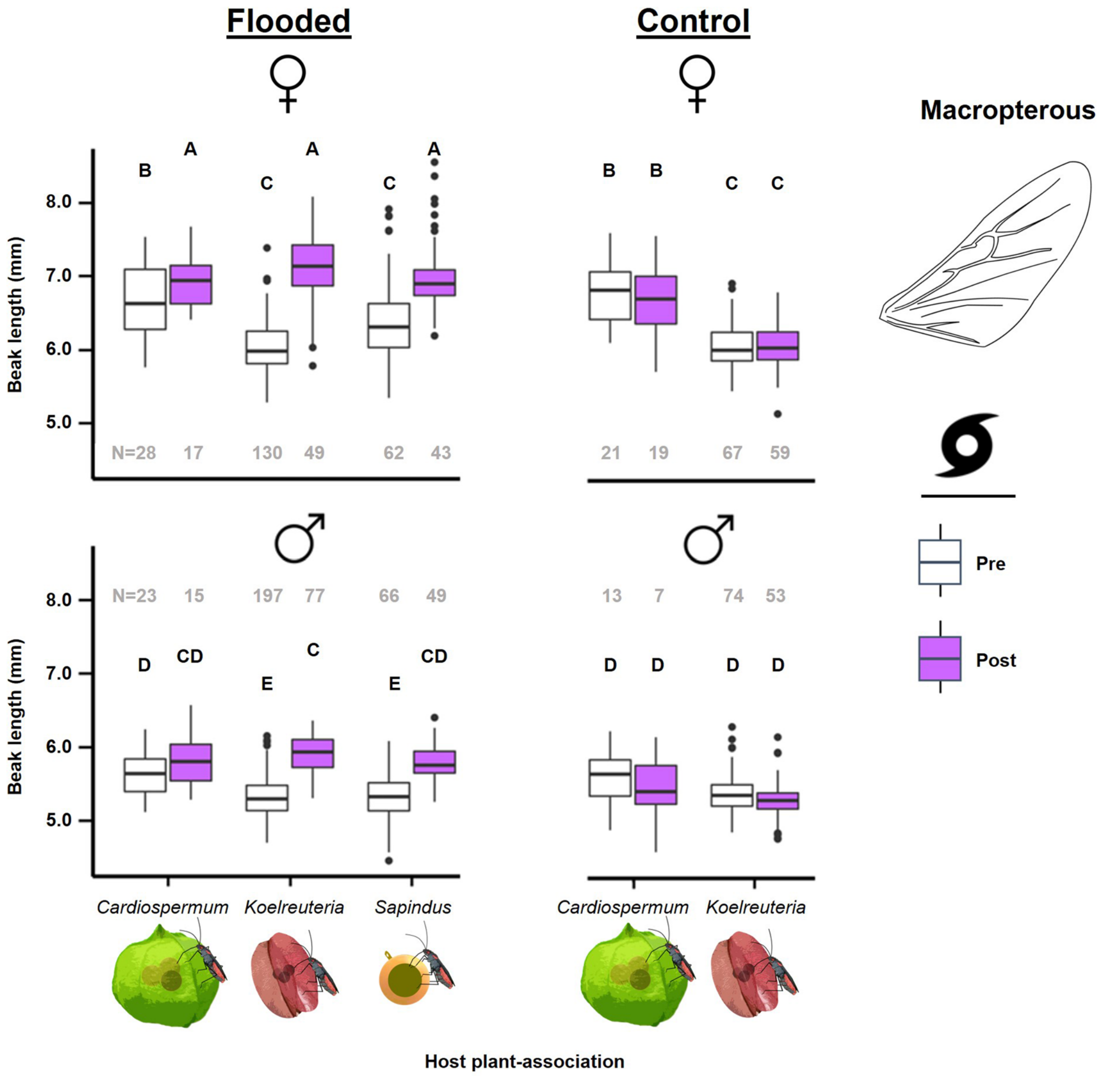
Extended Data Fig. 3 | Pre-hurricane regional patterns of soapberry bug beak length. Boxplot summarizing regional patterns of beak length in soapberry bugs sampled before the hurricane separated by sex (male and female) and wing form (macropterous insects in orange and brachypterous insects in blue). Model selection using linear mixed models suggests that females have longer beaks than males and macropterous individuals have longer beaks than brachypterous individuals (LMM: $F_{(1, 1079,)} = 18.286$, $P < 0.001$; Supplementary Table 6) The upper and lower edges of each box indicate the first and third quartile, the midline indicates the median value and the whiskers show the 95% confidences intervals with dots as outliers. Box plots labelled with different letters are significantly different (Tukey's test: $P < 0.01$, see Supplementary Table 23). Sample sizes provided in grey below each boxplot.



