Long-term reductions in anthropogenic nutrients link to improvements in Chesapeake Bay habitat

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Great effort continues to focus on ecosystem restoration and reduction of nutrient inputs thought to be responsible, in part, for declines in estuary habitats worldwide. The ability of environmental policy to address restoration is limited, in part, by uncertainty in the relationships between costly restoration and benefits. Here, we present results from an 18-y field investigation (1990–2007) of submerged aquatic vegetation (SAV) community dynamics and water quality in the Potomac River, a major tributary of the Chesapeake Bay. River and anthropogenic discharges lower water clarity by introducing nutrients that stimulate phytoplankton and epiphyte growth as well as suspended sediments. Efforts to restore the Chesapeake Bay are often viewed as failing. Overall nutrient reduction and SAV restoration goals have not been met. In the Potomac River, however, reduced in situ nutrients, wastewater-treatment effluent nitrogen, and total suspended solids were significantly correlated to increased SAV abundance and diversity. Species composition and relative abundance also correlated with nutrient and water-quality conditions, indicating declining fitness of exotic species relative to native species during restoration. Our results suggest that environmental policies that reduce anthropogenic nutrient inputs do result in improved habitat quality, with increased diversity and native species abundances. The results also help elucidate why SAV cover has improved only in some areas of the Chesapeake Bay.

ecology | eutrophication | restoration | submerged aquatic vegetation

Submerged aquatic vegetation (SAV) is a critical habitat for invertebrates, fish, and waterfowl (1–4), but SAV ecosystems are declining worldwide (5). Habitat restoration can improve biodiversity and ecosystem function, but recovery to predisturbance states is rare (6). Light attenuation limits SAV abundance in the Chesapeake Bay and other populated estuaries (5, 7, 8). Chesapeake Bay restoration goals are based, in part, on observed links between nutrients, light limitation, and SAV abundance (9–11), and nutrient reduction remains a key objective (12, 13). The watershed spans 165,000 km^2 in six states, and nutrient loads come from many sources, thus restoration is a substantial endeavor. Despite some progress, increases in abundances of key species and habitats have been limited (12–14), leaving the effectiveness of restoration in doubt.

In the Chesapeake Bay and its tributaries, SAV habitat has historically changed in abundance and diversity because of disease, anthropogenic impacts, and major tropical storms (15, 16). By the late 1970s, many previously vegetated areas were devoid of vegetation. SAV then began to recover while efforts to reduce nonpoint source and sewage impacts improved. Increases in SAV abundance across the bay were observed from 1985 to 1993 (17, 18). Potomac River restoration effort included the implementation of a nitrification system at the Blue Plains Wastewater Treatment Plant (Fig. 1) in 1980 as well as phosphorus-effluent filters in 1982 and a new nitrification-denitrification system between 1998 and 2001. SAV reappeared in the upper tidal Potomac River in 1983 with the proliferation of an exotic species, *Hydrilla verticillata* (hydrilla). Other native and exotic species also began to reappear, with 12 species present by 1985 (19). Research suggested that transport of SAV propagules (e.g., seeds, plants, and tubers) was high enough to repopulate bare areas if light availability improved (16).

Studies across the Chesapeake Bay have found correlations between SAV total abundance, nutrients, and water clarity (10, 18), but consistent bay-wide improvements in water quality and increases in SAV total abundance remain to be observed. Through 2001, in situ nitrogen in the tidal Potomac River correlated negatively to SAV Shannon diversity, and chlorophyll *a* and total suspended solids also correlated negatively to SAV abundance (4). The relationships between anthropogenic nutrient inputs and long-term SAV shifts in species composition and community structure have not, however, been examined until now.

Our methodology included analyzing species-specific SAV abundances (1990 to 2007) over an area of the Potomac River from Washington DC to ~90 km downstream (Fig. 1). We analyzed the following environmental and water-quality data during the growing season (April to October): Potomac River discharge, total nitrogen (TN) and phosphorus (TP) load at Little Falls, TN and TP inputs from the Blue Plains Wastewater Treatment Plant (WTP), in situ TN, TP, total suspended solids (TSS; includes both phytoplankton and suspended sediment) (Fig. 2 *A–D*), chlorophyll *a*, Secchi depth, temperature, and salinity (*SI Materials and Methods*). We collated species-specific abundance data from annual aerial photographs and field surveys conducted at the approximate peak of the growing season in the tidal freshwater and upper-oligohaline zones of the Potomac River (4). SAV community parameters included total abundance, native and exotic SAV abundances (cover area in km^2), Pielou evenness, and Shannon diversity as well as multivariate Bray-Curtis similarity indices of species composition and rank-abundance distributions (RADs) (Fig. 2 *E–G*).

