Measuring the Strength of Spatial Sorting

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Abstract

Empirical work suggests that spatial sorting—a mechanism of evolutionary change fueled by phenotype-dependent dispersal—may lead to phenotypic shifts on ecological timescales. However, we currently lack a quantitative framework to measure the strength of spatial sorting. To address this gap, we present a quantitative genetics model of spatial sorting and identify an evolutionary parameter in the model to measure the strength of spatial sorting. This parameter, referred to as the standardized sorting gradient, is structurally akin to the standardized selection gradient, which is commonly used to measure the strength of natural selection. To show the utility of our approach, we analyzed binary wing-morphology data of soapberry bugs (*Jadera haematoloma*) recolonizing flooded habitats extirpated by a hurricane. We found that non-random recolonization resulted in a standardized sorting gradient of 0.90 ± 0.08, which ranked in the top 5 percentile compared to standardized selection gradients documented in the scientific literature. Genetic crosses further revealed that the binary trait, short and long-wing forms, is heritable h2 = 0.65 ± 0.13) and yielded a standardized evolutionary response of 0.58 ± 0.13. Our results underscore that, like natural selection, spatial sorting, too, can yield rapid evolution, providing quantitative evidence that non-random dispersal may produce novel eco-evolutionary dynamics.

Introduction

Extreme climatic events are becoming common due to rising carbon emissions and concomitant planetary warming (Solow 2015; Stott 2016). These climatic perturbations may impose strong selection on populations, which, in turn, may fuel rapid evolution (Grant et al. 2017). Indeed, many studies have documented strong selection in response to extreme events (Boag and Grant 1981; Brown and Brown 1998; Bumpus 1899; Donihue et al. 2018; Grant and Grant 1993). These studies underscore a common theme—an extreme event yields non-random mortality wherein some individuals live past the event because of a genetically determined trait that confers a survival advantage. When these survivors reproduce, the mean phenotype of the population changes, resulting in evolution by natural selection (Darwin and Wallace 1858). These rapid phenotypic shifts can, in turn, alter vital rates of populations, leading to novel eco-evolutionary dynamics (Hendry 2017)

Recent empirical work suggests that extreme events can also produce drastic phenotypic changes by a relatively lesser known evolutionary mechanism that relies on non-random dispersal (Comerford et al. 2023). Extreme events can extirpate some local populations in a patchy landscape, creating empty patches (van Bergen et al. 2020). These local extinctions create an opportunity for non-random immigration from nearby extant populations wherein a subset of individuals colonize the empty patches because of a genetically determined trait that confers a dispersal advantage. When these immigrants with traits that confer dispersal advantage mate with each other, the mean phenotype in hitherto empty patches changes relative to the nearby extant populations, resulting in evolution by spatial sorting (Shine et al. 2011).

Although a growing number of studies suggest that spatial sorting can also lead to rapid evolution (Comerford et al. 2023; Duckworth 2008; Forsman et al. 2011; Hanski et al. 2004; Hill

et al. 1999; MacKay and Lamb 1979; Peroni 1994; Phillips et al. 2006), we lack a quantitative framework to measure the strength of spatial sorting, especially after an extreme event. This gap in the literature stems from two reasons. First, extreme events are hard to predict, making it challenging to plan longitudinal studies to quantify their evolutionary impacts (Grant et al. 2017). Second, the theory of spatial sorting is still in its infancy (Bolnick and Otto 2013; Novak and Kollár 2017; Peischl and Gilbert 2020; Phillips and Perkins 2019). Unlike Breeder's equation (Lush 1937) and its extensions (Falconer 1960; Lande and Arnold 1983; Walsh and Lynch 2018) that provide a quantitative framework to measure the strength of selection using standardized selection gradients, we do not have a formal quantitative genetics theory that may allow biologists to study phenotypic evolution by spatial sorting. Addressing these knowledge gaps is crucial for empirically evaluating whether spatial sorting is strong enough to influence ecology, producing novel spatial eco-evolutionary dynamics (Miller et al. 2020; Ochocki and Miller 2017; Phillips et al. 2006; Weiss-Lehman et al. 2017).

