Mean conditions predict salt marsh plant community diversity and stability better than environmental variability

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Environmental variability and the frequency of extreme events are predicted to increase in future climate scenarios; however, the role of fluctuations in shaping community composition, diversity and stability is not well understood. Identifying current patterns of association between measures of community stability and climatic means and variability will help elucidate the ways in which altered variability and mean conditions may change communities in the future. Salt marshes provide essential ecosystem services and are increasingly threatened by sea-level rise, land-use change, eutrophication and predator loss, yet the effects of temporal environmental variation on salt marshes remain unknown. We synthesized long-term plant community monitoring data from 11 sites on both coasts of the United States. We used an information-theoretic approach and linear models to determine the associations among long-term mean conditions, interannual environmental variability, and plant community stability and diversity. We found that salt marsh community stability and diversity were more strongly related to long-term means of temperature and precipitation than to interannual variation. Warm and wet environments had fewer species and less turnover among years. Our results suggest that communities in cool, dry environments may be more resilient to climate warming due to greater species richness and turnover. Mean conditions are sufficient to predict contemporary patterns of salt marsh plant community dynamics, but environmental variability may have stronger impacts as it increases with climate change.

Studies of climate effects on communities frequently focus on mean conditions, but variability of the environment through time may have equally important effects on species' demographics, interactions and distributions (Gaines and Denny 1993, Vasseur et al. 2014, Bulleri et al. 2014). Climate change is predicted to increase variability of several environmental factors including temperature and precipitation (Easterling et al. 2000, Cayan et al. 2009, IPCC 2014) which have important effects on terrestrial primary production, diversity and stability. A better understanding of the effect of environmental variability on diversity and stability of ecological communities is critical for predicting their response to ongoing climate change.

Theory predicts that environmental variability can simultaneously affect diversity via two categories of processes (Adler and Drake 2008). Greater environmental variability is expected to enhance diversity when fluctuations increase potential for temporal niche partitioning, known as the "storage effect" (Chesson 1985, Warner and Chesson 1985, Tilman and Pacala 1993). When species have different requirements and tolerances, variation over time in conditions can reverse the order of competitive dominance among species, preventing competitive exclusion of those that would be lost in a constant environment (Warner and Chesson 1985, Chesson 2000). In contrast, increased environmental variation can lead to loss of species due to reduced geometric mean fitness and increased risk of stochastic extinction during periods of low population density, thereby decreasing diversity. The balance between these two effects of variation is the basis for the 'intermediate disturbance hypothesis' (Grime 1973, Connell 1978, Huston 2014) which predicts a peak in diversity at an intermediate level of environmental variation (Adler and Drake 2008, D'Odorico et al. 2008).

Empirical studies support predictions that the effect of environmental variation on community diversity depends on the intensity and frequency of variability (Menge and Sutherland 1976, Shurin et al. 2010). In classic studies of intertidal boulder communities, boulders that were disturbed at intermediate frequency had the highest diversity while frequently disturbed boulders and those that were rarely disturbed both had low diversity (Sousa 1979). Similarly, in tree communities, low and high temperature variability were generally associated with lower species richness (Letten et al. 2013), likely because high variability caused higher rates of extinction while low variability led to competitive exclusion (Sousa 1979). However, in some ecosystems, richness always increased with variability indicating that the pattern is not consistent (Letten et al. 2013). Thus, empirical support for a unimodal relationship between species diversity and the

level of variability is mixed (Mackey and Currie 2001, Shea et al. 2004).

By means of its effects on diversity, variability may also affect community stability. Long-term grassland experiments show that plots with greater species richness are more resistant and resilient to environmental change such as drought (Tilman and Downing 1994, Tilman 1996). Species-rich communities are also more stable over time, showing less year-to-year variation in species' and total abundances (Kuiters 2013). However, other studies show that community stability is maintained by particularly stable dominant species, suggesting that diversity does not always augment stability (Grman et al. 2010, Sasaki and Lauenroth 2011). Stability and diversity may or may not show the same relationships to environmental variability, but knowledge of both relationships is necessary to fully understand how the environment affects community function.

