

EVOLUTIONARY ECOLOGY

Rapid plant trait evolution can alter coastal wetland resilience to sea level rise

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Rapid evolution remains a largely unrecognized factor in models that forecast the fate of ecosystems under scenarios of global change. In this work, we quantified the roles of heritable variation in plant traits and of trait evolution in explaining variability in forecasts of the state of coastal wetland ecosystems. A common garden study of genotypes of the dominant sedge *Schoenoplectus americanus*, “resurrected” from time-stratified seed banks, revealed that heritable variation and evolution explained key ecosystem attributes such as the allocation and distribution of belowground biomass. Incorporating heritable trait variation and evolution into an ecosystem model altered predictions of carbon accumulation and soil surface accretion (a determinant of marsh resilience to sea level rise), demonstrating the importance of accounting for evolutionary processes when forecasting ecosystem dynamics.

Organismal traits have long been understood to drive ecosystem functions such as elemental cycling (1, 2). There is mounting evidence that heritable trait variation within species can mediate ecosystem processes at a magnitude comparable with that of trait variation between species (Fig. 1B) (3, 4), and that traits can evolve at a fast enough pace to generate feedbacks that alter ecosystem dynamics on the timescale of current anthropogenic environmental change (Fig. 1C) (5). Together, this suggests that evolutionary processes play a larger role in the regulation of ecosystem function than previously imagined (6–8) (Fig. 1). Despite growing appreciation for this possibility, efforts to predict ecosystem function that account for genetic variation and evolutionary processes remain limited in number and scope (4, 9–12), in part because empirical studies are still needed to explicitly demonstrate whether heritable variation and rapid evolution are important drivers of ecosystem change. Studying the heritable trait variation of organisms is a necessary step toward understanding whether organismal evolution can influence ecosystem dynamics (6). Examining heritable trait variation over historical time might further reveal how organismal evolution elicits substantial ecosystem-level change (13, 14).

In coastal marshes, dominant plants act as ecosystem engineers by contributing to soil surface accretion, a process that has allowed

marshes to keep pace with sea level rise for millennia and is critical to their resilience (15). Further, the combination of high plant productivity and low decomposition rates from anoxic conditions in coastal marsh soils results in disproportionately high carbon accumulation rates per area relative to the soils of other ecosystems (16, 17). Models and empirical syntheses have demonstrated how traits and the growth of dominant marsh plants contribute to these and other ecosystem processes (18, 19). Because coastal marshes typically have low plant species diversity, intraspecific trait variation may play an important role in ecosystem processes (12, 20) (Fig. 1, B and C).

Belowground plant traits exert a strong influence on marsh ecosystem processes. For example, marsh accretion responds strongly to annual root turnover, which expands marsh soils, and plant-mediated decomposition, which reduces soil volume (21, 22). Belowground structures are consequently major contributors to carbon pools, and belowground productivity is tightly linked to carbon accumulation. Empirical estimates of belowground trait variation, heritable or otherwise, are sparse (23, 24), resulting in the common simplifying assumption that belowground traits vary following a fixed proportion to aboveground traits (Fig. 1D). This is a potentially unrealistic assumption—especially considering work that suggests that root-to-shoot ratios can rapidly evolve and exhibit substantial plasticity in response to stress (25, 26)—that can bias predictions (27, 28).

In this work, we paired a common garden experiment with an ecosystem model (29) to quantify the role of heritable variation in plant traits and of trait evolution in explaining variability in forecasts of carbon accumulation and soil surface accretion (Fig. 1). We characterized heritable trait variation using 16 genotypes