This paper has two major goals. First, we derive a quantitative genetics model of spatial sorting starting from the first principles. This model is analogous to the Breeder's equation and serves several functions, such as facilitating a conceptual understanding of how spatial sorting drives the evolution of quantitative traits and providing a standardized measure to quantify the strength of spatial sorting, which we refer to as standardized sorting gradient. Based on the knowledge gained from the model, biologists can plan what data to collect, how to analyze it, and how to interpret the results in the broader context of evolutionary theory. Second, to demonstrate the utility of the quantitative genetics model, we analyze wing morphology data of red-shoulder soapberry bugs (*Jadera haematoloma*; hereafter soapberry bug) from a multi-year monitoring experiment (2016-2020) in the Greater Houston area that overlapped with Hurricane Harvey in

2017 (Comerford et al. 2023). Specifically, using the survey data, we estimate the standardized sorting gradient to quantify the strength of spatial sorting due to the phenotype-dependent recolonization of habitats extirpated by the hurricane. We also perform experimental crosses to evaluate if the wing morphology has a genetic basis and to test if the non-random recolonization could have resulted in an evolutionary response.

Quantitative genetics model of spatial sorting

Consider a landscape consisting of vacant and occupied patches. The occupied patches are inhabited by a population of N parents. We denote the trait value of the ith parent as ϕ_i, such that the mean trait value of the parents is given by $\bar{\phi} = \mathbb{E}(\phi)$. The bar is a shorthand for the mean or expectation. Next, some parents disperse from occupied patches to vacant patches, such that the dispersal probability of a parent is determined by its phenotype. To capture this phenotype-dependent dispersal, we define an indicator variable V_i, which is one if the ith parent disperses to the vacant patch and zero otherwise. We use W_i to denote the lifetime reproductive success of the ith parent.

Based on these notations, we can show that the mean trait value of parents in vacant patches after non-random dispersal and before reproduction is

$$\bar{\phi}_{vw} = \frac{\sum_{i=1}^{N} V_i W_i \phi_i}{\sum_{i=1}^{N} V_i W_i}. \tag{1}$$

This equation is obtained by adding the trait value of parents that disperse to the vacant patches and then dividing this sum by the number of parents that disperse to the vacant patches. We can re-express the above equation compactly as

$$\bar{\phi}_{vw} = \frac{\mathbb{E}(VW\phi)}{\mathbb{E}(VW)}$$

$$= \frac{\mathbb{E}(VW)\mathbb{E}(\phi) + \mathbb{C}\mathrm{ov}(VW, \phi)}{\mathbb{E}(VW)} \tag{2}$$

$$= \overline{VW}^{-1}\mathbb{C}\mathrm{ov}(VW, \phi) + \bar{\phi}.$$

By re-arranging the terms in equation (2), we find that the change in the trait of parents due to spatial sorting (here defined as, the mean trait value of parents in vacant patches after dispersal minus the mean trait value of parents in the occupied patches before dispersal) is given by

$$\begin{aligned} s_{vw} &= \bar{\phi}_{vw} - \bar{\phi} \\ &= \overline{VW}^{-1}\mathbb{C}\mathrm{ov}(VW, \phi) \\ &= \sigma_{\phi}^{2}\beta_{vw,\phi}\,, \end{aligned} \tag{3}$$

where σ_{ϕ}^{2} is the phenotypic variance of the trait and $\beta_{vw,\phi}$ is the slope of the regression line between relative sorting fitness, $V_i W_i / \overline{VW}$, and the trait value of an individual, ϕ_i. Intuitively, the above equation suggests that the magnitude of phenotypic change due to spatial sorting is governed by the variation in the trait of parents before dispersal and the strength of the statistical association between the number of offspring that a parent leaves in vacant patches after dispersal and its trait value. This association arises because parents with traits that confer them a dispersal advantage are more likely to disperse and, therefore, likely to leave more offspring in the vacant patches.

