RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration
SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Revegetation decisions have genetic consequences: actively and passively restored salt marshes display different genetic diversity and composition

Katie P. Sperry[1,2], Sarah C. Crosby[3], Anna E. Bartholet[1], Anne Randall Hughes[1]

Genetic diversity facilitates common restoration goals like creating resilient and adaptable populations. Yet, the genetic consequences of restoration are rarely considered. To inform and motivate the inclusion of genetic diversity into restoration decision-making, we assessed the genetic diversity of the salt marsh foundation species *Spartina alterniflora* in three types of salt marshes: actively planted restored sites, passively colonized restored sites, and natural marshes. We found that active restoration was associated with higher genetic diversity, whereas passive restoration and natural marshes were equivalently associated with lower genetic diversity. All three marsh types had disparate genetic composition, but only actively restored sites contained seemingly non-local genotypes. These distinct genetic outcomes likely have proportionally distinct implications for eco-evolutionary processes. Our work adds to growing evidence that genetic diversity can be influenced by restoration decisions and should therefore be considered during restoration planning and in restoration policy.

Key words: active versus passive restoration, biodiversity-ecosystem function, genetic diversity, habitat restoration, population genetics, salt marsh, *Spartina alterniflora*

Implications for Practice

- Revegetation practices (planting or allowing for colonization) are associated with different plant genetic diversity and composition. As such, the genetic consequences of revegetation ought to be considered while choosing a strategy.
- Neither revegetation strategy was associated with reduced genetic diversity compared to natural populations, a promising sign that neither choice results in genetically depauperate populations.
- The genetic consequences of many active plantings are dependent on the propagation practices of commercial nurseries; clarifying these practices in advance can inform likely genetic outcomes during the restoration planning process.

Introduction

Biodiversity is being lost across ecosystems and taxa (Pimm et al., 2014; Chase et al., 2020), to the detriment of ecological functioning and stability (Hautier et al., 2015; Fanin et al., 2018) and human wellbeing (Cardinale et al., 2012; Stange et al., 2021). Of particular concern, given ecosystems' need to respond to rapid global climate change, is the loss of genetic diversity (Leigh et al., 2019; Exposito-Alonso et al., 2022). Evolution acts on genetic variation; therefore, populations with low genetic diversity may be less adaptable to changing environmental conditions (Etterson, 2004; Hoffmann & Sgró, 2011).

Beyond evolutionary potential, genetic diversity's benefits extend to ecological dynamics in populations, communities, and ecosystems. Within populations, genetic diversity can promote productivity (Crutsinger et al., 2006; Kotowska et al., 2010) and stability (Hughes & Stachowicz, 2004; Wernberg et al., 2018). Genetic variation of a single species can have cascading impacts across associated species and trophic groups (rev. by Whitham et al., 2006; Hughes et al., 2008), including promoting diversity at higher trophic levels (Crutsinger et al., 2006; Zerebecki & Hughes, 2023) and deterring invasion (Crutsinger et al., 2008), and can augment ecosystem processes like nutrient cycling (Semchenko et al., 2017). Such effects are especially prominent in systems dominated by foundation species (Whitham et al., 2006), where intraspecific variation can have impacts of similar magnitude as species-level variation (Bolnick et al., 2011; Des Roches

Author contributions: KPS, ARH, SCC designed the study; KPS, AEB, SCC conducted the field work; KPS, AEB conducted the molecular work; KPS analyzed the data; KPS, ARH interpreted the data and drafted the manuscript; all authors reviewed and edited the final draft of the manuscript.

[1]Department of Marine and Environmental Science, Northeastern University, 430 Nahant Road, Nahant, MA, U.S.A.
[2]Address correspondence to K. P. Sperry, email katieprosperry@gmail.com
[3]The Maritime Aquarium at Norwalk, 10 North Water Street, Norwalk, CT, U.S.A.

© 2025 The Author(s). Restoration Ecology *published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.*
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
doi: 10.1111/rec.70122
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.70122/suppinfo

et al., 2018). In sum, genetic diversity promotes both short-term resiliency and functioning as well as long-term evolutionary potential, leading to an increased recognition for the need to manage for genetic diversity (Des Roches et al., 2021; Hoffmann et al., 2021).

Habitat restoration, the managed recovery of degraded or recreation of extirpated ecosystems, is a key management tool for addressing biodiversity loss (Suding, 2011) and is an increasingly popular conservation strategy (Suding et al., 2015; Strassburg et al., 2020). For example, the United Nations declared 2021–2030 the "decade on ecosystem restoration" (United Nations General Assembly, 2019), and recent bills in the United States have featured hundreds of millions of dollars for restoration (U.S. Department of the Interior, 2022). Despite its inclusion in restoration guidelines (Mcdonald et al., 2016), actionable recommendations for effectively restoring genetic diversity are limited (Hughes et al., 2018; Hoban et al., 2020). Therefore, a gap persists between recognizing its value and knowing how restoration affects genetic diversity.

Existing work has found that genetic diversity is generally lower in restored systems compared to natural systems (Wei et al., 2023), mirroring the difference in species diversity between restored and natural systems (Rey Benayas et al., 2009). Moreover, restored populations often have distinct genetic composition and/or lower diversity of functional traits than natural systems (Espeland et al., 2017; Holl et al., 2022). As a result, restored ecosystems are often ecologically and evolutionarily distinct compared to natural ecosystems (Espeland et al., 2017; Höfner et al., 2022; Holl et al., 2022).

Restoration practices vary, however, and these differences can influence the degree of variation between restored and natural populations (Espeland et al., 2017; Höfner et al., 2022; Wei et al., 2023). In plant-focused restoration, revegetation can happen actively through the addition of plants, or passively by creating appropriate environmental conditions for native species and relying on colonization via dispersal (Jones et al., 2018). Active planting is more often associated with differences in genetic diversity in restored versus natural populations than passive approaches, though a wide variety of outcomes have been observed (Wei et al., 2023). Within active planting efforts, disparate approaches can modulate genetic outcomes. In particular, sowing seeds results in higher genetic diversity than planting seedlings (Wei et al., 2023). Additionally, how biotic source material (seeds or plants) is collected and propagated matters. High demand for large quantities of source material encourages collecting from the most productive individuals at the peak time of maturation, which can lead to genetic homogenization and trait selection that may be maladaptive in the long term (Holl et al., 2022).

Among passive restoration efforts, genetic outcomes also vary (Wei et al., 2023). Here, variation in outcomes is likely due to differences in the balance of seed-based recruitment versus clonal spread for plant establishment (Christie & Knowles, 2015; Aavik & Helm, 2018). Recruitment both within the population and from nearby sources will impact genetic outcomes. As such, landscape-level processes that impact dispersal, such as habitat connectivity or metapopulation dynamics, are influential (Christie & Knowles, 2015; Aavik & Helm, 2018).

While past work has broadly shown that passive and active restoration can impact genetic outcomes, direct comparisons within systems can yield operational insight for restoration decision makers by assessing the extent and directionality of differences and investigating potential mechanisms behind genetic outcomes. Here, we examined genetic diversity and composition in the foundational salt marsh grass species *Spartina alterniflora* across three types of salt marshes: natural (unrestored) marshes, actively revegetated restored marshes, and passively revegetated restored marshes. Salt marshes are among the most widely restored coastal ecosystems (Grabowski et al., 2012), suggesting that impacts of restoration practice on genetic diversity could have widespread implications. Further, salt marsh restoration is critical, as these systems provide economically valuable ecosystem services (Barbier et al., 2011; zu Ermgassen et al., 2021) and are among the most vulnerable coastal ecosystems (Gedan et al., 2009), having already faced widespread losses (Bromberg & Bertness, 2005; Campbell et al., 2022).

Salt marsh restoration is an excellent model for characterizing the genetic outcomes of restoration decisions. These intertidal grasslands are typically dominated by one or a few foundational grass species, such as our focal species, *S. alterniflora*. For such species, decisions regarding restoration approaches are expected to directly influence the genetic diversity and composition of the restored population (Kettenring et al., 2014). In addition, because *S. alterniflora* is well-suited for in situ and ex situ propagation, source material for active planting can be collected from existing marshes or purchased from commercial nursery stocks, with implications for both the genetic and phenotypic similarity to nearby natural populations. We hypothesized that actively and passively restored sites would be consistently associated with different genetic outcomes, though the directionality of this predicted difference was unclear from a priori reasoning.