of *Schoenoplectus americanus*—a dominant sedge in North American coastal marshes and the subject of extensive global change research related to coastal wetlands—and focused on belowground traits that are known to influence carbon sequestration and accretion. We characterized trait variation and evolution (Fig. 1, B and C) by applying a resurrection ecology approach (14, 30–32) in which we “resurrected” genotypes from time-stratified seed banks from four nearby marshes in the Chesapeake Bay (figs. S1 to S3 and table S1). For genotypes from two of the four marshes, we assessed the role of genotype provenance (marsh of origin; Corn Island or Sellman Creek), and age cohort [ancestral (1931 to 1973) or descendant (1994 to 2016)] in driving trait variation. To assess potential nonadditive interactions that can be important when scaling up from genotype to ecosystem (Fig. 1B), we compared traits of the 16 genotypes grown in monoculture (four propagules of one genotype; $n = 3$ monocultures per genotype, totaling 48 monocultures) with those grown in polyculture (one propagule each of four genotypes; $n = 48$ total polycultures). We quantified the potential impact of eco-evolutionary dynamics on ecosystem processes using estimates of heritable variation and evolution from the common garden experiment to parameterize a marsh ecosystem model. Together, these approaches provide a framework for integrating data from common garden experiments typical in the field of evolutionary biology to predictions at the ecosystem scale appropriate for forecasting ecosystem responses to global change.

Characterizing heritable variation in *S. americanus* traits

S. americanus exhibited considerable heritable variation in all traits measured in the common garden experiment (fig. S4). Comparably more heritable variation was observed in belowground traits—such as the magnitude and distribution of belowground biomass (fig. S4, B, D, and F)—than in aboveground traits (fig. S4, A, C, E, and G). For example, heritable variation explained on average 49.5% of variation in the shape of the root depth distribution [intraclass correlation coefficient (ICC), 49.5; 95% confidence interval (CI) (15.7, 77.3)] and 69.1% of variation in root-to-shoot ratio [ICC, 69.1; (43.7, 87.7)]. These findings demonstrate the importance of explicitly characterizing variation in belowground traits, as their variation does not align with that of traits aboveground.

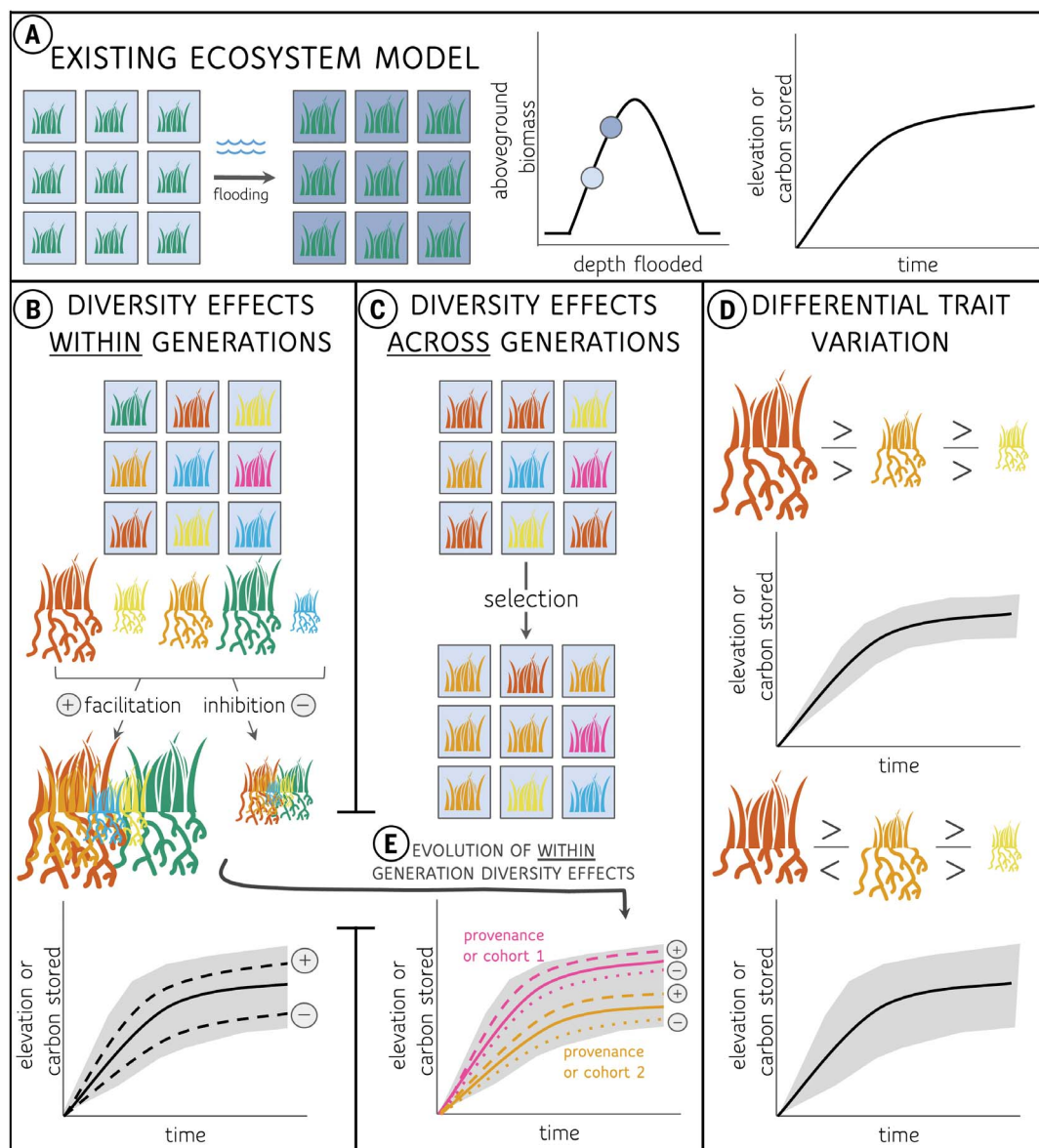
Heritable variation in *S. americanus* traits was structured by evolution captured across space (across the two provenances for which there were multiple genotypes; ~2 km of distance) and time (~50 years between ancestral and descendant cohorts) (Fig. 2). Differences