Next, upon reproduction, only the genetic component of the total phenotypic variation is passed to the offspring (Falconer 1960; Walsh and Lynch 2018), which yields a net evolutionary response of

$$\begin{aligned} \Delta\bar{\phi} &= h^2 s_{vw} \\ &= \sigma_{A}^{2}\beta_{vw,\phi} \end{aligned} \tag{4}$$

where σ_{A}^{2} is the genetic variance of the trait, and $h^2 = \sigma_{A}^{2}/\sigma_{\phi}^{2}$ is the heritability of the trait.

Note that the equation of evolution by spatial sorting (Eq. 4) is structurally similar to the Breeder's equation (Phillips and Perkins 2019). Consequently, we adopt the naming convention of variables in equation (4) that are analogs to their counterpart variables in the Breeder's equation. We refer to s_{vw} as the *sorting differential*, $\beta_{vw,\phi}$ as the *sorting gradient*, $V_i W_i$—the number of offspring the ith parent leaves in the vacant patches after dispersal—as the *sorting fitness* of i, $\overline{VW}$ as the *mean population sorting fitness*, and $V_i W_i / \overline{VW}$ as the *relative sorting fitness* of i.

More importantly, the similarities between the two models offer insights into what measure to use to quantify the strength of spatial sorting. We propose that the strength of spatial sorting should be measured using the sorting gradient of the standardized phenotypic trait, which we refer to as the *standardized sorting gradient*—$\beta'_{vw,\phi} = \sigma_\phi \beta_{vw,\phi}$. In the case of a single phenotypic trait, $\beta'_{vw,\phi} = \sigma_\phi \beta_{vw,\phi} = \sigma_\phi^{-1} s_{vw} = s'_{vw}$, where s'_{vw} is the *standardized sorting differential*. Using the standardized sorting gradient to quantify the strength of spatial sorting offers several advantages. First, the sorting gradient is closely connected to the equation of evolutionary change by spatial sorting (Eq. 4) and, therefore, has a predictive value in the context of quantifying evolutionary changes in phenotypic traits. Second, standardizing phenotypic traits provides a measure of the strength of spatial sorting, which can be compared across biological systems by putting traits on a common scale (Matsumura et al. 2012). Third, due to the structural congruence between the equations of evolution by natural selection and spatial sorting, standardized sorting gradients can be compared with standardized selection gradients to evaluate the relative magnitude of the two evolutionary forces in generating phenotypic shifts.

The quantitative genetics model presented above also shares several limitations of the Breeders equation (see Table 13.2 in Walsh and Lynch (2018) for a comprehensive list). For one, the model does not account for genetic correlations between multiple traits (Lande and Arnold

1983) arising from pleiotropy and linkage. These correlations can dramatically change our inferences about the direction and the magnitude of spatial sorting obtained from univariate analysis. For example, conducting separate univariate analyses on two strongly correlated traits with the same signed phenotypic shifts will yield the same signed sorting gradients. However, a joint multivariate analysis may reveal that the traits may have opposite signed sorting gradients, even though the observed phenotypic shifts after spatial sorting have the same sign. This situation can arise when the indirect response to spatial sorting due to genetic correlations on one of the traits is much larger in magnitude than the direct response. Another key assumption of the model is that individuals disperse to empty patches during spatial sorting, making the model formulism analytically intuitive and simplifying the estimation of sorting gradients using phenotypic data. However, this assumption is unlikely to hold in general (*e.g.*, range limits and invasion fronts), complicating theoretical modeling and quantification of trait clines due to spatial sorting in many natural settings.