Methods

Field Sites

Thirty-five salt marshes across southern New England, United States (Massachusetts, Rhode Island, and Connecticut) were sampled in July and August of 2021 (Connecticut) and 2022 (Massachusetts and Rhode Island) (Fig. 1). Each site fell into one of three categories: actively restored sites ($n = 12$), passively restored sites ($n = 11$), or natural marshes ($n = 12$). For the majority of actively and passively restored sites, restoration included hydrological modification to eliminate invasive vegetation (e.g. *Phragmites australis*). Actively restored sites had vegetation, including *Spartina alterniflora*, planted after hydrological modification (or other restoration action). Passively restored sites had no vegetation planted following the restoration action, and therefore vegetation was the result of colonization from nearby sources or germination from a seed bank. Natural marshes were sites with no documented major restoration.

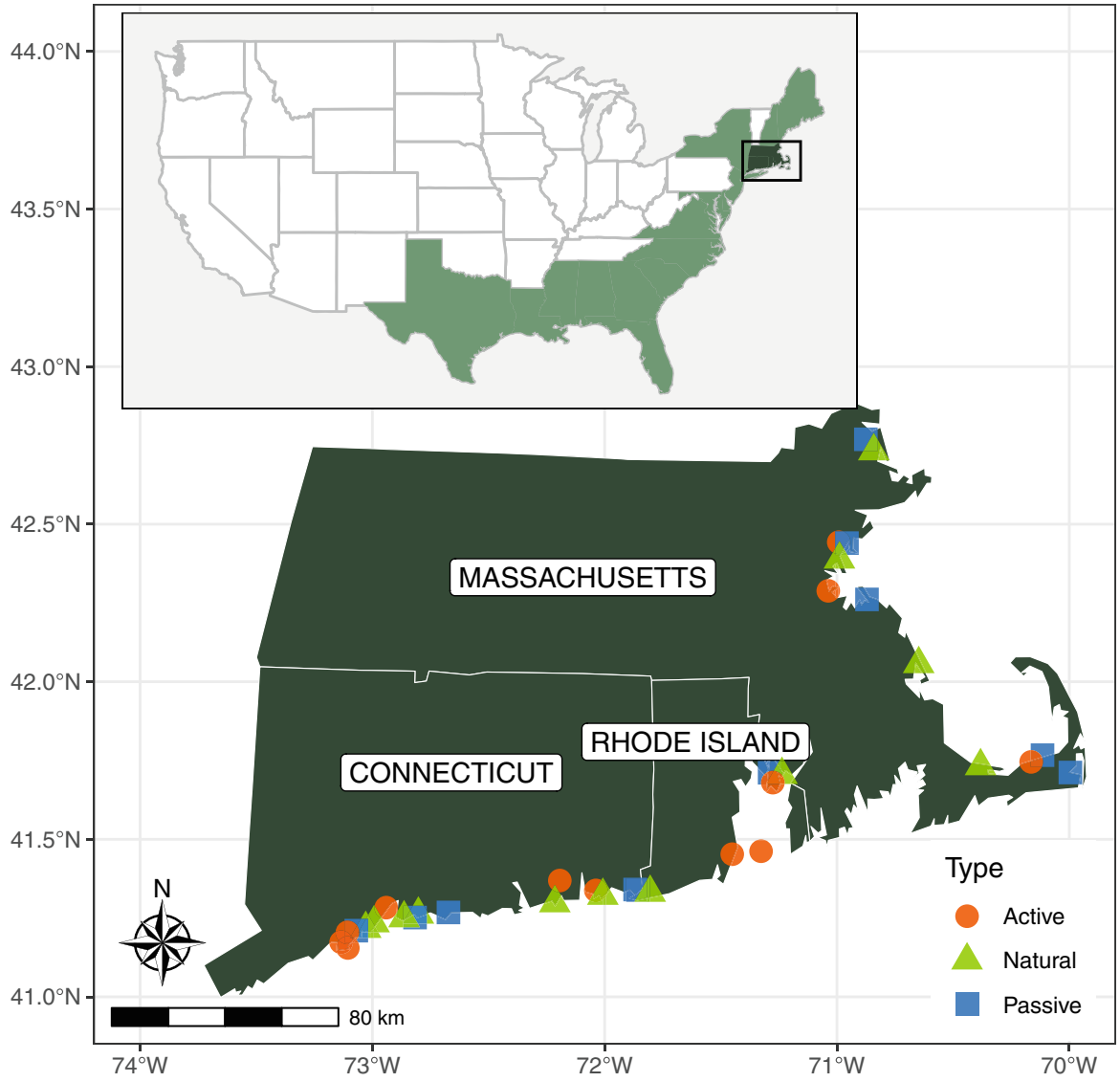


Figure 1. Map of sampling sites in Massachusetts, Rhode Island, and Connecticut, United States. Inset country map shows study location (dark green), and states where *Spartina alterniflora* is native (light green). Site location is shown, and site type is indicated by color and shape (actively restored sites = orange circles; passively restored sites = blue squares; natural marshes = green triangles).

For all Massachusetts and Rhode Island sites and passively restored sites in Connecticut, candidate sites were preliminarily identified through conversations with those involved in regional salt marsh restoration, or via satellite imagery exploration and online research. For each site, ownership and management were determined, and restoration history was confirmed by these parties before inclusion. Data from actively restored sites and natural marshes in Connecticut were also included in a companion study focused on the structure and function of restored and natural marshes (Crosby et al., 2024).

Across restored sites, the year of restoration ranged from 2010 to 2019, with an average restoration year of 2015. Actively restored sites ranged from 3 to 9 and averaged 5.5 years old, and passively restored sites ranged from 3 to 12 and averaged 8.45 years old.

Field Sampling

At each site, a 40 m transect was laid parallel to and 1 m back from the main marsh creek. Every four meters along the transect, a 1 m^2 sampling quadrat was established, yielding 10 sampling quadrats each three meters apart. Within each quadrat, 10 *S. alterniflora* individuals were haphazardly selected and a 10 cm portion of their innermost leaf was clipped. Thus, leaf tissue samples from 100 individuals were collected at each site, with a total of 3500 samples collected across all sites. Upon

collection, tissue samples were stored in silica for DNA preservation.

Laboratory

Tissue samples were processed between the fall of 2021 and spring of 2023 at Northeastern University's Marine Science Center. DNA purification and extraction followed Hughes and Lotterhos (2014). In brief, approximately 0.25 g of tissue was ground in a mill grinder (RETSCH MM 400), and DNA was extracted and purified using Omega Bio-Tek *E*-Z Plant DNA kits. To identify each sample's genotype, we amplified DNA at 12 microsatellite markers developed for *S. alterniflora* (Blum et al., 2004, Sloop et al. 2005). Amplification via polymerase chain reactions (PCR) for each sample occurred in 10 μL total volume with the following reagents: 1 μL DNA template, 5 μL 2X type-it multiplex master mix (Qiagen), 2 μL sterilized molecular-grade water, 0.25 μL each primer (10 mM) for each of 4 markers, and 0.25 μL each reverse primer (10 mM) for each of four markers. Three PCRs with four markers were performed for each sample to amplify DNA at all 12 markers. Forward primers were fluorescently labeled with NED, VIC, 6-FAM, and PET dyes. Loci were multiplexed for fragment length analysis. Using a T100 thermal cycler (Bio-Rad), PCR cycling conditions included initial activation/denaturation at 95°C for 5 minutes, followed by 28 cycles of 95°C for 30 seconds, 60°C for 90 seconds, and 72°C for 30 seconds, and final extension at 60°C for 30 minutes. PCR products were separated on a 3730xl Genetic Analyzer (Applied Biosystems) with capillary electrophoresis at the Yale DNA Analysis facility. Fragment analysis was performed using GeneMarker 2.6 (SoftGenetics, 2013).