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Fig. 1. Potential consequences of heritable variation in *S. americanus* on marsh accretion and carbon sequestration.

(A) Current marsh accretion models do not account for heritable variation in traits and only account for plastic responses of aboveground biomass to flooding. Increased flooding from light to dark blue environments increases aboveground biomass. (B) Heritable variation may have nonadditive, within-generation consequences. For example, interactions between genotypes can lead to facilitation (+) or inhibition (−) shifting the mean trait values of polycultures and thus shifting the mean prediction for ecosystem processes. (C) Selection may shift plant trait means, inducing evolutionary change. (D) Variation in belowground traits may not scale with variation in aboveground traits; thus capturing belowground trait variation is important for accurately predicting variation in ecosystem processes. (E) Within-generation diversity effects [from (B)] can evolve [from (C)]. In (B) to (E), different colored plants represent different genotypes of the same species.



in heritable trait variation were reflected in patterns of genetic variation elucidated with single-nucleotide polymorphism (SNP) genotyping (fig. S3 and table S3). Heritable variation attributable to genotype, provenance, and age cohort explained roughly 15 to 50% of observed variation across all traits (Fig. 2A, blue shading, and fig. S5) and, for most traits, exceeded the variation explained by experimental covariates (Fig. 2A, light gray shading; initial propagule weight, variation in flooding due to peat levels, and spatial blocking). Differences in the shape of root depth distributions were strongly consistent within age cohort and provenance (Fig. 2, A and B) [regression coefficient of age (β_{age}) = -0.015 (-0.022 , -0.007); regression coefficient of provenance (β_{prov}) = -0.023 (-0.031 , -0.015)]. Root-

ing depth became shallower over time within both provenances, with more root biomass proportionally allocated near the marsh surface in descendant genotypes (Fig. 2B). Root-to-shoot ratios exhibited strong signatures of provenance, with genotypes from Corn Island having root-to-shoot ratios that were 17.2% (1.9%, 34.4%) higher than those of genotypes from Sellman Creek (fig. S6). Comparisons of ancestral and descendant genotypes also revealed that root-to-shoot ratios have declined by 8.3% (-5.2% , 19.6%) since the mid-20th century (fig. S6), indicating that over time, plants have allocated fewer resources toward belowground biomass. We hypothesize that belowground traits may have evolved in response to anthropogenic nitrogen loading, which has increased throughout the Chesapeake Bay

over the most recent century (33). Shifts in root depth distribution in coastal marsh vegetation have previously been posited to represent differences in how plants access nutrients belowground (34). Excess nitrogen may have alleviated nutrient limitation, reducing the need for plants to invest in traits that improve access to belowground resources (35).