Data Analysis

Soapberry Bugs

The soapberry bugs' ancestral range in the USA falls along the southern U.S. border with Mexico and the states abutting the Gulf Coast (Tsai et al. 2013). In humid tropical regions, including the Greater Houston area, soapberry bugs breed throughout the year. Upon mating, the females lay eggs in 1 cm deep holes beneath their host plants of the soapberry family (Carroll 1988). It takes about 10 days before the larval nymphs emerge from the eggs. Subsequently, the nymphs undergo five molting stages (also referred to as instars) over the next 29 ± 4 days before

reaching sexual maturity. These newly molted adult females avoid mating for 6 ± 1 days, after which they lay eggs throughout most of their 60-day lifespan (Carroll 1991) (see Fig. S1).

Females usually disperse before reproduction due to prolonged mate guarding by males (Carroll 1988) and the general tendency of females to begin histolysis of flight muscles post-oogenesis (Carroll et al. 2003). Soapberry bugs have binary wing morphologies—long-winged 'macropterous' and short-winged 'brachypterous' forms (Fig. 1A) (Dingle and Winchell 1997). These binary forms are strongly associated with dispersal abilities—macropterous insects have fully developed wings that allow them to fly long distances, while flightless brachypterous insects lack flight muscles. Previous studies suggest that this discrete-wing polyphenism is determined by juvenile hormones, which, in turn, are regulated by many genes with small effects, in addition to resource availability in the environment (Dingle 2001; Dingle and Winchell 1997).

Hurricane Harvey

Warm sea surface temperatures are perfect incubators for tropical storms in the Gulf of Mexico (Chen et al. 2008; Risser and Wehner 2017). On 25th August 2017, Hurricane Harvey struck southeastern Texas, releasing in excess of 1500 mm of precipitation in a span of seven days (Trenberth et al. 2018). This one in ten-thousand-year event led to intense flooding across the Greater Houston area (Emanuel 2017; Van Oldenborgh et al. 2017). However, not all regions were affected equally. Variation in ground porosity and subsidence led to prolonged flooding in some areas while others remained unaffected (Miller and Shirzaei 2019). Fortuitously, the hurricane occurred during a multi-year population survey by Comerford et al. (2023), which was initiated a year before the hurricane and continued for an additional three years.

Monitoring Scheme

Comerford et al. (2023) noted the insect abundances and the morphological form of soapberry bugs every 2 weeks at fifteen sites across the region (Fig. 1A). The survey data revealed two important observations. First, four of the fifteen sites that did not experience prolonged flooding (hereafter called unflooded sites) maintained a stable population throughout the survey (blue points in Fig. 1A). The remaining eleven flooded sites (pink points in Fig. 1A) experienced a local extinction of insects (Fig. 1 B and C). Extinction was confirmed by a gap of 4.5 to 27 months gap in insect detection at the flooded sites, exceeding the ~100 days life expectancy of soapberry bugs (from the egg stage to the death of an insect). In addition, inundation experiments by Comerford et al. (2023) showed that after a week of submergence, egg survival drops precipitously and is zero after ten days. This provided further corroborative evidence for local extinction because females lay eggs in the soil beneath the host plants (Carroll 1988), and the topsoil at the flooded sites was inundated for 7 to 90+ days after the hurricane (Fig. 1C). Second, post-hurricane, the flooded sites were re-established only by macropterous insects, while the unflooded sites had a much lower proportion of macropterous insects (Fig. 2A). This observation is consistent with the theory of spatial sorting—since macropterous insects are better dispersers than flightless brachypterous insects, insects recolonizing the flooded sites have a higher proportion of macropterous forms relative to the insect population in the unflooded sites.

Strength of Spatial Sorting

To measure the strength of spatial sorting in soapberry bugs, we took six weeks of post-hurricane data from flooded and unflooded sites, starting from the first co-detection of male and female insects at a site (Comerford et al. 2023). We made this choice because it takes about six

weeks for an egg to develop into a penultimate nymph (the last stage before the insect reaches reproductive maturity). During this development period, the instars can be visually distinguished from adults, which allows us to avoid individuals from our analysis who were born in the flooded patches after recolonization (see Fig. S1). The survey revealed that, in the six weeks after the hurricane, 47 of the 108 sampled individuals at the unflooded sites (or 43%) had macropterous forms. In contrast, all 88 individuals sampled at the flooded sites had macropterous forms.