Two markers proved uninformative due to high failures and were excluded from further analyses; as such, 10 markers were used in this study. The quality of these 10 markers was assessed by calculating null allele frequency and linkage disequilibrium (Supplement S1). Additionally, samples that failed at two or more markers were excluded. Thus, 3307 samples were eligible for subsequent analyses.

Statistical Analyses

Genotypic richness, allelic richness, observed and expected heterozygosity, inbreeding coefficients (Gis), and population differentiation (Fst) were calculated in GENODIVE 3.06 (Meirmans, 2022). Clonal assignments were made using an infinite allele model, excluding missing data, and with a threshold of zero—where individuals were considered distinct multilocus genotypes (MLGs) if they differed at a single locus. Genotypic and allelic richness, heterozygosity measures, and Gis were calculated for each 1 m^2 sampling quadrat, including clonal replicates, to quantify genetic diversity as it would be experienced in the ecological system. Fst was calculated per site, only including unique MLGs (i.e., excluding clonal replicates at each site, $n = 944$) to better meet the assumptions of Hardy–Weinberg equilibrium.

Subsequent statistical analyses were performed in R 4.3.0 (R Core Team, 2023) with RStudio 2023.03.1 (RStudio Team, 2023), save STRUCTURE analyses (Structure 2.3.4, described in Pritchard et al., 2000). Only unique MLGs were included during Analysis of Molecular variance (AMOVA), Discriminant Analysis of Principal Components (DAPC), and STRUCTURE analyses to assess between-population structure and not within-site clonal dynamics.

Diversity. Linear mixed effect models assessed whether marsh type (active, passive, or natural) predicted genetic diversity. We assessed two metrics of genetic diversity: allelic and genotypic richness. Allelic richness is the number of alleles per loci found per individual per quadrat. Genotypic richness is the number of MLGs found in each quadrat. For both allelic and genotypic richness, we included marsh type as a main effect and site as a random intercept. Normality was assessed with Shapiro–Wilk tests. Residuals for the linear mixed effect model predicting allelic diversity were non-normal ($W = 0.99$, $p < 0.05$), though because sample sizes were above 100 for each category, non-normality is unlikely to be an issue given the Central Limit Theorem. Residuals for the linear mixed effect model predicting genotypic diversity were normally distributed ($W = 0.99$, $p > 0.05$). To assess which restoration types differed from one another, post-hoc pairwise comparisons using estimated marginal means were conducted with the emmeans package, adjusting *p*-values with Tukey multiple comparisons (Lenth et al., 2024). We tested for the influence of time since restoration on our response variables by comparing linear mixed effects models with and without time since restoration as a fixed effect using model selection (Akaike Information Criterion, Supplement S2). To see if genetic diversity in natural sites varied geographically, we regressed site's average genotypic richness by both latitude and longitude using simple linear models.

Composition. To assess how genetic variation was partitioned across categories of interest, we performed an AMOVA testing hierarchical variation attributed to site nested within marsh type. Additionally, we performed AMOVAs assessing hierarchical variation attributed to site nested within type nested within state, and for the variation attributed solely to site (Table S1). For each, Monte Carlo tests with 999 permutations assessed statistical significance. AMOVA methods used the poppr package in R (Kamvar et al., 2014) and followed Grünwald et al. (2017).

Genetic differentiation among sites (Fst) of different was compared with an Analysis of Variance (ANOVA), and post hoc pairwise comparisons were made using Tukey tests adjusted for multiple comparisons. A Shapiro–Wilk test for normality found that ANOVA residuals were not normally distributed ($W = 0.979$, $p < 0.05$), but sample sizes were above 100 for each group. The relationship between each pairwise site comparison's genetic differentiation and geographic distance (i.e. isolation-by distance) was assessed with a mantel test.

We assessed latent population structure using DAPC (Jombart et al., 2010) with the adegenet package in R (Jombart, 2008). For these analyses, we excluded clones to only

assess unique MLGs ($n = 944$) and also excluded samples with missing data at any alleles ($N = 645$, $n_{active} = 298$, $n_{passive} = 168$, $n_{natural} = 179$).

Genetic clusters (k) were found and assigned to samples using successive K-means for 1:35 clusters (representing our 35 field sites) and 150 principal components. Clustering solutions at different values of K were compared with Bayesian Information Criterion (BIC), and $K = 10$ was chosen to minimize BIC. To avoid over-fitting the DAPC model, the optimal number of principal components to retain during final discriminant analysis was assessed using a-scores. We found a maximized a-score at 14 principal components. As such, we ran a DAPC for 10 clusters with 14 retained principal components. To assess population structure across broader scales of organization, we also conducted DAPC for $K = 2$, 3, 4, 5, and 6, with 7, 7, 7, 8, and 7 principal components, respectively. DAPC results were visually assessed with a scatterplot demonstrating cluster relationships, bar plots assessing overall cluster frequencies across types, and site-specific posterior probability cluster assignment plots.

To complement DAPC, we performed Bayesian clustering analyses using STRUCTURE (Pritchard et al., 2000). Ks 1:35 were assessed, with a burn-in period of 100,000 and 500,000 Markov Chain Monte Carlo reps using the dataset with clonal replicates excluded. We assumed an admixture ancestry model and correlated allele frequencies.

Results

Diversity

We genotyped 3307 individuals, which were grouped into 944 unique MLGs. Almost all genotypes were unique to a single site, with the exception being four genotypes each found at two sites. Additionally, most genotypes were unique to a single 1 m^2 quadrat, with 807 genotypes found in one and 137 found in two or more.

Both allelic and genotypic richness differed across marsh types (Fig. 2A, allelic richness: $F_{[2,32]} = 6.958$, $p < 0.01$; Fig. 2B, Genotypic richness: $F_{[2,32]} = 4.195$, $p < 0.05$). Post hoc pairwise comparisons showed that actively restored sites differed from passively restored sites (allelic richness: t-ratio$_{32} = 3.129$, $p < 0.05$; genotypic richness: t-ratio$_{32} = 2.489$, $p < 0.05$) and from natural marshes (allelic richness: t-ratio$_{32} = 3.302$, $p < 0.01$; genotypic richness: t-ratio$_{32} = 2.509$, $p < 0.05$), whereas passively restored sites and natural marshes had equivalent levels of diversity (allelic richness: t-ratio$_{32} = -0.100$, $p > 0.05$; genotypic richness: t-ratio$_{32} = 0.035$, $p > 0.05$). For both genetic diversity metrics, models excluding time since restoration had the most support (Table S2). Average genotypic richness in natural sites did not vary by site latitude ($r^2 = 0.031$, $p > 0.05$) nor longitude ($r^2 = 0.0029$, $p > 0.05$).