Aboveground traits also evolved, but less so than belowground traits, as evidenced by smaller effect sizes of age cohort and provenance. For example, on average, stems became thinner over time, with stem widths declining 5.6% (-3.3% , 14.4%) between ancestral and descendant cohorts (fig. S7). This pattern mirrors changes in stem morphology exhibited by *S. americanus* subjected to 30 years of elevated CO_2 exposure—a change that can affect

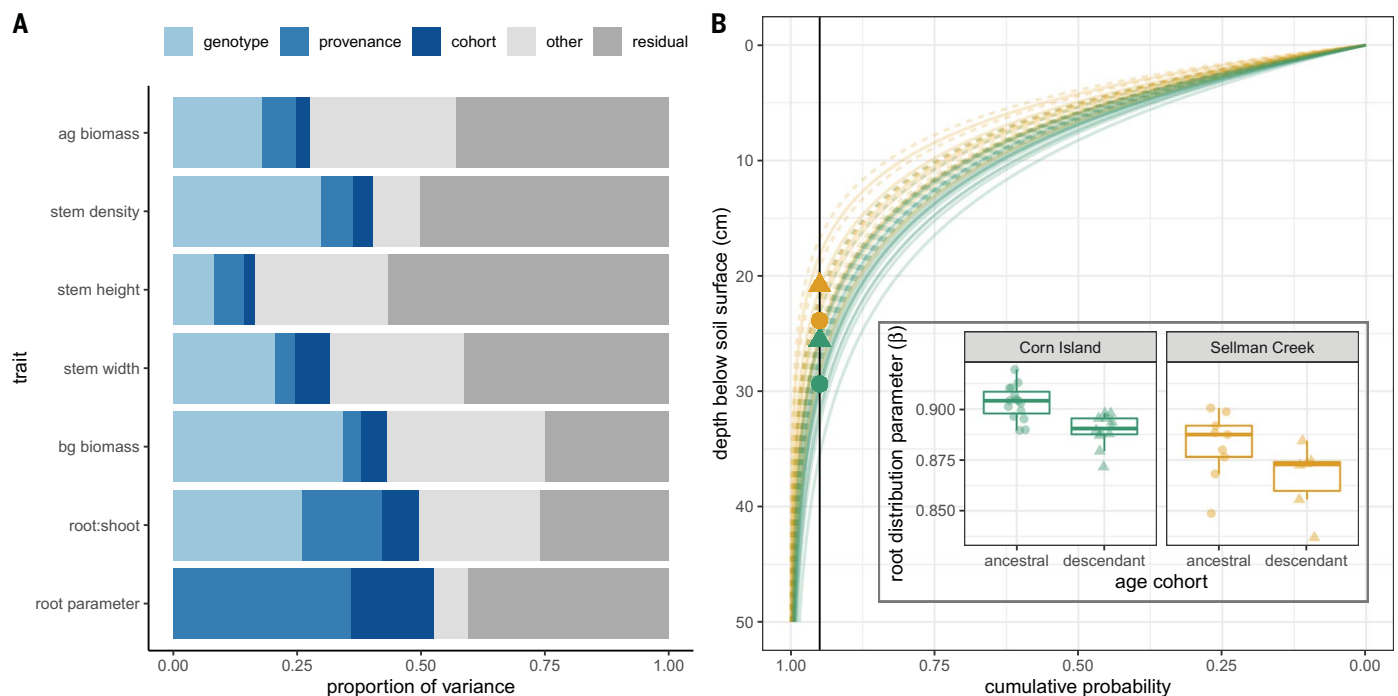


Fig. 2. Provenance and age cohort explain considerable variation in traits, particularly for root depth distribution. (A) Using (generalized) linear mixed models with provenance and age cohort as fixed effects and genotype as a random effect, for each trait we decomposed observed trait variation into five categories: genotype, provenance, cohort, other (covariates in the model that accounted for exogenous variation because of experimental setup: initial propagule weight, variation in flooding because of peat level, and spatial blocking), and residual. Labels “ag biomass” and “bg biomass” represent

aboveground and belowground biomass, respectively. (B) Differences in belowground biomass distribution with depth according to provenance and age cohort. Differences in the parameter β (root distribution parameter) are shown in the inset and were applied to the equation $1 - \beta^{\text{depth}}$ to predict the cumulative proportion of belowground biomass with depth shown in the main figure (34, 45). The vertical line at 95% cumulative probability indicates the depth at which 95% of belowground biomass is contained, which is a parameter in the Cohort Marsh Equilibrium Model (CMEM) (29).

the ability of marshes to withstand storm surges (36). Like belowground traits, on average, more variation in aboveground traits was attributable to provenance than age cohort. For example, mean stem heights differed according to provenance, with plants from Sellman Creek being 3.0% (−1.5%, 7.5%) taller than those from Corn Island (fig. S8), whereas only a 0.3% (−3.8%, 4.7%) difference in stem height was found between ancestral and descendant plants.