We assume the visible morphological form of an insect has a threshold response to an underlying unobserved continuous trait, called liability, such that when the liability of a parent insect is above zero, the individual takes the macropterous (brachypterous) form (Fig. 2B) (Dingle et al. 2009; Roff 1996). The variation in the liability is assumed to be determined by environmental and genetic factors and can be thought of as the concentration of some substance (Falconer 1960).

Assuming that the liability of insects has a normal distribution (Fig. 2B), the mean liability of the insects in the unflooded sites can be expressed as

$$\bar{\phi}\sigma_{\phi}^{-1} = \sqrt{2}\,\mathrm{Erf}^{-1}(2p - 1) \tag{5}$$

(blue triangle in Fig. 2B), where p is the proportion of macropterous insects at the unflooded sites and Erf^{-1} is the inverse error function. Note that the mean liability of insects can only be measured in units of standard deviation of phenotypic distribution (σ_{ϕ}). Intuitively, equation (5) identifies the mean liability of insects in the unflooded sites, $\bar{\phi}$, such that the area under the liability distribution from the threshold value (zero) to infinity is p. Next, because only macropterous insects were found at the flooded sites (see Comerford et al. 2023), we assume that only insects with a liability greater than zero participate in the recolonization of the flooded sites. Thus, the mean liability of the insects at the flooded sites ($\bar{\phi}_{vw}$) is the mean liability of macropterous insects in the unflooded sites (see the proof in supplementary information). This is given by the mean of

the liability distribution of insects at the unflooded sites truncated from below at zero (pink triangle in Fig. 2B):

$$\bar{\phi}_{vw}\sigma_{\phi}^{-1} = \bar{\phi}\sigma_{\phi}^{-1} + \sqrt{2\pi p^2}^{-1}\, e^{-\frac{1}{2}\left(\frac{\bar{\phi}}{\sigma_{\phi}}\right)^2}. \tag{6}$$

By rearranging the terms in the above equation, we can show that the strength of spatial sorting quantified by standardized sorting gradient is given by

$$\beta'_{vw,\phi} = s'_{vw} = \sigma_{\phi}^{-1}(\bar{\phi}_{vw} - \bar{\phi}) \tag{7}$$

$$= \sqrt{2\pi p^2}^{-1}\, e^{-\frac{1}{2}\left(\frac{\bar{\phi}}{\sigma_{\phi}}\right)^2}.$$

To calculate $\beta'_{vw,\phi}$, we first calculate $\bar{\phi}\sigma_{\phi}^{-1}$ using $p = 0.43$ as input in equation (5), and then use the estimated value of $\bar{\phi}\sigma_{\phi}^{-1}$ and p to calculate $\beta'_{vw,\phi}$ using equation (7). We found a statistically significant standardized sorting gradient ($\beta'_{vw,\phi}$= s'_{vw}= 0.90 ± 0.08; see supplementary code). When we compared the magnitude of the standardized sorting gradient to the magnitude of standardized selection gradients documented in the scientific literature, it ranked in the top 5 percentile among ~1400 previous studies (Kingsolver et al. 2001).

Heritability and Evolutionary Response to Spatial Sorting

To test if spatial sorting could have resulted in an evolutionary change, we performed multigenerational crosses to estimate the heritability (see supplementary for details). This multigenerational breeding experiment was conducted under standardized laboratory conditions, which allowed us to control for plasticity and maternal effects.