We used multivariate statistics to determine correlations between matrices (R) of SAV species composition and RAD similarity to multivariate environmental-variation similarity using the above environmental parameters and randomization tests to determine significance (20) (*SI Materials and Methods*). We conducted all correlations using the nonparametric Spearman-rank correlation (r_s). Last, we examined the covariance of each species with each other species over time as an indicator of compensatory dynamics.

Results and Discussion

We found evidence that restoration efforts have improved Potomac River water quality and were linked to important SAV habitat improvements and lesser proportion of exotic species. Multidimensional species composition and RAD similarity were significantly correlated to environmental and water-quality similarity,

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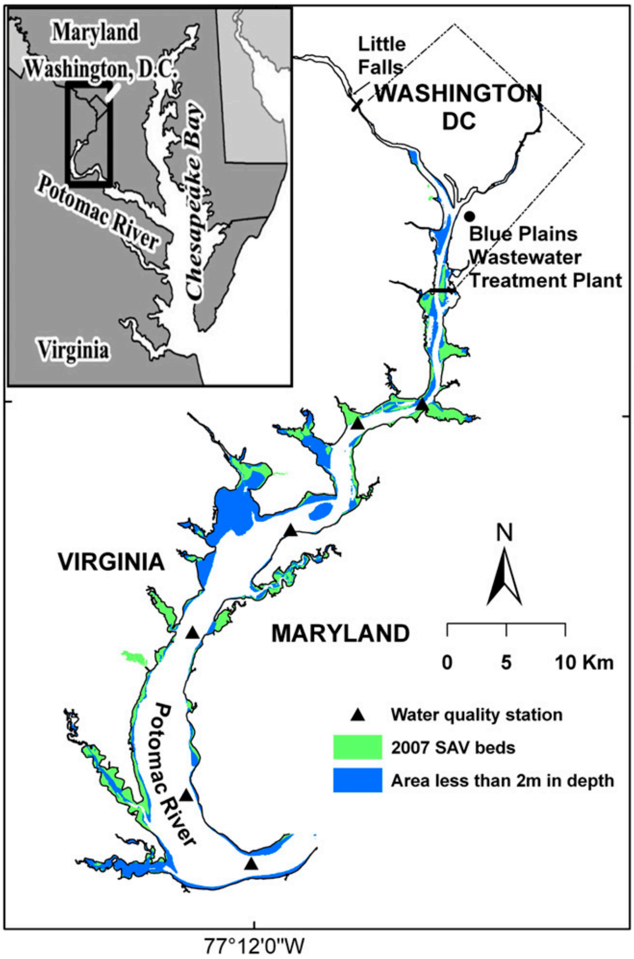

Fig. 1. Map illustrating the study area. *Inset* locates it within the Chesapeake Bay watershed. Also indicated are Little Falls, the Blue Plains Wastewater Treatment Plant, the locations of the in situ water-quality measurement stations, the 2007 SAV coverage, and the area of potential SAV habitat extending to 2-m depth.

with both species-composition and RAD similarities having TN WTP, in situ TN, and TSS as the top three most explanatory variables for change over time ($R > 0.57$, $P < 0.001$). Of those, TN WTP is itself an anthropogenic variable, whereas in situ TN and TSS are related to natural and anthropogenic inputs through point and nonpoint sources that ultimately limit light. The multivariate analysis suggests that the species composition and relative abundance and structure (RADs) were influenced by differential responses to these light-limiting factors.