Assessing the strength of nonadditive interactions between genotypes

Given that there are high levels of standing genetic diversity within populations of *S. americanus*, even at fine spatial scales of a few meters (30), it is possible that interactions among genotypes result in nonadditive effects, in which trait values for a mixture of genotypes are not equal to the sum of trait values for individual genotypes (37–39) (Fig. 1B). Consequently, characterizing the direction and strength of nonadditive effects can be important for scaling trait variation from genotype to ecosystem. Mechanisms that give rise to nonadditivity can include facilitation (a

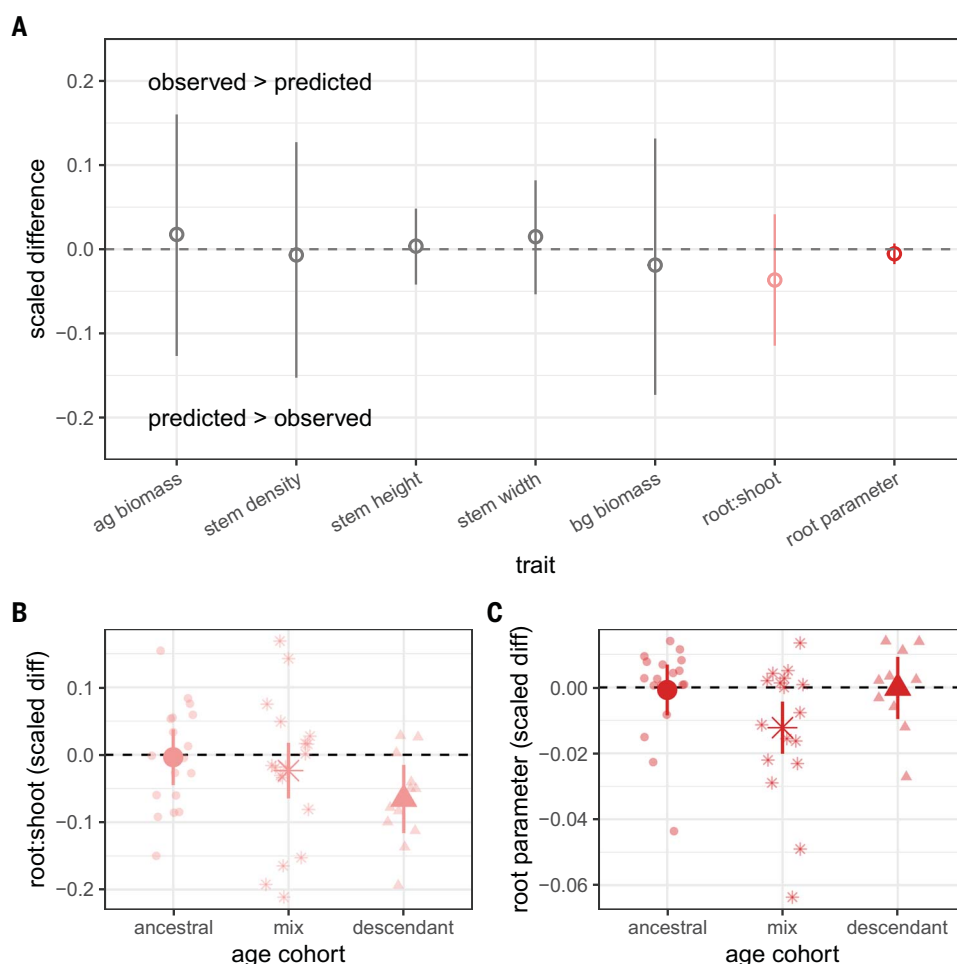
positive nonadditive interaction), inhibition (a negative nonadditive interaction), and selection effects (a positive or negative nonadditive interaction) (37). Overall, comparisons of *S. americanus* genotypes grown in monoculture with those grown in polyculture did not reveal strong evidence of nonadditive interactions (Fig. 3A). However, for two belowground traits—root-to-shoot ratio and root depth distribution—variation in the strength of the nonadditive interactions depended on whether the polycultures were composed of ancestral genotypes, modern genotypes, or a mix of both (Fig. 3, B and C and fig S9). Root-to-shoot ratios were substantially lower than additive expectations for polycultures composed of descendant genotypes but not for those composed of ancestral genotypes [$\beta_{\text{anc vs desc}} = -0.06$ (−0.13, 0.00)] (Fig. 3B), suggesting that the strength of within-species interactions can rapidly evolve. Root depth distributions in mixed polycultures were shallower than additive expectations, but those composed of only ancestral or descendant genotypes were similar to additive expectations [$\beta_{\text{mix vs anc}} = 0.01$ (0.00, 0.02); $\beta_{\text{mix vs desc}} = 0.01$ (0.00, 0.02)] (Fig. 3C). Mixing genotypes from different age co-