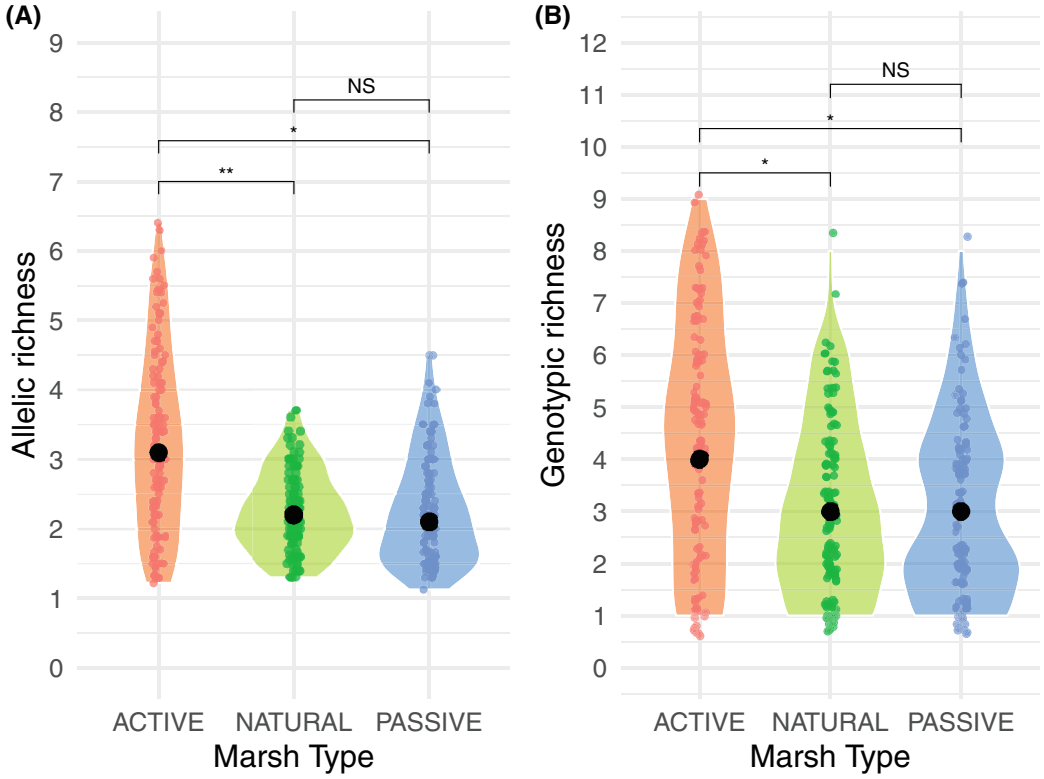


Figure 2. Violin plots displaying the distribution and median of (A) allelic and (B) genotypic richness across three marsh types: actively restored sites, natural marshes, and passively restored sites. (A) Allelic richness, or the mean number of alleles per loci per individual. (B) Genotypic richness, or the number of genotypes found in a 1 m^2 sampling plot per site. Symbols above violin plot comparisons indicate post hoc significance: **denotes a p-value of less than 0.01, *denotes a p-value of less than 0.05, and NS denotes no difference.

Table 1. Genetic diversity metrics across marsh categories. Values are the mean (standard deviation) for each marsh type, calculated at the level of the sampling plot. Genotypic richness is the number of unique MLGs; allelic richness is the number of alleles per locus; observed heterozygosity is the measured frequency of heterozygotes per locus per sample; expected heterozygosity is the expected frequency of heterozygotes per locus per sample assuming Hardy–Weinberg equilibrium; inbreeding coefficient assess the difference between observed and expected heterozygosity.

Type	*Genotypic richness*	*Allelic richness*	*Observed heterozygosity*	*Expected heterozygosity*	*Inbreeding coefficient (Gis)*
Active	4.40 (2.27)	3.27 (1.32)	0.53 (0.12)	0.49 (0.17)	−0.20 (0.44)
Passive	3.06 (1.72)	2.28 (0.79)	0.47 (0.13)	0.36 (0.13)	−0.41 (0.40)
Natural	3.08 (1.65)	2.25 (0.58)	0.52 (0.16)	0.37 (0.11)	−0.45 (0.46)

The increased diversity at actively restored sites was of equivalent magnitude for both measures; on average, there were 1.4 times more genotypes present per 1 m^2 sampling plot and 1.4 times more alleles per locus in actively restored sites than in passively restored sites or natural marshes (Table 1). Additional genetic diversity metrics are presented in Table 1. The absolute values of diversity were lower when using the reduced marker set, but the relative diversity of natural, actively restored, and passively restored marshes was consistent (Supplement S1).

Composition

AMOVA indicated genetic differentiation among marsh types and sites. Actively restored sites, passively restored sites, and natural marshes were genetically differentiated from one another ($p < 0.05$), though the estimated magnitude of this difference was small (0.74%). Within each type, sites were differentiated from one another ($p < 0.05$), which accounted for 6.52% of overall genetic variation.

Site-level genetic differentiation (Fst) also varied across marsh types (Fig. 3, $F_{[5,1,184]} = 48.67$, $p < 0.001$). Post hoc pairwise comparisons showed that Fst between sites was lowest among actively restored sites and highest among natural sites, with other comparisons falling in between (Fig. 3). Differentiation for natural sites and either actively or passively restored sites was equivalent (Fig. 3). A Mantel test for the correlation of geographic distance and genetic differentiation (Fst) between sites found no effect of isolation-by-distance (Obs = 0.019, $p > 0.05$).

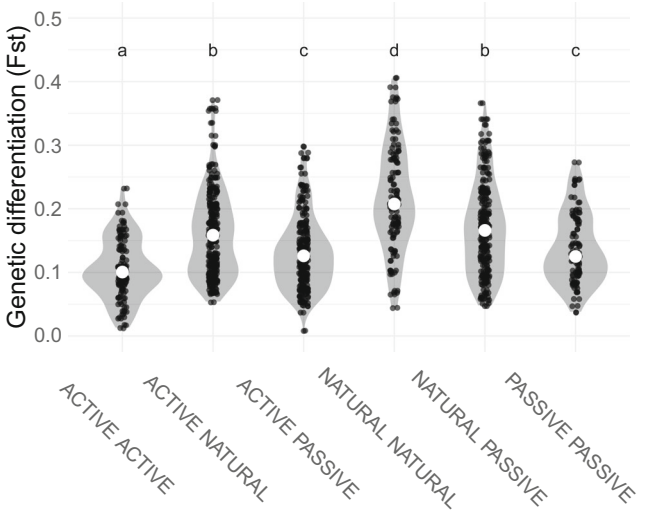


Figure 3. Violin plot of genetic differentiation (Fst) among all pairwise combinations of marsh types. Each boxplot shows the median and spread for all pairwise comparisons of marshes belonging to the shown categories. Letters above the violin plots indicate whether Fst differed across marsh type combinations.

All three marsh types were characterized by unique genetic composition. Because DAPC is recommended over STRUCTURE for clonal populations (Grünwald et al., 2017) we focus on the DAPC results here; STRUCTURE results are in Supplement S4. *K*-means clustering for DAPC suggested 10 genetic clusters (Fig. 4C), and at $K = 10$, clusters were differently represented across the three marsh types (Fig. 4A). Notably, cluster 5 was almost wholly unique to natural marshes (Fig. 4A), and site-specific exploration showed that cluster 5 was overwhelmingly in one natural site (Lathrop; Fig. 5), which is distinct in a DAPC scatterplot (Fig. 4C). Cluster 6 largely differentiated actively restored sites from other types; it was in many actively restored sites and less commonly found elsewhere (Figs. 4A & 5). At lower *K*s, genetic composition in actively restored sites became more distinct from passively restored sites and natural marshes (e.g. $K = 2$; Fig. 4B), suggesting that at broader scales of comparison, passively restored sites and natural marshes group together while actively restored sites differentiate. This pattern was also found with STRUCTURE analysis (Supplement S4), though the degree of differentiation was somewhat sensitive to the number of markers used (Supplement S1).

Different marsh types also varied in how clusters were distributed across sites. Any given natural marsh contained relatively few clusters, with several marshes having only a single cluster (e.g. Branford; Fig. 5). Moreover, each natural marsh tended to have different clusters than other natural populations (e.g. Branford vs. oyster; Fig. 5), consistent with the observed high Fst among natural sites. In contrast, populations of either restoration type were more likely to have many clusters, particularly those that were actively restored (Fig. 5).

Discussion

Genetic variation is foundational to ecological and evolutionary processes that facilitate the common restoration goals of functional and resilient populations (Hughes et al., 2008; Hoffmann & Sgró, 2011; Wernberg et al., 2018). Here, we add to a growing body of evidence that restoration decisions can