The effects of environmental variability on community stability are less well understood than those on diversity. One of few empirical studies on the topic found no consistent pattern of association between interannual variability in rainfall and the stability of grassland communities, although negative covariance among species was more prevalent in more variable environments (Hallett et al. 2014). Theory predicts that when species' abundances negatively covary, fluctuations in community composition will promote stability of total biomass in the face of environmental variation (Ives et al. 1999). When species respond similarly to environmental fluctuations, community composition is predicted to be stable as the environment changes, while community biomass will vary as all species increase or decrease in synchrony (Loreau and de Mazancourt 2008). However, there is little empirical evidence indicating how stability of community composition or biomass are related to environmental variation through time.

Differences in mean environmental conditions over space and time can also have important effects on community diversity and subsequently on stability. Increased precipitation is associated with increases in plant species richness in grasslands (Adler and Levine 2007, Cleland et al. 2013) and some salt marshes (Allison 1992), although the opposite relationship has been shown in others (Canepuccia et al. 2013). Increases in temperature led to a decrease in species richness in salt marshes (Gedan and Bertness 2009, Baldwin et al. 2014) and alpine plant communities (Klein et al. 2004), while in forests, mean temperature was not a good predictor of diversity (Letten et al. 2013). The associations between herbaceous plant community richness and temperature and precipitation means and variation therefore remain unclear.

The effects of environmental means and variability on diversity or stability have rarely been compared in plant communities (but see Cleland et al. 2013, Hallett et al. 2014), yet understanding these relationships is critical to predicting how changing environmental conditions will affect communities. If mean environmental conditions are the main drivers of community dynamics, managers can focus on future means, which are more commonly predicted than variability (de Elía et al. 2013). If means and variability both contribute, research efforts must be broadened from the effect of changing means. Thus, understanding these relationships will help management and research focus on the most impactful changes.

We conducted a continental-scale comparison of means and interannual variability of temperature and precipitation and their associations with plant community diversity and stability in salt marshes on both coasts of North America. Salt marshes are ideal for examining these relationships as they occur over broad geographic areas that encompass large ranges in both environmental means and variability. They provide critical ecosystem services including protection from floods and waves, which are likely to become increasingly important as climate change causes elevated sea levels and altered storm patterns. Finally, the relationship between environmental variability and diversity remains relatively unexplored in salt marshes, and the association between environment and salt marsh stability is even more poorly understood. This may be partly because salt marsh vegetation is less variable and diverse than other herbaceous plant communities, but understanding why salt marshes vary will provide insights into the main drivers of community dynamics in insensitive ecosystems. This is particularly useful given the importance of salt marshes as ecological study systems. Salt marshes experience environmental variability despite their constancy, and understanding how salt marsh diversity and stability covary with current variation in climate conditions will allow us to better anticipate how and to what extent they will change in future scenarios.

We synthesized long-term salt marsh plant community monitoring data from marshes along latitudinal gradients on both coasts of the United States. We asked several questions: 1) what is the association between environmental variability and plant species richness? 2) is environmental variability associated with negative covariance and high turnover or do species respond similarly to variability? 3) are species richness and stability more closely related to mean conditions than variability? This is particularly likely if variability is low or unpredictable (e.g. non-directional or stochastic as opposed to periodic) as these may be difficult conditions to which to adapt. 4) Are these relationships the same on the east and west coast of the US? A better understanding of these relationships will improve our predictions of how communities will respond to future changes in variability of temperature and precipitation (Easterling et al. 2000). Understanding these relationships will also clarify whether knowledge of mean conditions is sufficient to predict the richness and variability of communities or whether variability must be accounted for in order to make accurate predictions.

Methods

Data set

We identified eleven salt marsh sites in the United States in which plant species composition has been monitored by reserve managers and other scientists (Fig. 1b). While data were available from a relatively small number of sites, eleven is comparable to the number of sites used in other studies of environmental effects on plant communities (Cleland et al. 2013, Hallett et al. 2014). Sites consisted of NOAA National Estuarine Research Reserve System sites,



Figure 1. Geographic trends in means and interannual variability of (a, b) maximum temperatures, (c, d) minimum temperatures and (e, f) precipitation. Larger circles indicate larger means or variability. Sites are labeled with their abbreviations in (b). Full site names (clockwise from PIE) are Plum Island Estuary LTER (PIE), Narragansett Bay NERR (NAR), Virginia Coast Reserve LTER (VCR), Sapelo Island (SAP), Point aux Pins (PAP), Coastwide Reference Monitoring System (CRMS), Los Peñasquitos Lagoon (LPL), Carpinteria Salt Marsh Reserve (CAR), San Francisco Bay (SFB), South Slough NERR (SO), Padilla Bay NERR (PDB).