horts in our experiment may have increased the functional diversity of rooting behavior, allowing for better resource partitioning without the need for deeper rooting (Fig. 3C).

Scaling heritable variation in plant traits to ecosystem outcomes

Observed heritable trait variation and rapid evolution drove downstream effects on soil surface accretion and carbon accumulation (Fig. 4). We ran simulations of a marsh accretion model (29) based on conditions at the Global Change Research Wetland (Edgewater, MD, USA), which are typical of large areas of the Chesapeake Bay. We accounted for heritable variation in peak aboveground biomass, root-to-shoot ratio, and depth of the 95% cumulative root distribution (while accounting for between-trait covariances) (figs. S10 and S11 and table S2). We projected that heritable trait variation could result in differences in marsh elevation gain of up to 5 cm by the year 2100 [mean elevation = 34.2 cm NAVD88 (North American Vertical Datum, 1988), (32.1, 37.1)]; (Fig. 4A), which is approximately one-third of the elevation differential between mean and high tides and thus is consequential

Fig. 3. Genotypes do not exhibit strong nonadditive interactions in polyculture overall, but there is evidence that within-species interactions have evolved since the mid-20th century. (A to C) The “scaled difference” on the y axes indicates the difference between a trait exhibited by genotypes grown in polyculture versus what would be expected of genotypes grown in monoculture (scaled by the mean value of the trait for easier comparison across traits). (A) Scaled differences across traits overall indicate no significant nonadditive interactions. Points indicate the mean difference, and bars indicate 95% confidence intervals. The strength of within-species interactions for (B) root-to-shoot ratio and (C) root depth distribution varies systematically based on the composition of the polyculture. For (B) and (C), points with error bars represent marginal means with 95% confidence intervals.



to how much flooding plants will experience. These differences also result in average vertical accretion rates that could vary more than 1.5-fold [mean vertical accretion rate = 1.45 mm/year (1.18, 1.81)] (Fig. 4B, width of histogram). Predicted rates of carbon accumulation at our sites varied up to 0.32 metric tons C ha⁻¹ year⁻¹ because of heritable variation [mean C accumulation rate = 0.35 (0.21, 0.53); Fig. 4C, width of histogram], which would lead to estimates of soil carbon storage through 2100 varying by more than two-fold in highly organic peat-forming marshes, such as those in the Chesapeake Bay.

Vertical accretion rates were 8% higher and carbon accumulation rates were 18% higher for ancestral cohorts than descendant cohorts (Fig. 4, B and C). This suggests that modern *S. americanus* marshes may be less resilient to sea level rise and store less carbon compared with marshes from the mid-20th century because of organismal evolution. Across space, changes in plant traits drove soil accretion at Corn Island to be 3% higher than at Sellman Creek and drove soil carbon accumulation rates to be 6% higher (Fig. 4, A to C, green versus gold). Additional evidence from a separate ex-

periment suggests that our estimates of the impact of heritable variation and rapid temporal evolution on accretion and carbon accumulation are robust and possibly conservative (40) (figs. S12 and S13 and table S4).