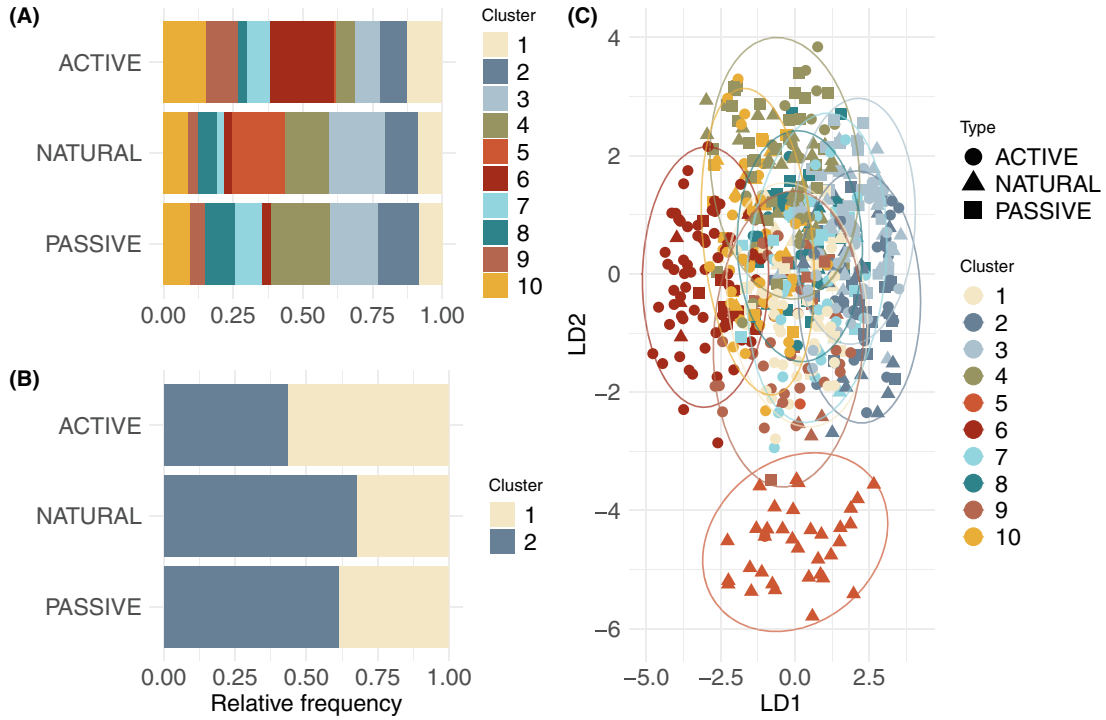


Figure 4. DAPC primary cluster assignments for MLGs across marsh categories. (A) $K = 10$, the optimized number of clusters selected with BIC. (B) $K = 2$, to illustrate differentiation at the broadest level of comparison. (C) Scatterplot of DAPC results for $K = 10$. Points are individual MLGs, where color represents predominant cluster assignment and shape represents marsh type (active = circle; natural = triangle; passive = square). Cluster assignments for each MLG are the cluster to which they were most likely to belong (i.e. the cluster with the highest posterior probability for each sample).

have substantial and consistent effects on this variation (e.g. Breed et al., 2013; Jordan et al., 2019; Wei et al., 2023). Specifically, we found that passively restored *Spartina alterniflora* populations had comparable genetic diversity to natural populations, whereas actively restored populations had increased richness and differentiated composition. We have previously found increased genetic diversity in actively planted salt marshes relative to natural marshes in Connecticut (Crosby et al., 2024). Here, we show this holds across a greater region and additionally show that diversity depends on revegetation method.

Genetic diversity increases adaptive potential and reduces the risk of inbreeding depression, thus facilitating population persistence (Hufford & Mazer, 2003; Christie & Knowles, 2015). On ecological timescales, genetic diversity can impact resistance and resilience (Hughes & Stachowicz, 2004; Whitham et al., 2006; Wernberg et al., 2018). In *S. alterniflora* specifically, intraspecific diversity can increase ecosystem functions like primary production and erosion resistance via heritable traits (Bernik et al., 2021; Zogg & Travis, 2022; Zerebecki & Hughes, 2023). Thus, more diverse active and less diverse passively restored populations may exhibit commensurate adaptability and functioning.

Both actively and passively restored sites had distinct genetic composition from natural marshes, though not to the same degree. Our results are consistent with the expectation that incoming propagules for passively restored sites were from nearby sources, whereas seedlings or plugs for actively restored sites can be sourced from anywhere. Actively restored populations commonly contained a distinct genetic cluster found less frequently elsewhere, suggesting it was not produced locally. Non-local genotypes may decrease population functioning via maladaptation or outbreeding depression (Hufford & Mazer, 2003). Thus, the distinct composition of actively restored populations may result in negative effects that counteract the predicted benefits of the higher genetic diversity in these same populations. Concerns of maladaptation are lesser in passively restored populations, which were less differentiated from natural marshes. While clusters were differently represented at fine scales of comparison, they appeared similar when assessed more broadly.

Genetic outcomes in actively restored sites are likely caused by sourcing and planting practices. Our results suggest that commercial nurseries use practices resulting in high genetic diversity, such as rearing plants from seed and/or collecting seed stock from numerous source sites. *Spartina alterniflora* reproduces asexually via clonal propagation and sexually via seed, creating a wide potential range in diversity depending on a population's predominant reproduction mode. The higher genetic diversity in actively restored populations may be due to the common practice of growing plant stock from seed at commercial nurseries in the eastern United States, as indicated by interviews with growers (Kollars & Hughes unpublished data). Conversely, clonal reproduction is common in

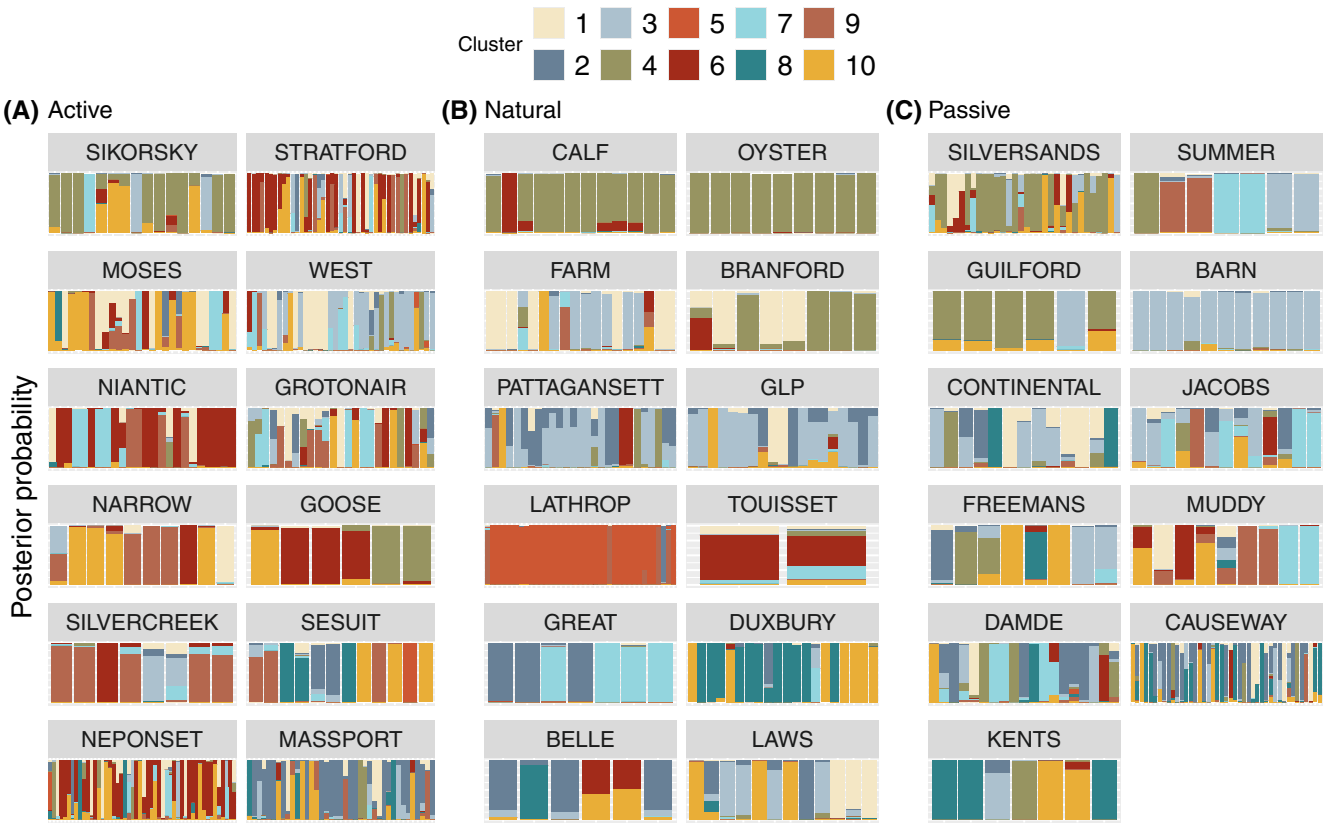


Figure 5. Posterior probabilities for each MLG at every site for $K = 10$, grouped by marsh type. (A) Actively restored sites, (B) passively restored sites, and (C) natural marshes. In each grouping, sites are arranged geographically along the coast, from western Connecticut on the top left to northern Massachusetts on the bottom right. Each bar shows the posterior probability cluster assignment from DAPC for each MLG.

natural populations, comparatively lowering diversity (Hughes & Lotterhos, 2014; Noto & Hughes, 2020). Higher genetic diversity may also reflect that seed stock was collected from multiple sites, increasing the likelihood of sampling new alleles (Breed et al., 2013; Jordan et al., 2019; Wei et al., 2023). Though site-specific information on the location or number of sources was unavailable for most sites, commercial nurseries that commonly supply plants for restoration in this region often gather seed at multiple sites (Kollars & Hughes unpublished data). Thus, the practices of multi-site collection and growing out plant stock from seed likely yielded increased genetic diversity in planted populations and ought to be continued. Documenting sourcing-specific information in future planting efforts would aid assessment of how specific practices impact genetic outcomes.