Relationships observed in the multidimensional analysis were corroborated by results from bivariate correlations. Indices of species composition and RAD similarity, native abundance, total abundance, evenness, and Shannon diversity increased over time ($r_s = 0.59$ to 0.78, $P \leq 0.03$), whereas TN WTP, in situ TN, TP, and TSS decreased over time ($r_s = -0.69$ to -0.79, $P \leq 0.01$) (Fig. 2 *B*–*G*). Higher values in the index of species composition [multidimensional scaling (MDS) x-ordinate] were significantly correlated to total abundance, the abundances of native and exotic species, the ratio of native to exotic species, Shannon diversity, RAD (MDS x-ordinate), and evenness ($r_s \geq 0.66$, $P \leq 0.01$) (Fig. 3*A*). Decreases in TN WTP, in situ TN, TP, and TSS were significantly correlated to increases in total abundance and species-composition index (MDS *x*-ordinate; $r_s = -0.52$ to -0.84, $P \leq 0.05$) (Fig. 3*B*) as well as increases in Shannon diversity and RAD index (MDS *x*-ordinate) (Table S1 and Fig. S2). In 2007, for example, when TSS concentration and nutrient loads were relatively low, there were 11 species, and the first seven ranks ranged across an order of magnitude in abundance (Fig. 2 *H* and *I*). Conversely, in 1994, when those loads were higher, nine species were detected with lower evenness, and the first seven ranks spanned nearly four orders of magnitude with a greater dominance of exotics.

Secchi depth (21) was negatively correlated to TSS ($r_s = -0.54$, $P = 0.04$). Correlations between Secchi depth and SAV community parameters were sensible in sign, but none were significant (Table S1 and Fig. S2) (Fig. 3*B*). TN WTP was highly correlated to in situ TN ($r_s = 0.84$, $P < 0.001$), but in situ TP was not correlated to TP WTP. Total N and TP load at Little Falls was not significantly correlated to in situ TN, in situ TP, or any of the SAV parameters. The ratio of TN WTP to TN load at Little Falls ranges between 0.07 and 0.68, with an average of 0.30. According to that measure of WTP nutrient dominance, TN WTP loading could almost double overall TN loading during some years. TP WTP was unrelated to SAV community parameters in all cases. The ratio of TP WTP to TP load at Little Falls loading ranges between 0.01 and 0.14, with an average of 0.06, which may be related to the perceived lesser influence of TP WTP.

Decreased water-column chlorophyll *a* was significantly correlated to increased total abundance ($r_s = -0.60$, $P = 0.02$) and exotic abundance ($r_s = -0.67$, $P = 0.01$; Table S1 and Fig. S2 and Fig. 3*B*). Other SAV community correlations with chlorophyll *a* were not significant, which might be related to epiphytic algal growth. In situ nutrients can stimulate the growth of algal epiphytes. Algal and invertebrate epiphytes can cover SAV tissue and limit light in a way that would not be necessarily discerned from water-quality data from the channel, but no epiphyte time-series data were available for the study area.

Many of the studied parameters had significant correlations with time. We, therefore, repeated the bivariate correlation analysis with any significant temporal trends removed from the data and found that, although not all previously significant correlations remained significant, TSS was still similarly correlated to total abundance, species composition, and RADs ($r_s \geq -0.69$ to -0.82, $P \leq 0.006$) (*SI Materials and Methods*).

Higher river-discharge years can be associated with cooler temperatures and greater nutrient and TSS loading from nonpoint sources. In 1936, the SAV cover in the study area was potentially decimated by a high discharge of about three times that observed during our study period (22). In our study, river discharge was not correlated to in situ temperature, TN, TP, or TSS. Variations in river discharge were also not correlated to SAV community parameters, and no long-term change in growing-season water temperature was observed. However, low SAV abundances were observed in 1996 and 2003, years with tropical storms and resulting average daily river discharge $>400\ \mathrm{m^3s^{-1}}$ during the growing season (Fig. 2). Such climate perturbations provide an example of how thresholds in factors other than nutrients can have a clear impact on SAV.

Variation in species composition and RADs are widely believed to be driven by niche-based differences in environmental tolerances or competition for resources (23–25). Correlations between temporal shifts in water quality, species composition, and RADs may be related to differential responses between species to changing conditions. Differences in species-specific responses to TSS, nutrients and other factors in terms of growth rates, photosynthetic efficiencies, depth of colonization in various light conditions, and production and transport of propagules (16, 19, 26, 27) may be explanatory factors in the observed changes in species composition.