The effect of evolution on ecosystem processes captured in this work is comparable with the effects of rapid environmental change. For example, the magnitude of evolution's influence on vertical accretion that we found is similar to the modeled effect of shifts in salt marsh mineral accretion rates from changes in *S. americanus* stem morphology over 11 years of exposure to elevated CO₂ in a different but related study (36). Additionally, by running simulations of the ecosystem model in which we varied the total amount of sea level rise, we found that the percent difference in carbon accumulation rate between ancestral and descendant genotypes was approximately equal to an additional 4 cm of sea level rise by 2100. The effects of organismal evolution on carbon accumulation are particularly notable given that they would partially offset predicted large increases in future carbon storage in response to global change factors such as increasing atmospheric CO₂ (41, 42).

Much of the projected variation in our predictions of marsh accretion and carbon accumulation was attributable to belowground trait variation (Fig. 4E), which suggests that further study of the effects of genotypic variation on belowground traits can improve forecasts of coastal marshes in which surface accretion is predominantly driven by organic matter accretion. This was revealed by running simulations in which we only accounted for between-genotype variation in aboveground biomass, keeping belowground traits (root-to-shoot ratio and depth of the 95% cumulative root distribution) constant, which aligns with the simplifying assumption that belowground traits covary with aboveground traits (Fig. 1D). Failing to account for heritable variation in belowground traits beyond the variation in aboveground biomass dramatically decreased the predicted uncertainty for accretion and carbon sequestration (Fig. 4, A, D, and E). For example, the variance in final predicted marsh elevation decreased by 68% when only variance in aboveground biomass was included in the simulations (Fig. 4E). Accounting for heritable belowground trait variation also altered the average predictions