Long-Term Ecological Research sites (LTER; Brinson and Christian 2014, Deegan and Warren 2012), and several other marshes (Coastal Protection and Restoration Authority of Louisiana 2013). We chose sites that represent a broad latitudinal gradient along the two coasts. Plant composition differed among sites with more succulent forbs in southwest coast marshes and more graminoid species elsewhere, although both groups were widespread across sites. Thus differences in plant type may affect community dynamics but these marshes also show many similarities in functional group composition.

In nine sites, data were collected from replicated permanent plots over a minimum of five years, and in two additional sites (South Slough and Padilla Bay; Fig. 1b), plant community composition was measured in different plots each year. Species abundances were generally measured as percent cover in 1-m² plots, but data collection methods varied among sites (Supplementary material Appendix 1 Table A1). However, methods within each site were consistent over time. We excluded any plots that were subjected to experimental treatments.

Within most sites, plots spanned representative plant communities from the high to low marsh. Three sites did not have plots across the whole elevational range: Plum Island Estuary, the Coastwide Reference Monitoring System marshes in Louisiana, and Carpinteria Salt Marsh, although Carpinteria included plots in several different zones. Elevation data were not available, so we are not able to determine the effect of elevation on salt marsh communities, although it is likely to be important (Bertness and Hacker 1994, Janousek and Folger 2014). However, elevation is unlikely to drive the patterns we see here because both high and low marsh plant communities were represented in most sites without systematic bias in sites lacking that range of plant communities. In addition, tidal ranges and mean sea level differed among sites (Supplementary material Appendix 1 Table A2), but they were unassociated with variation in plant community dynamics (Supplementary material Appendix 1 Table A3).

Precipitation and air temperature data were obtained from the closest available weather station to each site using a combination of NOAA databases and local meteorological measurements, for example collected at LTER sites. We obtained daily maximum and minimum temperatures. Climate data were used from the same time period for which we had plant data. We chose not to use longer sets of climate data so that we could determine the response of communities to current climatic conditions rather than historic conditions. On average, weather stations were 16.7 km from the site from which vegetation data were collected with a maximum distance of 33 km at Los Peñasquitos Lagoon.

Data analysis

We calculated long-term means of temperature and precipitation as well as interannual variability. We calculated seasonal variability as well, but it was very strongly correlated with interannual variability so it was excluded from analysis. Long-term means for each site were calculated over the years in which plant communities were sampled. The annual mean of minimum temperature, for example, is the mean of all daily minimum temperatures during a year. Annual means were calculated based on the growing season (November of the previous year – October of the calendar year; Cleland et al. 2013). Peak biomass in most sites is in October, and most sites have summer growing seasons, although warmer sites have longer growing seasons (e.g. LPL in California, Fig. 1b) with growth beginning in December or January. Using the year based on the growing season allows us to calculate annual means over the same biologically-relevant time period for all sites.

Interannual variability (A_i) was calculated using a multiplicative time series variance decomposition approach (Chatfield 2004, Cloern and Jassby 2009, Shurin et al. 2010). This method of estimating variability is based on the ratio of the means of two different time scales and expresses variation as a percent deviation from the mean. For each month j in each year i, the annual components of variability (A_i) for each environmental variable, X, were calculated as

$$A_i = \overline{X}_i / \overline{X}_{L7}$$

where \overline{X}_i is the mean value for year *i*, and \overline{X}_{LT} is the long-term mean across all years. For each site, standard deviations of all A_i -values in the time series were calculated as a measure of variability (Cloern and Jassby 2009, Shurin et al. 2010). While extreme events are important forms of environmental variation, our measures of variation may not encompass every possible type of variability, so extreme events may play important roles that are not accounted for here.

To determine how community stability is affected by environmental variability, we calculated several metrics that address different aspects of stability. We calculated temporal turnover, the variance ratio, and stability of total plant cover at the site level. Temporal turnover measures the proportion of species that appear and disappear from one year to the next and is calculated as the ([the number of species lost] + [the number of species gained])/(the total combined number of species observed in the current and previous year) (Rusch and van der Maarel 1992, Cleland et al. 2013). The variance ratio was used as a measure of negative covariance. It compares the variance of plant cover at the community level (*C*) to the variance of cover of each population (P_i) (Schluter 1984, Houlahan et al. 2007, Hallett et al. 2014):

variance ratio =
$$\frac{\operatorname{var}(C)}{\sum_{i=1}^{n} \operatorname{var}(P_i)}$$

where

$$var(C) = \sum_{i=1}^{n} var(P_i) + 2\left[\sum_{i=1}^{n} \sum_{j=1}^{i=1} cov(P_i P_j)\right]$$

A variance ratio of less than one suggests that negative covariance is dominant in the community, while a value greater than one suggests that synchrony is most common.