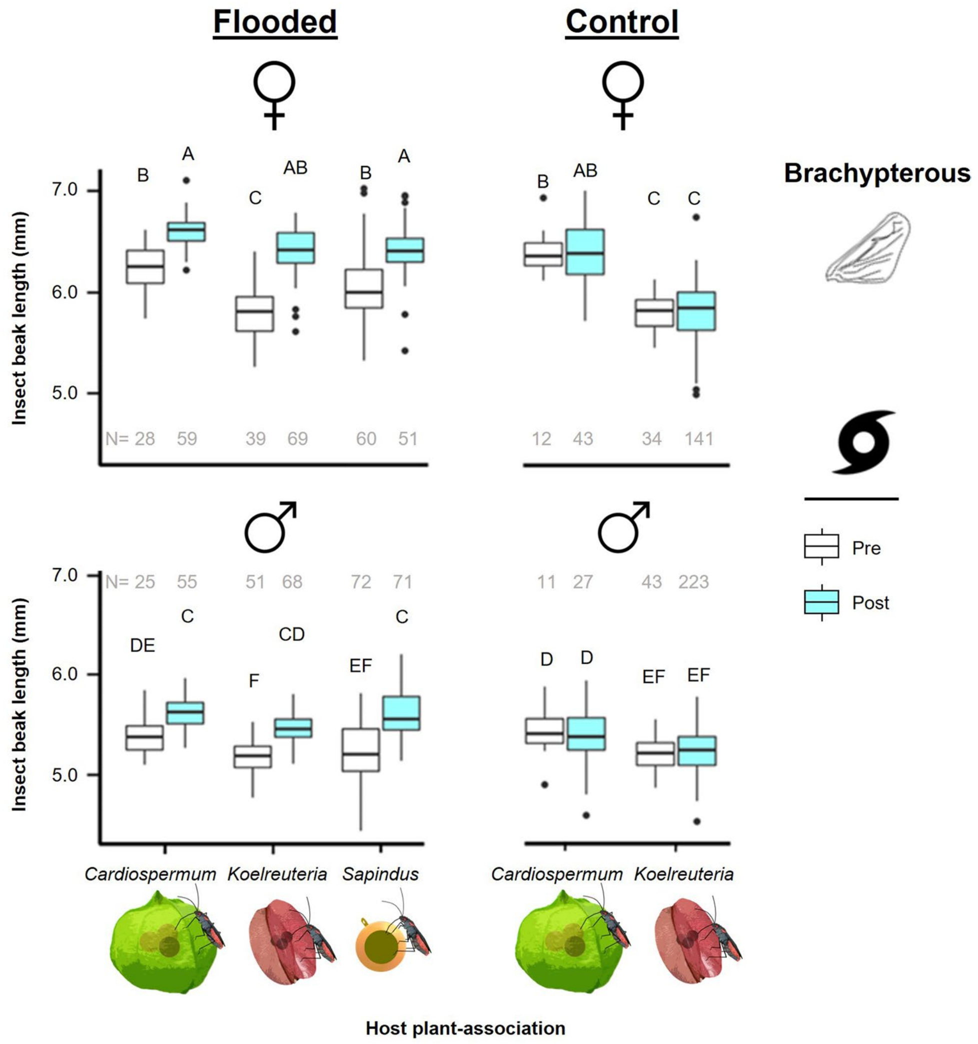
Extended Data Fig. 4 | Soapberry bug beak length before and after hurricane. Line plots illustrating hurricane-associated beak length changes of soapberry bugs at flooded (left) and control sites (right). Insect beak lengths are compared pre- and post-hurricane with the pink column in the middle marking the timing of Hurricane Harvey. Each coloured line represents an individual sampling site. The colour of each line represents the host association with *Cardiospermum* (green), *Sapindus* (orange) and *Koelreuteria* (blue). Box plots on left (pre-hurricane) and right (post-hurricane) illustrate the overall median, first and third quartile, 95% confidence intervals and outliers. Bars with asterisk indicate levels of significance per two-tailed Welch's test with (*) <0.05 and (***) <0.001, with test statistics provided at the top of each panel. Sample sizes in grey. Plots are aligned by horizontally by sex and wing form to account for previously demonstrated dimorphic differences in beak length (see Extended Data Fig. 3).