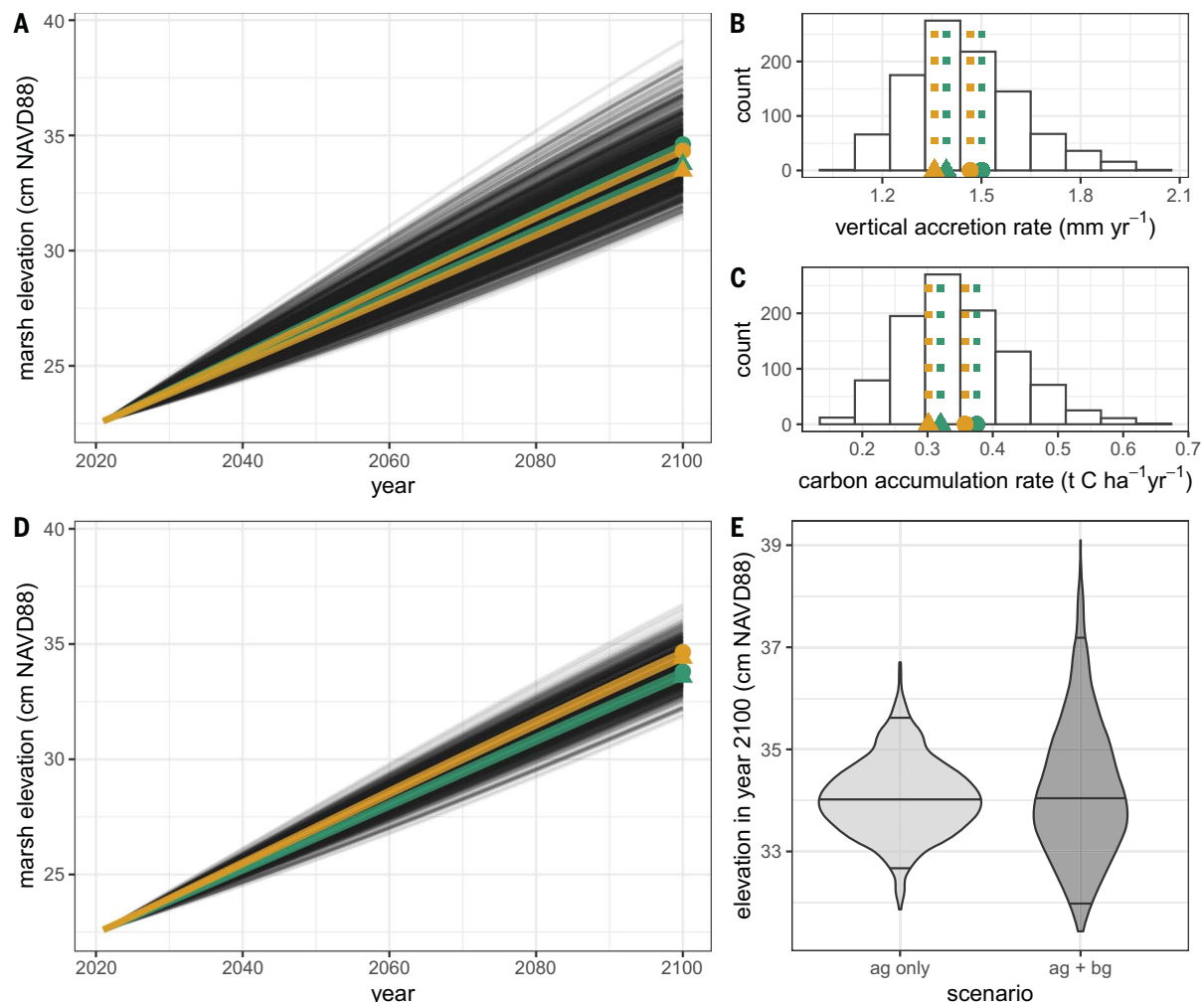


Fig. 4. Accounting for heritable trait variation and evolution alters forecasts of marsh ecosystem structure and function. (A) Using CMEM (29), we simulated marsh elevation gain to the year 2100. Light gray lines indicate model simulations ($n = 1000$) that account for variation in aboveground biomass, root-to-shoot ratio, and 95% cumulative root distribution depth due to genotype. Green and gold lines indicate mean predictions for genotypes from Corn Island and Sellman Creek, respectively, and the shapes at year 2100 indicate age cohorts (circle, ancestral; triangle, descendant). (B) Average vertical accretion rate explained by variation in traits due to heritable

variation (histogram) and average provenance and age cohort trait values (points). (C) Average carbon accumulation rate explained by variation in traits due to heritable variation (histogram) and average provenance and age cohort trait values (points). (D) Simulations of CMEM that account for heritable variation in only aboveground biomass due to genotype, provenance, and age cohort. (E) Distribution of final predicted elevation of CMEM simulations for scenarios in which aboveground and belowground traits were varied ["ag + bg" from (A)] and for which only aboveground biomass was varied ["ag only" from (D)].

for each age cohort and provenance. Notably, differences in ecosystem outcomes between age cohorts were larger than those between provenances when belowground trait variation was considered (Fig. 4A), but the opposite was true when only aboveground trait variation was considered (Fig. 4D). However, although belowground trait variation drove variation in ecosystem processes in a highly organic marsh in the Chesapeake Bay, heritable variation and evolution of aboveground plant traits may play a larger relative role in marshes in which accretion rates are driven by mineral sediment capture aboveground, a

process mediated by stem density and morphology (36).

Observed shifts in plant traits in long-term studies of coastal marshes have been previously thought to reflect plastic responses induced by exposure to environmental pressures (Fig. 1A). For example, there is evidence that *S. americanus* morphology has changed in response to elevated CO_2 and increased nitrogen deposition over the course of 30 years, with putatively plastic trait changes having substantial consequences for model predictions of aboveground sediment capture rate (36). Our findings, along with additional evi-

dence of the adaptive capacity of *S. americanus* (14, 30), offer an updated perspective suggesting that plants can evolve at a pace and magnitude that feeds back on ecosystem-level processes (6). Failure to account for heritable variation and rapid evolutionary change in ecosystem models (43, 44) might therefore mischaracterize the role that organismal response plays in ecosystem resilience to environmental change that could systematically alter ecosystem-level predictions. For example, our results suggest that failing to account for decadal-scale evolutionary change may overestimate the potential for coastal marshes

to build elevation and store carbon. It is increasingly apparent that organismal evolution and ecosystem development occur on similar time scales, which can elicit feedbacks (6). Integrative approaches will thus be increasingly important as anthropogenic change continues to challenge our ability to forecast the resilience of at-risk ecosystems such as coastal marshes (12).

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S13
Tables S1 to S4
References (47–70)

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