Finally, we calculated another measure of community stability using aggregated species abundances (total percent cover of all species) to determine whether stability of total abundance differs across sites. For sites in which percent cover values were not relativized (allowed to sum to more or less than 100%), we aggregated cover of all species as a proxy for total plant abundance in each site and year and calculated the community stability (μ/σ where μ is overall mean abundance and σ is the standard deviation over all years; Lehman and Tilman 2000, Hallett et al. 2014). We did not include sites in which data were relativized (limited to 100%) as this was not a measure of total abundance.

We calculated species richness at the site level as a measure of community diversity. To account for different sampling efforts in different sites we used the 'specaccum' function from the vegan package in R to construct rarefaction curves based on the number of species found as a function of the number of plots sampled (Oksanen et al. 2015). Because plot areas differed among sites (Supplementary material Appendix 1 Table A1), we standardized rarefaction curves for each site by multiplying the number of plots sampled by plot area to obtain a plot of area sampled versus number of species found. We found the largest sampling area for which all sites had data (55 m²) and used the richness value on the rarefaction curve at that point as our rarefied species richness. One site, South Slough, had unusually high richness. It was classified as an outlier since it was above the third quartile by more than 1.5 times the interquartile range (Fig. 2c). We performed subsequent analyses both including and excluding this point.

We examined patterns of association between measures of community stability and diversity and temperature and precipitation variability on both coasts. We used an information-theoretic model-averaging approach to determine which environmental variables best explained stability and diversity, analyzing temperature and precipitation separately as there was insufficient power to combine them. We compared fixed effects linear models that included a coast by latitude interaction term as well as mean and interannual variability of either temperature or precipitation. The coast by environment interaction terms did not improve the fit of the models and so were excluded. Normality of residuals was assessed by visual inspection, and we found that transformation was unnecessary.

We determined the importance of each variable by considering models containing all possible combinations of predictors (Grueber et al. 2011). Models were ranked according to AICc values and models within four AIC



Figure 2. Long-term mean precipitation(a, d), interannual variability of precipitation (b, e), and coast (c, f) as predictors of species richness (a-c) and turnover (d-f). Black circles represent marshes on the east coast and gray triangles indicate the west coast. Insets are partial regression plots which indicate the relationship between the independent variable (e.g. mean precipitation) and the dependent variable (e.g. richness) holding all other variables constant. Thus these plots indicate the effect of each individual environmental variable alone on the dependent variable. A line in a partial regression plot indicates a variable that was in the model and has a high importance value, and those plots are based on the best model. A partial regression plot without a line indicates a variable which was not in the model, and plots are based on the full model. Asterisks indicate that the effect of coast was significant.

units of the best model (delta = 4) were used to determine importance of each variable in the top models. The importance of each variable was calculated as the sum of Akaike weights for all top models in which that variable was included (Bartoń 2015). We also used the top models to estimate parameter values for each variable. The predictive value of mean, interannual variability, coast and latitude were assessed based on their importance value and the probability of the parameter not being zero. Predictors with large importance values and parameter estimates that were likely not zero (p < 0.05 or p < 0.1) were deemed important. We corroborated model-averaging results using model selection (Supplementary material Appendix 1 Table A4). Model averaging approaches perform better than model selection when variables show collinearity (Freckleton 2011, Grueber et al. 2011), but our model-selection and model-averaging approaches produced largely consistent results.

We tested the influence of collinearity on our results using variance inflation factors and collinearity plots. Because of collinearity among means and variability in other variables, we only tested the effects of precipitation and minimum daily temperature as these were sufficiently uncorrelated (Supplementary material Appendix 1 Fig. A1–A2). However, trends were consistent among minimum and maximum temperatures, suggesting that the choice of temperature metric is not driving observed patterns. All analyses were done in R ver. 3.2.0 (<www.r-project.org>).