Extended Data Fig. 5 | Host plant-associated beak length before hurricane. Boxplot of host-associated beak lengths from soapberry bugs collected before the hurricane. Insect beak lengths are compared between host association denoted by colour with *Cardiospermum* (green), *Koelreuteria* (blue) and *Sapindus* (orange) and separated by sex (females – top; males – bottom) and wing form (macropterous – left; brachypterous – right; see Extended Data Fig. 3). Model selection using linear mixed models suggest that sex, wing form and host association are all important predictors of insect beak length (LMM: $F_{(2,1079)} = 2.88$, $P = 0.057$; Supplementary Table 16). The upper and lower boxes indicate the first and third quartile, the midline indicates the median value and the whiskers show the 95% confidence intervals with dots as outliers. Boxes labelled with different letters are significantly different (Tukey's test: $P < 0.05$, see Supplementary Table 17). Sample sizes in grey within panels.



Extended Data Fig. 6 | Beak length before and after hurricane for macropterous soapberry bugs. Boxplot of spatial sorting's effect on eroding a history of natural selection driven host-associated beak length differentiation in macropterous soapberry bugs. Divergent host-associated beak lengths (s ee Extended Data Fig. 5) are compared pre- (white) versus post-hurricane (purple). Insect host association is denoted by images of the insect feeding on each of their given host plants: *Cardiospermum* (green), *Koelreuteria* (red) and *Sapindus* (orange). Model selection using linear mixed models found the three-way interaction to be significant (LMM: $F_{(1, 518.5)} = 22.88$, $P < 0.001$; Supplementary Table 24), however, a post hoc Tukey's test suggests that host-associated beak lengths where no longer significantly different post-hurricane at the flooded sites (Tukey: $P > 0.1$). All *Sapindus*-associated sites flooded during the hurricane, so none were available in controls. Plots are aligned vertically by site condition with flooded sites on the left and unflooded control sites on the right. Plots are aligned horizontally by sex with females on the top and males on the bottom. The upper and lower edge of box plots indicate the first and third quartile, the midline indicates the median value and the whiskers show the 95% confidences intervals with dots as outliers. Boxes labelled with different letters are significantly different (Tukey's test: $P < 0.05$). Sample sizes in grey included in panels.