We collected 40 juvenile insects from three geographical locations (Austin, Stock Island, and Gulfport) separated by more than 350 km. The insects were reared under standardized laboratory conditions and randomly mated to generate 28 males and 28 females of the F1

generation of insects. Upon maturation, the morphological form of F1 insects was noted: we used the numerical value one (zero) to represent macropterous (brachypterous) insects. Subsequently, the insects were randomly paired to generate an F2 generation of insects. Upon eclosion from eggs, 14 F2 nymphs were selected haphazardly from each maternal line. The insects were reared under the same conditions as F1 insects, and their morphological form was noted upon maturation.

To estimate heritability, we fit a threshold animal model (De Villemereuil et al. 2016) with the morphology of F1 and F2 insects as input for parents and offspring forms, respectively. We found a statistically significant estimate of heritability of liability ($h^2 = 0.65 \pm 0.13$) (Hadfield 2010), suggesting that wing morphology is highly heritable.

Finally, we used the estimates of h^2 and s'_{vw} in equation (4) to calculate standardized evolutionary change ($\Delta\bar{\phi}' = \Delta\bar{\phi}\sigma_{\phi}^{-1} = h^2 s'_{vw}$). We find that non-random recolonization of the flooded sites would have resulted in a standardized evolutionary change ($\Delta\bar{\phi}'$) of 0.58 ± 0.13 in insect liability. The large magnitude of standardized evolutionary change suggests that evolution by spatial sorting may exert a strong influence on the spatial population dynamics of a species.

Discussion

We present a quantitative genetics model of spatial sorting that is structurally akin to the Breeder's equation (Eq. 4). The model suggests that the evolutionary change by spatial sorting can be partitioned into two components, sorting gradient and additive genetic variance, which can be estimated independently using dispersal traits of organisms measured during a recolonization event and an animal model with pedigree data as input, respectively. We propose that analogous to the Breeder's equation, the sorting gradient of standardized traits (i.e., $\beta'_{vw,\phi}$) can be used to quantify the strength of spatial sorting. This choice offers two advantages. First, putting traits on

a common scale (*i.e.*, in units of standardized deviation) allows evolutionary biologists to compare the strength of spatial sorting across biological systems (Matsumura et al. 2012). Second, biologists can juxtapose standardized sorting and selection gradients to assess the relative magnitude of phenotypic shifts arising from non-random dispersal (*i.e.*, spatial sorting) and non-random survival and reproduction (*i.e.*, natural selection).

Next, we applied our quantitative genetics model of spatial sorting to study the evolution of soapberry bugs' liability because of morphology-dependent recolonization of habitats extirpated by Hurricane Harvey in Greater Houston (Fig 1; Comerford et al. 2023). We found a statistically significant standardized sorting gradient ($\beta'_{vw,\phi}$) of 0.90 ± 0.08 (Fig. 2), which ranked in the top 5 percentile of standardized selection gradients documented in the scientific literature (Kingsolver et al. 2001). Genetic crosses revealed that insect liability is a heritable trait ($h^2 = 0.65 \pm 0.13$), yielding a standardized evolutionary change in liability ($\Delta\bar{\phi}'$) of 0.58 ± 0.13 due to spatial sorting.

The estimate of the standardized sorting gradient suggests that non-random colonization of habitats can produce phenotypic shifts comparable to the most extreme observed phenotypic shifts in natural populations (Kingsolver et al. 2001). And, since many natural populations have abundant heritable variation in dispersal-associated traits (Saastamoinen et al. 2018), spatial sorting may yield evolutionary changes on ecological timescales, producing novel eco-evolutionary feedback, which may impede or facilitate species persistence (Hendry 2017; Miller et al. 2020).

For instance, a continuous assortment of highly dispersive individuals at the periphery can produce accelerated invasions (Phillips et al. 2006), which may leave little time for managers to plan and act before the invader becomes geographically widespread, making subsequent management efforts prohibitively expensive. However, accelerated range expansion can also be beneficial: spatial sorting can rescue populations from extinctions due to changing climate by

allowing faster tracking of poleward moving climatic niches (Boeye et al. 2013). This mechanism of genetic rescue could be important when the climate velocity is higher than the mean species velocity. Alternatively, in fragmented landscapes with patchy distribution of suitable habitats, non-random dispersal may maintain dispersive phenotypes. As a result, spatial sorting may increase the resilience of patchy populations experiencing random extinctions by maintaining an elevated colonization rate (Heino and Hanski 2001).