Results

Salt marshes on the east and west coasts of North America showed substantial environmental differences (Fig. 1). Gulf coast sites were included among the east coast sites as analyses of environmental latitudinal and coastal trends showed that the most parsimonious model combined the two. West coast sites received less precipitation on average than east coast sites ($F_{1,8} = 6.8$, p = 0.031) with northwestern sites receiving more precipitation than east coast sites at the same latitude, and southwestern sites being much drier than southeastern (Fig. 1e). Temperatures were higher in the south on both coasts (Fig. 1a, c; maximum: p < 0.001, $R^2 = 0.81$; minimum: p < 0.001, $R^2 = 0.82$). The west coast had greater variability in precipitation, and this difference was most pronounced at low latitudes (Fig. 1f; $R_{model}^2 = 0.93$, p < 0.001). The east coast is more variable in temperature, particularly in the northeast (Fig. 1b, d; minimum temperature coast imeslatitude: $R^2_{model} = 0.79$, p = 0.027).

The amount of variation from the mean differed between the two environmental variables. Temperature varied by a maximum of 17.6% from the long-term mean, but most sites showed less than 10% variation. Precipitation was more variable with mean variation of 25% and maximum variation of 52.4%. Mean precipitation was typically more important than interannual variability in precipitation for predicting plant community richness and stability. Turnover was generally reduced in areas with higher mean precipitation (Table 1, Fig. 2d). There was a weaker relationship between turnover and interannual precipitation variability with lower rates of turnover in areas of more variability. Communities with lower mean precipitation also had lower species richness when we exclude one outlying point, South Slough (SO; Table 1, Fig. 2a).

Mean temperature was associated with some community metrics while interannual variation in temperature was not (Table 1). Areas with lower mean temperatures tended to have more turnover among years (Fig. 3d). Temperature was not associated with species richness Table 1, Fig. 3a–b), stability based on aggregated species abundances (stability of total abundance) or covariance ratio.

There were substantial geographical differences in community richness and dynamics with coast and latitude both being important. The west coast showed significantly greater turnover than the east coast (Table 1, Fig. 2f) and turnover also differed latitudinally (Table 1, Fig. 4b). Plant diversity was higher on average on the west coast than the east coast (Fig. 2c). The very high rarified species richness we observed at SO likely resulted from spatial turnover within the site.

Table 1. Importance values from models within 4 units of best AIC_c value from information-theoretic modeling. Larger values indicate that a term is present in more models and therefore more important. There is no value when the term was absent in the most highly weighted models. *indicates term was in model with a stepwiseAIC model selection method. **indicates term was in model with model selection and significant (p < 0.05) in ANOVA. *+ indicates term was in model with model selection and marginal (p < 0.1) in ANOVA. Estimated parameters (Est param) are also estimates based on the top models. p-values indicate whether the parameter estimates are significantly different from zero. Values less than 0.05 are in bold, those less than 0.1 are in black, and those greater than 0.1 are in italics.

			Turnover	Covariance ratio	Richness	Richness (w/outlier removed)
Precipitation	Coast (C)	Importance	0.27	0.12	0.42*+	0.22**
		Est param	0.20	0.21	11.4	-5.9
		p	0.069	0.50	0.099	0.12
	Mean	Importance	0.33**	0.086	0.10	1.00**
		Est param	-0.080	-0.0038	1.22	-4.4
		р.	0.060	0.98	0.75	0.0058
	Interannual	Importance	0.13	0.086	0.11*	0.17*
		Est param	0.57	0.039	-14.7	-14.9
		p	0.086	0.97	0.64	0.16
	Latitude (L)	Importance	0.62**	0.093	0.15*	_
		Est param	0.018	0.0084	0.69	_
		р.	0.041	0.76	0.20	_
	$C \times L$	Importance	_	_	_*	_
		Est param	_	_	_	_
		p	_	-	_	_
Minimum temperature	Coast (C)	Importance	0.48**	0.122	0.33*+	0.28*
		Est param	0.20	0.21	10.1	5.1
		p	0.067	0.50	0.095	0.15
	Mean	Importance	0.30	0.085	0.11	0.088*
		Est param	-0.029	-0.00066	-1.0	-0.37
		р.	0.098	0.99	0.30	0.52
	Interannual	Importance	0.12	0.094	0.05	_*
		Est param	-0.19	-1.42	1.4	_
		p	0.93	0.72	0.99	_
	Latitude (L)	Importance	0.33*	0.092	0.16	0.10*
		Est param	0.017	0.0084	0.70	0.27
		р.	0.071	0.76	0.20	0.43
	$C \times L$	Importance	_	_	_	_*+
		Est param	_	-	_	_
		р	_	-	-	_