This study provides a rare quantification of long-term exotic species dynamics many years after the invasion and establishment of several exotic species. Both stabilizing differences (niche partitioning that leads to coexistence) and fitness differences (one taxon has competitive advantage over another) between exotics and natives may have important roles in this system. According to invasion theory, exotic species should either be lost or exclude resident species if fitness differences dominate over stabilizing

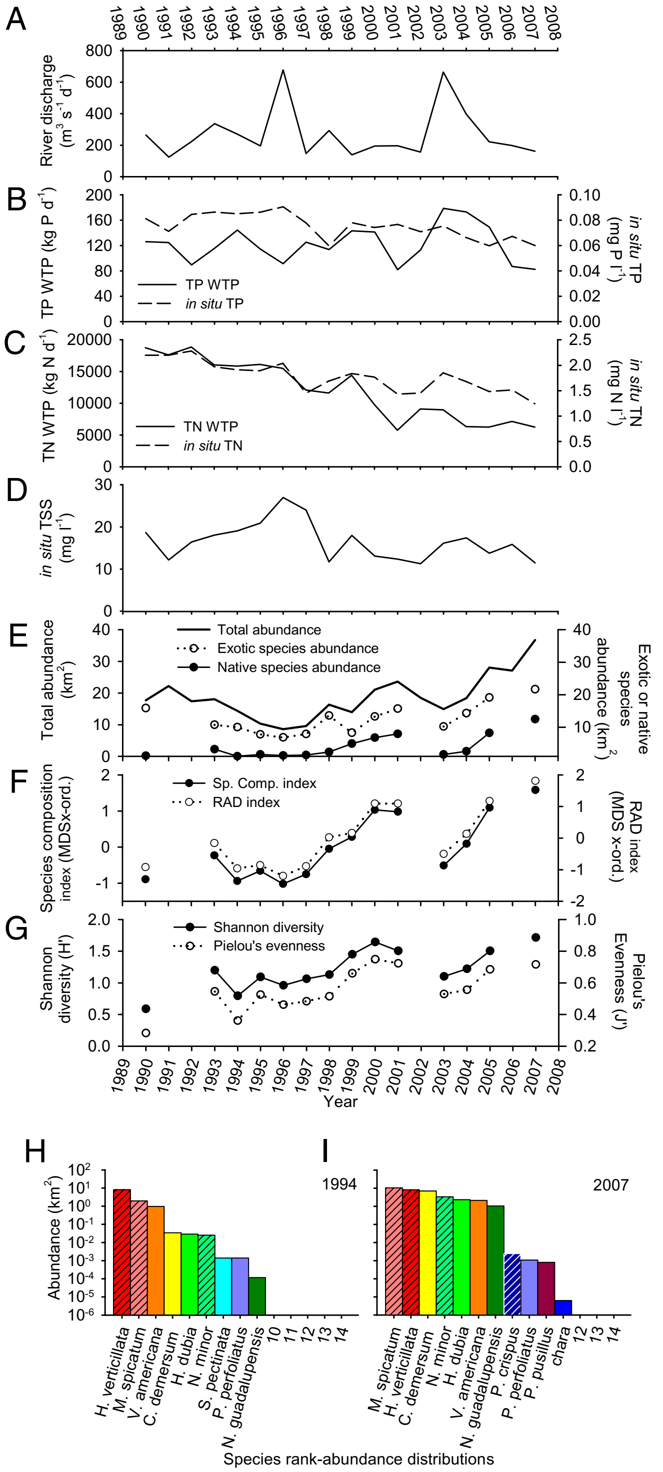

Fig. 2. Time-series data showing the variation of key environmental variables. (*A*) Potomac River water discharge at Little Falls (solid line). (*B*) TP WTP (solid line) and in situ TP (dashed line). (*C*) TN WTP (solid line) and in situ TN (dashed line). (*D*) TSS as well as SAV parameters including (*E*) total abundance (solid line), native abundance (solid line with dots), and exotic abundance (dotted line with circles). (*F*) Multivariate species composition (solid line with dots) and RAD similarity indices (dotted line with circles) MDS *x*-ordinates created using log(x + 1) transformed data and the Bray-Curtis similarity measure. Points closer together on the *y* axis are more similar than points farther apart on that axis. (*G*) Shannon diversity (solid line with dots) and Pielou evenness (dotted line with circles). RADs for (*H*) 1994 and (*I*) 2007 with hatch marks indicating exotic species. Species composition included *H. verticillata*, *Potamogeton crispus*, *Myriophyllum spicatum*, *Najas minor*, *Vallisneria americana*, *Ceratophyllum demersum*, *Najas guadalupensis*, *Heteranthera dubia*, *Potamogeton perfoliatus*, *Potamogeton pusillus*, *Stuckenia pectinata*, *Elodea nuttallii*, *Najas gracillima*, and the macroalgae, *Chara* spp. Numbers indicate empty ranks of the 14 species observed during the entire study.