Extended Data Fig. 7 | Beak length before and after hurricane for brachypterous soapberry bugs. Boxplot of spatial sorting's effect on eroding a history of natural selection driven host-associated beak length differentiation in brachypterous soapberry bugs. Divergent host-associated beak lengths (See Extended Data Fig. 5) are compared pre- (white) versus post-hurricane (light blue). Insect host association is denoted by images of the insect feeding on each of their given host plants: *Cardiospermum* (green), *Koelreuteria* (red) and *Sapindus* (orange). Model selection using linear models found the three-way interaction to be significant (LM: $F_{(1, 509)} = 4.12$, $P = 0.04$; Supplementary Table 25), however, post hoc Tukey's test suggests that that host-associated differences between beak lengths are no longer significant at flooded sites post-hurricane (Tukey: $P > 0.1$). All *Sapindus*-associated sites flooded during the hurricane, so none were available in controls. Plots are aligned vertically by site condition with flooded sites on the left and unflooded control sites on the right. Plots are aligned horizontally by sex with females on the top and males on the bottom. The upper and lower edge of box plots indicate the first and third quartile, the midline indicates the median value and the whiskers show the 95% confidence intervals with dots as outliers. Boxes labelled with different letters are significantly different (Tukey's test: $P < 0.05$). Sample sizes in grey included in panels.

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Our web collection on statistics for biologists contains articles on many of the points above.

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Policy information about availability of computer code

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Data analysis	All statistical analyses and data illustrations were conducted with R v.3.6.1.

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Study description	This is a multi-level study of the role of spatial sorting in promoting evolutionary change. We monitored 15 populations of the redshouldered soapberry bug across southeast Texas, including eleven that went extinct and were later recolonized. In addition to over three years of monitoring natural populations, we compliment with detailed lab measurements and experiments, to experimentally verify the critical, but overlooked role of spatial sorting in driving adaptation and maladaptation after an extreme weather event.
Research sample	The focal species for this study was the red-shouldered soapberry bug, Jadera haematoloma. We closely followed 15 populations and measured many hundreds of individuals that were in the path of the hurricane, as well as measurements of over 100 background populations and many thousands outside of the hurricane's path.
Sampling strategy	We monitored 15 populations of the red-shouldered soapberry bug for 6 months prior to the hurricane and for three years following the hurricane. Using field collected indivduals, we also performed lab experiments and measurements on eggs and adults.
Data collection	For field monitoring, insects were collected by hand over a period of 30 minutes and temporarily stored in a plastic container, where morphological measurements were made and then insects were returned to the population. For egg submersion study, eggs were placed into three treatments and then followed for emergence success of the nymphs.
Timing and spatial scale	We monitored 15 populations of the red-shouldered soapberry bug for 6 months prior to the hurricane and for three years following the hurricane between spring 2017 to fall 2020. The spatial scale was the region of southeast Texas near Houston with monitored populations spanning a 1500 sq. km. area.
Data exclusions	No data was excluded in this study.
Reproducibility	A subset of morphological measurements were repeated on the same individual insect on different days and repeatability was high (r=0.99).
Randomization	Individuals were measured per population in the field and population was included as a random effect in all models. In the lab based egg submersion study, families were repeated across treatments to control for genetic variation among families, and family ID was included as a random effect in the model.
Blinding	Blinding was not possible in the field; but was performed in the lab relative to the egg submersion study.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	The field work was performed over a three and a half year period before and after Hurricane Harvey hit southeast Texas. Populations

Field conditions	were monitored every two weeks and weather varied seasonally.
Location	Southeast Texas
Access & import/export	Insects that were monitored for the main part of this study were returned to the population after measurement. Other Jadera individuals were collected in accordance with local laws for a non-pest insects.
Disturbance	No disturbance was caused during this study.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☐	☒	Animals and other organisms
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	This study focused on the red-shouldered soapberry bug, Jadera haematoloma, a harmless, non-pest herbivorous Hemipteran.
Wild animals	No ethical approval or guidance is required for research on wild insect populations that are common in nature.
Reporting on sex	Information on the sex of the red-shouldered soapberry bug, Jadera haematoloma, has been provided in the manuscript.
Field-collected samples	Insects at all monitoring sites were collected temporarily, measured, and returned to their natural population. Insects brought back to the lab were preserved for morphological measurement or kept in lab colonies, raised on seeds from their native host plant, and some climbing substrate, and placed in a plastic shoe box with a fixed lid and a small water source.
Ethics oversight	No ethical approval or guidance is required for research on wild insect populations that are common in nature.

Note that full information on the approval of the study protocol must also be provided in the manuscript.