Figure 3. Long-term mean (a, c) and interannual (b, d) variability of minimum temperature as predictors of species richness (a, b) and turnover (c, d). Black circles represent marshes on the east coast and gray triangles indicate the west coast. Insets are partial regression plots. A line in a partial regression plot indicates a variable that was in the model, and those plots are based on the best model. A partial regression plot without a line indicates a variable which was not in the model, and plots are based on the full model.

Average species richness in individual plots at SO was relatively high (5.2 species per m² compared to a mean of 3.1 and a maximum of 5.8 across all sites) but was not the highest and therefore unlikely to be a result of measurement anomalies. Rather, this site had high mean precipitation and low variability as well as low minimum temperatures (Fig. 2a–b, 3a), suggesting that its somewhat anomalous species richness can be explained by its extreme environment compared to other sites in our survey.

Stability based on aggregated species abundances (stability of total abundance) and covariance ratio could not be explained by any environmental variable and showed little geographic trend (Fig. 4c–d, Supplementary material Appendix 1 Fig. A3). We cannot conclude whether negative covariance was more prevalent than synchrony as covariance ratios varied from less than one (negative covariance) to greater than one (synchrony), but many were so close to one that they do not distinctly suggest either mechanism (Supplementary material Appendix 1 Fig. A3).

Differences among sites in plot size had the potential to introduce error into our estimates of species richness as species richness is sensitive to area sampled. Plot sizes ranged from 0.25 m² to 4.6 m² (Table 1). However, across all sites, we found no correlation between plot size and species richness ($R^2 = 0.046$, p = 0.53) suggesting that plot size is unlikely to confound systematic trends in this analysis. Further, there was no significant interactive effect of any combination of plot size, coast or latitude on species richness confirming that there was no geographic relationship between plot size and species richness. Finally, there was also not a significant relationship between plot size and turnover or negative covariance (turnover: $R^2 = -0.12$, p = 0.80; covariance ratio: $R^2 = 0.054$, p = 0.25).

Discussion

Our analysis indicates that continental-scale patterns of plant species richness and community dynamics in salt marshes are more strongly correlated with long-term means of precipitation and temperature than interannual variation. Areas with higher mean minimum temperatures showed lower temporal turnover, while wetter sites had fewer species and lower turnover. Wetter climates and higher temperatures may lead to stronger competition and the dominance of a few species of consistently high abundance. These findings suggest that mean conditions are better predictors of community richness and stability than interannual variation in salt marshes.

Mean conditions showed a stronger relationship to species richness and turnover than did environmental variability. In grasslands and forests, interannual variability was an important predictor of stability and diversity, respectively (Letten et al. 2013, Hallett et al. 2014). In salt marshes, community stability may be less affected by interannual variability than in grasslands because salt marsh plants are largely perennials and may be better able to tolerate fluctuations from year to year compared to annual plants that often dominate grasslands. In addition, the predictability of interannual variation may determine the extent to which it affects communities. For instance, richness of zooplankton communities was related to interannual environmental variability only when there was a directional trend (e.g. acidifying lakes; Shurin et al. 2010). Finally, the degree of variability observed here may not have been sufficient to have strong effects on diversity or stability. Temperature typically varied by less than 10% from the mean. Precipitation variation showed a stronger relationship to community metrics, which may be because it demonstrates much more variation from the mean, varying by 20-50%. Thus, mean conditions may be more closely associated with community metrics than interannual variability unless species can easily respond to fluctuations, variability is predictable, or the magnitude of variability is large.

Contrary to our initial predictions, species richness and community stability were associated with variability in



Figure 4. Geographic trends in species richness and stability. Larger circles indicate larger values with larger covariance ratio values signaling less negative covariance.

precipitation but not temperature variability. Higher variability in precipitation among years was generally associated with decreased species richness (Fig. 2b), suggesting that little temporal niche partitioning occurred (Warner and Chesson 1985). This may be because salt marsh species are mainly perennials so abundance is unlikely to change dramatically among years unlike in grasslands with many rare, annual species (Cleland et al. 2013). Richness is likely to be lower in areas with high variability because the risk of extinction is generally higher (Sousa 1979, Shurin et al. 2010). High interannual precipitation variability was also associated with decreased species turnover (Fig. 2e), possibly because the few species that are able to tolerate variable environments thrive in environments with few competitors (Pennings and Callaway 1992, Bertness and Hacker 1994). Precipitation variability may be more important than temperature variability because precipitation is more variable than temperature and therefore more likely to affect plants and community dynamics.