In conclusion, our quantitative genetics model and empirical analysis provide evidence that, like natural selection, spatial sorting can produce phenotypic shifts on ecological timescale, which may, in turn, have reciprocal effects on spatial ecological dynamics. These novel ecological dynamics may play an important role in the Anthropocene in determining the redistribution of biodiversity as alien species are introduced beyond their biogeographical realm and native species shift their geographical distribution to track their climatic niches.

Author Contribution

NG conceived and designed the study based on feedback from TEJ and MSC. MSC led the survey and performed the crosses. NG built the model and analyzed the data with feedback from TEJ. NG wrote the paper with feedback from all authors. Authors declare no conflict of interest.

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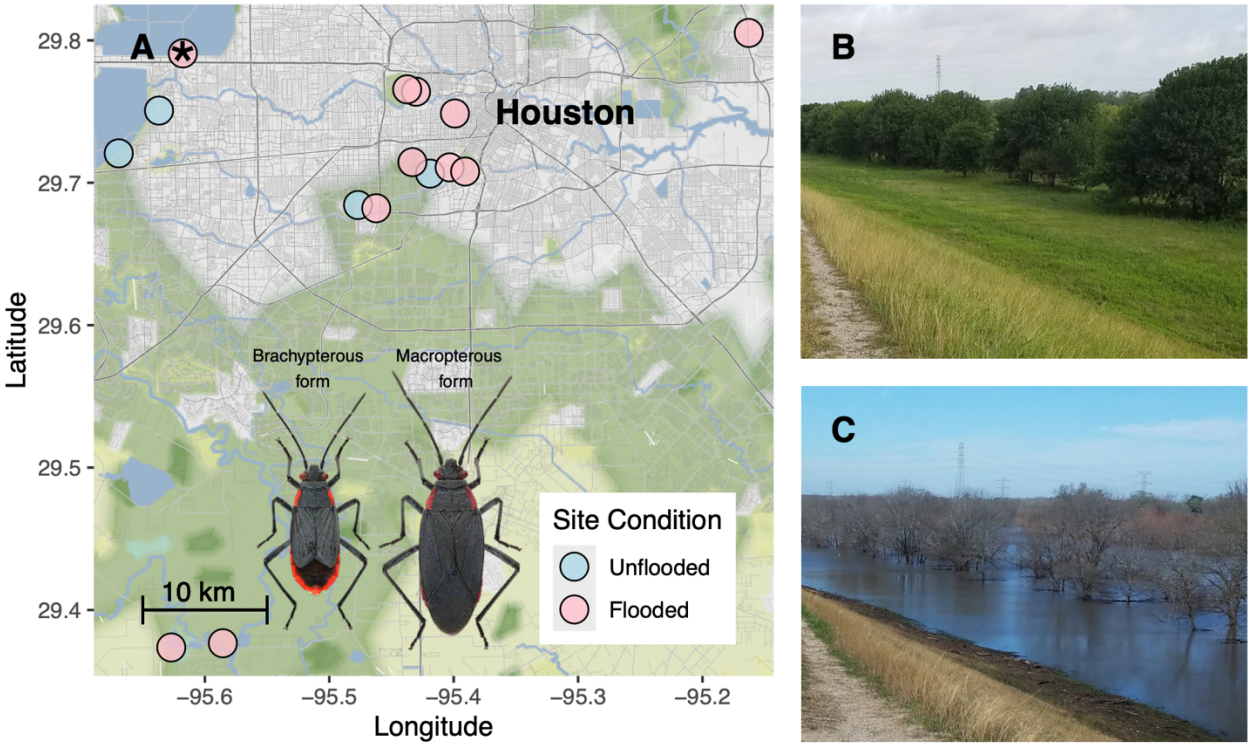