differences in the community (28). Although the ratio of native to exotic abundance was not directly correlated to TN WTP, TN, or TSS, species-composition was significantly correlated to the relative dominance of natives. When nitrogen loads decreased, species composition shifted such that natives became more dominant and diversity, evenness, and total SAV abundance increased. The ratio of exotics to natives had similar variation in the upper, middle, and lower reaches of the study area, with a notable exception when the ratio dropped in the upper reach only in 2000. These relationships suggest that native species fitnesses increased relative to exotic species fitnesses when nitrogen and TSS were reduced and that species composition consequently shifted, with native species increasing in abundance.

Competition seems to have played an important, albeit less than dominant, role in SAV community dynamics. Compensatory dynamics were not found here (as measured by negative covariance between species) (24); however, the apparent differential responses to water quality between exotics and natives suggest a role for competition (fitness differences) (Fig. 3). If competitive interaction without substantial negative covariance between species is common, it could explain the ostensible paradox between the apparent rigor of competition theory and its lack of dominance in observations.

Environmental variables like nutrients and TSS have apparent influences on SAV community structure and SAV abundance, but other factors probably contribute to unexplained variation in correlations. For example, negative impacts from river discharge and positive feedbacks from the water-clarifying ecosystem functions of bivalves and SAV have been observed (3, 8, 29). Filter-feeding bivalves and SAV itself can improve water clarity and provide positive feedback for SAV abundances (14), but the limited bivalve biomass time-series data for the study area were not correlated to SAV dynamics (*SI Materials and Methods*). Both positive and negative feedback mechanisms have been suggested between SAV and waterfowl, with greater waterfowl counts linked to greater SAV abundance in the study area (4). Spatial differences between water-quality sample stations in the main channel and the shores and embayments where SAV often resides probably also explain some variation (30).

Although long time-series data on species-specific SAV community dynamics are unavailable bay-wide, the relationships observed in this study may be representative of SAV habitats throughout the Chesapeake Bay. Because nutrient and environmental conditions across the bay are not uniform, the responses to restoration in terms of SAV cover can be masked in bay-wide analyses (8, 18). Areas like the Potomac River study area, which has had reductions in nutrients and TSS, show signs of SAV recovery (13, 18). However, water quality has recently been declining for other parts of the Chesapeake Bay, possibly explaining why bay-wide SAV abundance has not improved appreciably in the last decade (13, 14, 17, 18). Although the certainty with which nutrients can be asserted as a causal factor varies from study to study, a recent review of 215 studies worldwide found that estuaries with reduced nutrients generally had increases in SAV abundance (5).

Our results suggest that reduced nutrient inputs and improved water clarity result in improvements in SAV habitat abundance with reductions in the proportion of exotic species. Other estuaries globally that have substantially reduced nutrients have also documented increases in SAV cover (5, 31–37). The Chesapeake Bay Program has had a three-tier set of threshold goals for restoring SAV. Tier I is the maximum historical cover of SAV as determined by aerial photography. It has been hypothesized that, with comprehensive restoration, the Tier III goal of SAV extending to