While site-level diversity was high for actively restored sites, among-site diversity was low and characterized by a common set of genetic clusters. Compositional similarity among actively restored populations suggests that a similar planting stock was utilized for salt marsh plantings in the region, in keeping with the presence of few commercial nurseries producing salt marsh plants for regional restoration. Genetic homogenization from planting has been found in other actively revegetated systems across smaller spatial scales (Höfner et al., 2022), but the relatively large scale of our study (the approximately 4000 km of coastline across southern New England, United States) may increase the risks and implications of biotic homogenization (Holl et al., 2022).

Seed collection, propagation, and planting practices have high potential to cause genetic change (Basey et al., 2015; Jordan et al., 2019), but we lack an understanding of which steps are most influential. We have previously found that actively restored populations in Connecticut were genetically similar to plugs purchased from commercial nurseries (Crosby et al., 2024), underscoring the tight relationship between plant stock and planted populations and therefore the importance of producing stock with diversity and provenance in mind. Collaboration between scientists and practitioners, including commercial nurseries, to co-produce such knowledge would be valuable for determining genetic best practices (Beier et al., 2017; Cook et al., 2021).

In contrast to plantings where human decision-making during restoration can be linked to genetic outcomes, ecological processes related to landscape connectivity, dispersal, and establishment dictate genetic outcomes in passively restored populations (Aavik & Helm, 2018). *Spartina alterniflora*

populations in passively restored sites exhibited genetic diversity equivalent to natural salt marshes, suggesting that dispersal from nearby populations sufficiently establishes similar diversity within a few years after restoration. This is mostly consistent with past comparisons in marshes (Travis et al., 2002, 2004), and across systems (Wei et al., 2023), which have largely found equivalent or reduced genetic diversity in passively restored populations relative to natural ones.

Despite the similar amounts of genetic diversity between passively restored and natural marshes, they exhibit different compositional patterns. Natural marsh comparisons exhibited the most differentiation of any comparison type, while passively restored site pairings showed greater compositionally similarity to one another. Compositional similarity among passively restored populations suggests considerable dispersal across regional *S. alterniflora* populations. Regional dispersal is also supported by a lack of isolation-by-distance and by the absence of an effect of state in an AMOVA. Higher differentiation among natural marshes and lower differentiation among passively restored populations also likely reflects the increased relative importance of dispersal and seedling recruitment in recently restored marshes versus the influence of post-settlement processes such as competition and clonal spread common in long-established natural marshes (Travis et al., 2004; Hughes & Lotterhos, 2014). Although time since restoration was not a strong predictor of diversity in our study, sites of similar age were purposefully selected. Therefore, our data likely do not have sufficient age variability to assess temporal patterns in diversity. We would, however, expect passively restored populations to genetically differentiate over time, given past work showing geographic structure in natural *S. alterniflora* populations (Blum et al., 2004) and increased within-site genetic homogenization over time in *S. alterniflora* populations (Travis et al., 2004). Multi-year monitoring of genetic diversity, and using more phylogenetically informative markers, could illustrate evolutionary relationships within and among *S. alterniflora* populations. Such information would be useful to predict when and where passive restoration may be unsuitable or relied upon for establishment.

Encouragingly, neither revegetation strategy had lower genetic diversity than natural populations, a common baseline for restoration goals, thus suggesting that neither revegetation choice erodes the ecological and evolutionary benefits conferred by genetic diversity. This contrasts with other systems, where restoration uncommonly establishes diversity commensurate to natural references (Atkinson et al., 2022). While the increased genetic diversity found in actively restored populations may translate to additional provisioning of these benefits, additional assessments of potential non-local genotypes' maladaptation is needed. Additionally, active planting costs more than utilizing passive colonization (Holl & Aide, 2011). Further work should explicitly quantify the relationship between genetic diversity and its conferred benefits to help weigh eco-evolutionary and logistical strengths and drawbacks by addressing the question, how much diversity do we "need"?

Despite substantial literature demonstrating the effects of *S. alterniflora* genetic variation on population and community processes (Zerebecki et al., 2017; Zogg & Travis, 2022; Zerebecki & Hughes, 2023) and increasing interest in genetic management for conservation and restoration (Breed et al., 2019; Des Roches et al., 2021; Holl et al., 2022), coastal restoration practitioners view genetic diversity as less important for salt marshes than for other coastal systems (Hughes et al., 2020). Here, we demonstrate that whether considered or not, restoration choices are associated with appreciable differences in the genetic diversity of a common salt marsh foundation species. Going forward, considering the genetic consequences of specific actions could prove beneficial for the functioning and adaptability of restored populations.

Acknowledgments

We thank the editor and two anonymous reviewers for comments that improved the manuscript. This work was supported by the National Science Foundation (DGE-1938052 to K.P.S. and OCE-1851043 to A.R.H.). Funding for this work was also provided by Connecticut Sea Grant, University of Connecticut through Award Number NA18OAR4170081, Project Number 390251. These data and related items of information have not been formally disseminated by the National Oceanographic and Atmospheric Administration and do not represent any agency determination, view, or policy. This work was made possible by access to study sites from: Connecticut Department of Transportation, Branford Land Trust, Milford Land Conservation Trust, East Haven Land Trust, Groton-New London Airport, the Groton Long Point Association, The Nature Conservancy, The Connecticut Audubon Society, Bridgeport-Sikorsky Airport, Connecticut Department of Energy and Environmental Protection, Silver Sands State Park, the town of Guilford CT, the Narrow River Association, the town of Bristol RI, Aquidneck Island Land Trust, the Warren Land Conservation Trust, the Massachusetts Department of Conservation and Recreation, the town of Barnstable MA, Plum Island Ecosystems LTER, Duxbury Beach Reservation, the Chatham Conservation Foundation, the town of Brewster MA, and Massachusetts Department of Fish and Game. P. Cirillo helped with field work and DNA extraction, T. Hanley, S. Truskey, and N. Kollars assisted with molecular work and analysis, K. Rabbitt assisted with DNA extraction, and C. Nadeau advised on data analysis. Data to reproduce analyses are publicly available on Northeastern University's Digital Repository Service: https://repository.library.northeastern.edu/files/neu:h989ss82d. The authors have no conflicts of interest to disclose.