Figure 1: Map of survey sites across the Greater Houston area in Texas where Comerford et al. (2023) sampled soapberry bugs (**A**). Out of the fifteen sampling sites, eleven (pink) experienced local extinction due to prolonged flooding, while four sites (blue) maintained a stable population throughout the survey period. The photographs on the right show a flooded site (marked with an asterisk in **A**) before (**B**) and after (**C**) Hurricane Harvey from the same vantage point. The image of the macropterous and brachypterous forms of soapberry bug in **A** was taken from Tsai et al. (2013).

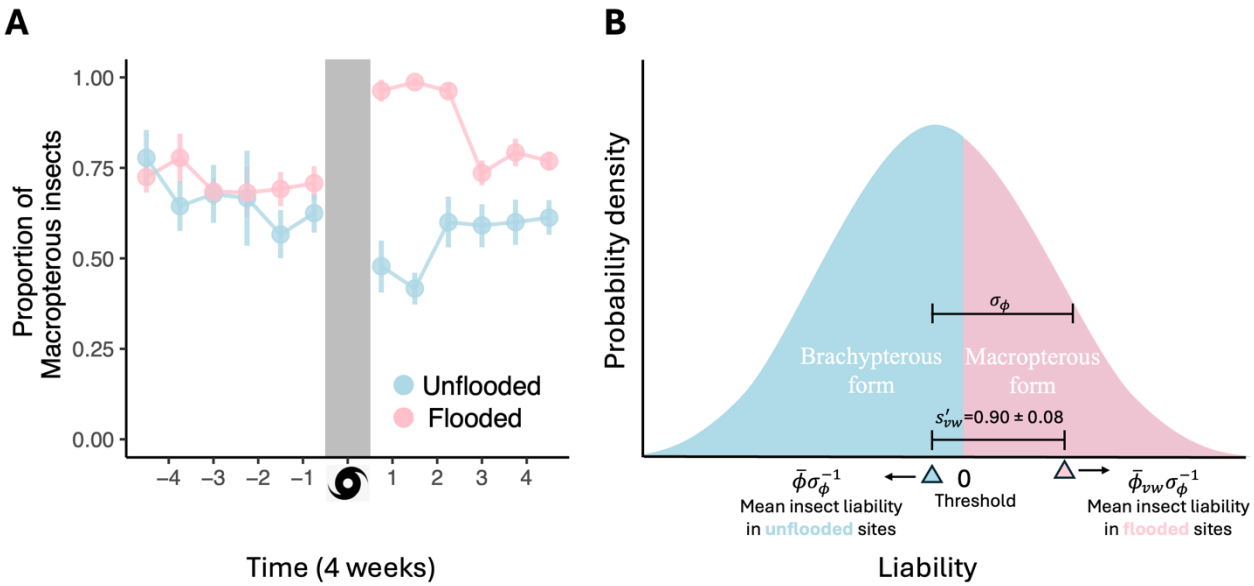

Figure 2: (**A**) The survey data of proportion (± 1 sd.) of macropterous insects suggests that post-hurricane, relative to unflooded sites (blue), immigrants in the flooded sites (pink) had a higher proportion of macropterous insects. (**B**) We find that the mean liability of insects in the flooded sites (pink triangle) is 0.90 ± 0.08 ($\beta'_{vw,\phi}$) standard deviation higher than that of insects in unflooded sites (blue triangle). The estimated standardized sorting gradient ($\beta'_{vw,\phi}$) is in the top 5 percentile of standardized selection coefficients observed in natural populations (Kingsolver et al. 2001). Genetic crosses show that the liability is a heritable trait ($h^2 = 0.65 \pm 0.13$). Consequently, spatial sorting resulted in a net evolutionary change of 0.58 ± 0.13σ_ϕ. The variation in the parameter estimates corresponds to standard error. For details on the statistical analysis, refer to the supplementary R codes.