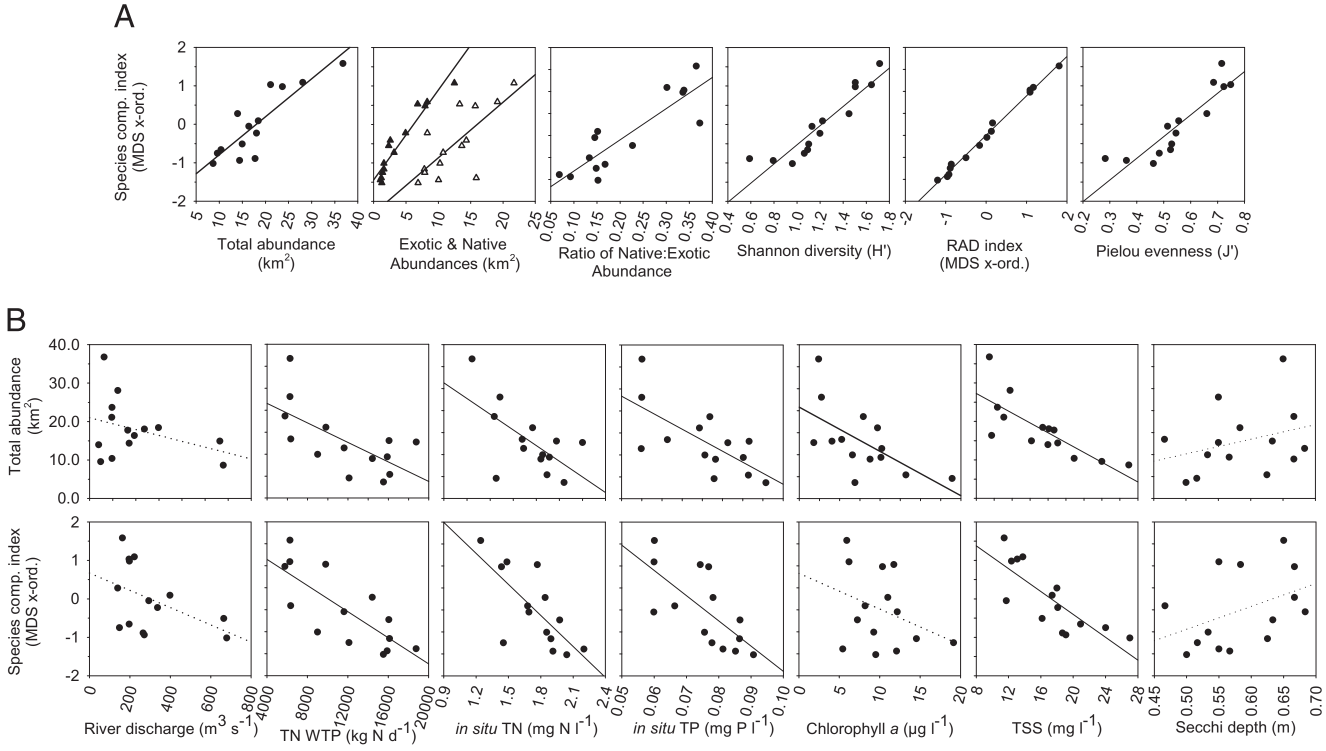

Fig. 3. Scatter plots of (*A*) species-composition similarity index (MDS *x*-ordinates) and total abundance, native and exotic abundance, the ratio of native to exotic abundance, Shannon diversity, RAD similarity index (MDS *x*-ordinates), and evenness and (*B*) total abundance and species-composition similarity index (MDS *x*-ordinates) vs. river discharge and water-quality factors, illustrating the interactions of the plotted variables (n = 14). Lines are only shown as a visual aid, with significant Spearman-rank correlations ($P \leq 0.05$) denoted by a solid line, whereas nonsignificant correlations are denoted with a dotted line. Native species are denoted by black triangles, and exotic species are denoted by open triangles.

nearly all areas shallower than 2-m depth in the Chesapeake Bay could be reached (27). The Tier I threshold of recovery to maximum historical extent is approximately met in the study area with SAV coverage of 37 km^2 in 2007.

Greater SAV cover would increase SAV ecosystem functionality and habitat availability and likely benefit invertebrates and waterfowl as well as important fisheries. If continued restoration to Tier III is successful, it could approximately double the 2007 SAV coverage in the study area (Fig. 1) and increase coverage severalfold bay-wide. Although nitrogen loading seems to have importance for SAV coverage, other factors such as river discharge and ecological interactions may also have important implications for SAV coverage in the future, which seemed to be the case with discharge in 1996 and 2003.

Materials and Methods

In addition to the methods described in the introduction, there are details on our analysis in *SI Materials and Methods*. This includes details on cover area quantification, water quality data, and multivariate statistical methods. Also included in the Supporting Information are results including a table of correlation results, scatter plots, and rank abundance distribution plots.

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