LITERATURE CITED

Aavik T, Helm A (2018) Restoration of plant species and genetic diversity depends on landscape-scale dispersal. Restoration Ecology 26:S92–S102. https://doi.org/10.1111/rec.12634

Atkinson J, Brudvig LA, Mallen-Cooper M, Nakagawa S, Moles AT, Bonser SP (2022) Terrestrial ecosystem restoration increases biodiversity and reduces its variability, but not to reference levels: a global meta-analysis. Ecology Letters 25:1725–1737. https://doi.org/10.1111/ele.14025

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2011) The value of estuarine and coastal ecosystem services. Ecological Monographs 81:169–193. https://doi.org/10.1890/10-1510.1

Basey AC, Fant JB, Kramer AT (2015) Producing native plant materials for restoration: 10 rules to collect and maintain genetic diversity. Native Plants Journal 16:37–52. https://doi.org/10.3368/npj.16.1.37

Beier P, Hansen LJ, Helbrecht L, Behar D (2017) A how-to guide for coproduction of actionable science. Conservation Letters 10:288–296. https://doi.org/10.1111/conl.12300

Bernik BM, Lumibao CY, Zengel S, Pardue J, Blum MJ (2021) Intraspecific variation in landform engineering across a restored salt marsh shoreline. Evolutionary Applications 14:685–697. https://doi.org/10.1111/eva.13148

Blum MJ, Sloop CM, Ayres DR, Strong DR (2004) Characterization of microsatellite loci in *Spartina* species (Poaceae). Molecular Ecology Notes 4:39–42. https://doi.org/10.1046/j.1471-8286.2003.00556.x

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA (2011) Why intraspecific trait variation matters in community ecology. Trends in Ecology & Evolution 26:183–192. https://doi.org/10.1016/j.tree.2011.01.009

Breed MF, Harrison PA, Blyth C, Byrne M, Gaget V, Gellie NJC, et al. (2019) The potential of genomics for restoring ecosystems and biodiversity. Nature Reviews Genetics 20:615–628. https://doi.org/10.1038/s41576-019-0152-0

Breed MF, Stead MG, Ottewell KM, Gardner MG, Lowe AJ (2013) Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. Conservation Genetics 14:110. https://doi.org/10.1007/s10592-012-0425-z

Bromberg KD, Bertness MD (2005) Reconstructing New England salt marsh losses using historical maps. Estuaries 28:823–832. https://doi.org/10.1007/BF02696012

Campbell AD, Fatoyinbo L, Goldberg L, Lagomasino D (2022) Global hotspots of salt marsh change and carbon emissions. Nature 612:701–706. https://doi.org/10.1038/s41586-022-05355-z

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, et al. (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67. https://doi.org/10.1038/nature11148

Chase JM, Blowes SA, Knight TM, Gerstner K, May F (2020) Ecosystem decay exacerbates biodiversity loss with habitat loss. Nature 584:238–243. https://doi.org/10.1038/s41586-020-2531-2

Christie MR, Knowles LL (2015) Habitat corridors facilitate genetic resilience irrespective of species dispersal abilities or population sizes. Evolutionary Applications 8:454–463. https://doi.org/10.1111/eva.12255

Cook CN, Beever EA, Thurman LL, Thompson LM, Gross JE, Whiteley AR, et al. (2021) Supporting the adaptive capacity of species through more effective knowledge exchange with conservation practitioners. Evolutionary Applications 14:1969–1979. https://doi.org/10.1111/eva.13266

Crosby SC, Hudson DM, Hughes AR, Bartholet A, Burns KT, Donato MK, et al. (2024) Structure and function of restored and natural salt marshes: implications for ecosystem resilience and adaptive potential. Estuaries and Coasts 47:1561–1578. https://doi.org/10.1007/s12237-024-01395-y

Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. Science 313:966–968. https://doi.org/10.1126/science.1128326

Crutsinger GM, Souza L, Sanders NJ (2008) Intraspecific diversity and dominant genotypes resist plant invasions. Ecology Letters 11:16–23. https://doi.org/10.1111/j.1461-0248.2007.01118.x

Des Roches S, Pendleton LH, Shapiro B, Palkovacs EP (2021) Conserving intraspecific variation for nature's contributions to people. Nature Ecology & Evolution 5:574–582. https://doi.org/10.1038/s41559-021-01403-5

Des Roches S, Post DM, Turley NE, Bailey JK, Hendry AP, Kinnison MT, Schweitzer JA, Palkovacs EP (2018) The ecological importance of intraspecific variation. Nature Ecology & Evolution 2:64. https://doi.org/10.1038/s41559-017-0402-5

Espeland EK, Emery NC, Mercer KL, Woolbright SA, Kettenring KM, Gepts P, Etterson JR (2017) Evolution of plant materials for ecological restoration: insights from the applied and basic literature. Journal of Applied Ecology 54:102–115. https://doi.org/10.1111/1365-2664.12739

Etterson JR (2004) Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. Evolution 58:1446–1456. https://doi.org/10.1111/j.0014-3820.2004.tb01726.x

Exposito-Alonso M, Booker TR, Czech L, Gillespie L, Hateley S, Kyriazis CC, et al. (2022) Genetic diversity loss in the Anthropocene. Science 377:1431–1435. https://doi.org/10.1126/science.abn5642

Fanin N, Gundale MJ, Farrell M, Ciobanu M, Baldock JA, Nilsson M-C, Kardol P, Wardle DA (2018) Consistent effects of biodiversity loss on multifunctionality across contrasting ecosystems. Nature Ecology & Evolution 2:269–278. https://doi.org/10.1038/s41559-017-0415-0

Gedan KB, Silliman BR, Bertness MD (2009) Centuries of human-driven change in salt marsh ecosystems. Annual Review of Marine Science 1:117–141. https://doi.org/10.1146/annurev.marine.010908.163930

Grabowski JH, Brumbaugh RD, Conrad RF, Keeler AG, Opaluch JJ, Peterson CH, Piehler MF, Powers SP, Smyth AR (2012) Economic valuation of ecosystem services provided by oyster reefs. Bioscience 632:900–909. https://doi.org/10.1525/bio.2012.62.10.10

Grünwald NJ, Everhart SE, Knaus BJ, Kamvar ZN (2017) Best practices for population genetic analyses. Phytopathology 107:1000–1010. https://doi.org/10.1094/PHYTO-12-16-0425-RVW

Hautier Y, Tilman D, Isbell F, Seabloom EW, Borer ET, Reich PB (2015) Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348:336–340. https://doi.org/10.1126/science.aaa1788

Hoban S, Bruford M, D'Urban Jackson J, Lopes-Fernandes M, Heuertz M, Hohenlohe PA, et al. (2020) Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. Biological Conservation 248:108654. https://doi.org/10.1016/j.biocon.2020.108654

Hoffmann AA, Miller AD, Weeks AR (2021) Genetic mixing for population management: from genetic rescue to provenancing. Evolutionary Applications 14:634–652. https://doi.org/10.1111/eva.13154

Hoffmann AA, Sgró CM (2011) Climate change and evolutionary adaptation. Nature 470:479–485. https://doi.org/10.1038/nature09670

Höfner J, Klein-Raufhake T, Lampei C, Mudrak O, Bucharova A, Durka W (2022) Populations restored using regional seed are genetically diverse and similar to natural populations in the region. Journal of Applied Ecology 59:2234–2244. https://doi.org/10.1111/1365-2664.14067

Holl KD, Aide TM (2011) When and where to actively restore ecosystems? Forest Ecology and Management 261:1558–1563. https://doi.org/10.1016/j.foreco.2010.07.004

Holl KD, Luong JC, Brancalion PHS (2022) Overcoming biotic homogenization in ecological restoration. Trends in Ecology & Evolution 37:777–788. https://doi.org/10.1016/j.tree.2022.05.002

Hufford KM, Mazer SJ (2003) Plant ecotypes: genetic differentiation in the age of ecological restoration. Trends in Ecology & Evolution 18:147–155. https://doi.org/10.1016/S0169-5347(03)00002-8

Hughes AR, Edwards P, Grabowski JH, Scyphers S, Williams SL (2020) Differential incorporation of scientific advances affects coastal habitat restoration practice. Conservation Science and Practice 2:e305. https://doi.org/10.1111/csp2.305

Hughes AR, Grabowski JH, Leslie HM, Scyphers S, Williams SL (2018) Inclusion of biodiversity in habitat restoration policy to facilitate ecosystem recovery. Conservation Letters 11:1–8. https://doi.org/10.1111/conl.12419

Hughes AR, Inouye BD, Johnson MTJ, Underwood N, Vellend M (2008) Ecological consequences of genetic diversity. Ecology Letters 11:609–623. https://doi.org/10.1111/j.1461-0248.2008.01179.x

Hughes AR, Lotterhos KE (2014) Genotypic diversity at multiple spatial scales in the foundation marsh species, *Spartina alterniflora*. Marine Ecology Progress Series 497:105–117. https://doi.org/10.3354/meps10565

Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proceedings of the National Academy of Sciences of the United States of America 101:8998–9002. https://doi.org/10.1073/pnas.0402642101

Jombart T (2008) Adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genetics 11:94. https://doi.org/10.1186/1471-2156-11-94

Jones HP, Jones PC, Barbier EB, Blackburn RC, Rey Benayas JM, Holl KD, McCrackin M, Meli P, Montoya D, Mateos DM (2018) Restoration and repair of Earth's damaged ecosystems. Proceedings of the Royal Society B: Biological Sciences 285:20172577. https://doi.org/10.1098/rspb.2017.2577

Jordan R, Breed MF, Prober SM, Miller AD, Hoffmann AA (2019) How well do revegetation plantings capture genetic diversity? Biology Letters 15:20190460. https://doi.org/10.1098/rsbl.2019.0460

Kamvar ZN, Tabima JF, Grünwald NJ (2014) Poppr: an R package for genetic analysis of populations with clonal, partially clonal, and/or sexual reproduction. PeerJ 2:e281. https://doi.org/10.7717/peerj.281

Kettenring KM, Mercer KL, Reinhardt Adams C, Hines J (2014) Application of genetic diversity-ecosystem function research to ecological restoration. Journal of Applied Ecology 51:339–348. https://doi.org/10.1111/1365-2664.12202

Kotowska AM, Cahill JF, Keddie BA (2010) Plant genetic diversity yields increased plant productivity and herbivore performance. Journal of Ecology 98:237–245. https://doi.org/10.1111/j.1365-2745.2009.01606.x

Leigh DM, Hendry AP, Vázquez-Domínguez E, Friesen VL (2019) Estimated 6% loss of genetic variation in wild populations since the industrial revolution. Evolutionary Applications 12:1505–1512. https://doi.org/10.1111/eva.12810

Lenth RV, Bolker B, Buerkner P, Giné-Vázquez I, Herve M, Jung M, Love J, Miguez F, Riebl H, Singmann H (2024) emmeans: estimated marginal means, aka least-squares means. https://cran.r-project.org/web/packages/emmeans/index.html (accessed 17 April 2024)

Mcdonald T, Gann GD, Jonson J, Dixon KW (2016) International standards for the practice of ecological restoration – including principles and key concepts. Communications standards. https://seraustralasia.com/wheel/image/SER_International_Standards.pdf (accessed 9 April 2024)

Meirmans PG (2022) GENODIVE version 3.0: easy-to-use software for the analysis of genetic data of diploids and polyploids. Molecular Ecology Resources 20:1126–1131. https://doi.org/10.1111/1755-0998.13145

Noto AE, Hughes AR (2020) Genotypic diversity weakens competition within, but not between, plant species. Journal of Ecology 108:2212–2220. https://doi.org/10.1111/1365-2745.13465

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science 344:1246752. https://doi.org/10.1126/science.1246752

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155:945–959. https://doi.org/10.1093/genetics/155.2.945

R Core Team (2023) R: a language and environment for statistical computing. https://www.R-project.org/ (accessed 17 April 2024)

Rey Benayas JM, Newton AC, Diaz A, Bullock JM (2009) Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325:1121–1124. https://doi.org/10.1126/science.1172460

RStudio Team (2023) RStudio: integrated development for R.

Semchenko M, Saar S, Lepik A (2017) Intraspecific genetic diversity modulates plant–soil feedback and nutrient cycling. New Phytologist 216:90–98. https://doi.org/10.1111/nph.14653

Sloop CM, McGray HG, Blum MJ, Strong DR (2005) Characterization of 24 additional microsatellite loci in Spartina species (Poaceae). Characterization of 24 additional microsatellite loci in Spartina species (Poaceae). Conservation Genetics. https://doi.org/10.1007/s10592-005-9084-7

SoftGenetics (2013) GeneMarker. https://softgenetics.com/PDF/GeneMarkerMTP_UserManual.pdf (accessed 17 April 2024)

Stange M, Barrett RDH, Hendry AP (2021) The importance of genomic variation for biodiversity, ecosystems and people. Nature Reviews Genetics 22:89–105. https://doi.org/10.1038/s41576-020-00288-7

Strassburg BBN, Iribarrem A, Beyer HL, Cordeiro CL, Crouzeilles R, Jakovac CC, et al. (2020) Global priority areas for ecosystem restoration. Nature 586:724–729. https://doi.org/10.1038/s41586-020-2784-9

Suding K, Higgs E, Palmer M, Callicott JB, Anderson CB, Baker M, et al. (2015) Committing to ecological restoration. Science 348:638–640. https://doi.org/10.1126/science.aaa4216

Suding KN (2011) Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annual Review of Ecology, Evolution, and Systematics 42:465–487. https://doi.org/10.1146/annurev-ecolsys-102710-145115

Travis SE, Proffitt CE, Lowenfeld RC, Mitchell TW (2002) A comparative assessment of genetic diversity among differently-aged populations of *Spartina alterniflora* on restored versus natural wetlands. Restoration Ecology 10:37–42. https://doi.org/10.1046/j.1526-100X.2002.10104.x

Travis SE, Proffitt CE, Ritland K (2004) Population structure and inbreeding vary with successional stage in created *Spartina alterniflora* marshes. Ecological Applications 14:1189–1202. https://doi.org/10.1890/03-5135

U.S. Department of the Interior (2022) Bipartisan Infrastructure Law supports ecosystem restoration. U.S. Department of the Interior. https://www.doi.gov/priorities/investing-americas-infrastructure/ecosystem-restoration/projects (accessed 17 April 2024)

United Nations General Assembly (2019) United Nations Decade on Ecosystem Restoration (2021–2030). https://documents.un.org/doc/undoc/gen/n19/060/16/pdf/n1906016.pdf?token=lB9pykgZPEyvDtubXK&fe=true (accessed 17 April 2024)

Wei X, Xu Y, Lyu L, Xiao Z, Wang S, Yang T, Jiang M (2023) Impacts of ecological restoration on the genetic diversity of plant species: a global meta-analysis. Journal of Applied Ecology 60:1149–1160. https://doi.org/10.1111/1365-2664.14390

Wernberg T, Coleman MA, Bennett S, Thomsen MS, Tuya F, Kelaher BP (2018) Genetic diversity and kelp forest vulnerability to climatic stress. Scientific Reports 8:1851. https://doi.org/10.1038/s41598-018-20009-9

Whitham TG, Bailey JK, Schweitzer JA, Shuster SM, Bangert RK, LeRoy CJ, et al. (2006) A framework for community and ecosystem genetics: from genes to ecosystems. Nature Reviews Genetics 7:510–523. https://doi.org/10.1038/nrg1877

Zerebecki RA, Crutsinger GM, Hughes AR (2017) *Spartina alterniflora* genotypic identity affects plant and consumer responses in an experimental marsh community. Journal of Ecology 105:661–673. https://doi.org/10.1111/1365-2745.12703

Zerebecki RA, Hughes AR (2023) Ecological consequences of genotypic diversity within a foundation plant, *Spartina alterniflora*, are pervasive but not universal across multiple stress gradients. Journal of Ecology 111:1794–1810. https://doi.org/10.1111/1365-2745.14147

Zogg GP, Travis SE (2022) Genotypic diversity reduces the negative effects of increased competition, herbivory, and tidal inundation on the productivity of *Spartina alterniflora*. Estuaries and Coasts 45:462–469. https://doi.org/10.1007/s12237-021-00962-x

zu Ermgassen PSE, Baker R, Beck MW, Dodds K, zu Ermgassen SOSE, Mallick D, Taylor MD, Turner RE (2021) Ecosystem services: delivering decision-making for salt marshes. Estuaries and Coasts 44:1691–1698. https://doi.org/10.1007/s12237-021-00952-z

Supporting Information

The following information may be found in the online version of this article:

Table S1. AMOVA results.
Table S2. Akaike information criterion results, for model performance regarding both allelic and genotypic richness.
Supplement S1. Microsatellite marker quality control.
Supplement S2. Time Since Restoration.
Supplement S4. STRUCTURE analyses plots.

Coordinating Editor: Martin Breed

Received: 2 July, 2024; First decision: 17 December, 2024; Revised: 9 June, 2025; Accepted: 11 June, 2025