Species richness and turnover both showed negative relationships to mean precipitation, consistent with results from other salt marsh studies. An observational study in Argentinean marshes found that diversity decreased as precipitation increased, similar to our results (Canepuccia et al. 2013). This may be because the effect of positive interactions outweighs that of negative interactions in high salinity, low precipitation environments, leading to weaker competition and subsequently greater diversity where there is little precipitation (Bertness and Callaway 1994, Canepuccia et al. 2013). In contrast, increases in mean annual precipitation are typically related to an increase in species richness in grasslands (Cleland et al. 2013, Hallett et al. 2014). Competition for water may be more prevalent in grasslands, whereas salt marshes are frequently inundated by tides and therefore require less precipitation to have enough water to grow. Precipitation in salt marshes is still somewhat important as a source of water but also as a moderator of soil salinity levels, and decreases in precipitation cause increases in soil salinity that may be more likely to lead to weaker competition and even facilitation (Pennings and Callaway 1992).

Species turnover decreased with increases in minimum temperature on both coasts but was unaffected by variability in temperature. We also observed greater richness in marshes with colder long-term means of minimum temperatures on the east coast of North America, unlike most ecosystems in which richness increases at low latitudes (Wallace 1878, Schall and Pianka 1978, Hillebrand 2004, but see Canepuccia et al. 2013, Marshall and Baltzer 2015). Turnover was lower at higher mean temperatures, potentially because greater richness results in more potential species that can arrive or leave a site in any year. This mechanism is consistent with grasslands, where turnover was driven mainly by the appearance and disappearance of rare species (Cleland et al. 2013). Because warm sites in our study were dominated by a few taxa, there were fewer rare species to contribute to turnover.

Interestingly, while studies that manipulate species richness have found that communities with greater species richness tend to be stable due to mechanisms such as negative covariance (Isbell et al. 2009, Gross et al. 2014), we found no significant relationship between the degree of covariance and richness. A study in grasslands found that greater interannual variability in precipitation was correlated with greater negative covariance but not with higher richness (Hallett et al. 2014). In our case, the degree of covariance was independent of both environmental conditions and species richness. The occurrence of negative covariance or synchrony in salt marshes may be related to other environmental conditions or historical factors. Alternatively, dominant species in salt marshes may be better adapted to variable conditions so that community stability is driven by the dynamics of these stable dominant species more than the interrelated dynamics of multiple species (Grman et al. 2010, Sasaki and Lauenroth 2011).

Similarly, we found no association between aggregate stability of total plant cover and temperature, precipitation or other measures of stability (Fig. 4). In grasslands, there was no geographic trend in aggregate stability, but negative covariance was more prevalent where aggregate stability was greater (Hallett et al. 2014). It is possible that total cover is a poor indicator of total abundance or biomass. Alternatively, another mechanism may maintain aggregate stability in salt marsh sites where asynchrony and the portfolio effect do not.

Finally, while environmental variables were related to differences among sites, there were also geographical differences, including higher species richness and turnover on the west coast (Fig. 1), that may be affected by biotic factors. For instance, succulents, which are well adapted to drought and salinity, were most common in the southwest. Species or populations that are well adapted to stressful rainfall conditions may not be as strongly affected by variable precipitation patterns and may display different patterns of diversity, stability and species interactions (Pennings et al. 2003, Noto and Shurin 2016). We may even expect to see nonlinear relationships between rainfall and community dynamics as the dominant plant type shifts among sites. Variable species composition may lead to more complex relationships to environmental conditions, but comparable data from more sites are needed to identify such transitions.

The latitudinal trends in richness and turnover that we observed may also be related to geographic variation in the intensity of herbivory driven by environmental gradients. In salt marshes on both coasts of the Atlantic, plants have been shown to experience stronger herbivory at low latitudes (Pennings and Silliman 2005, Pennings et al. 2007). The effects of precipitation and herbivory are difficult to disentangle as they can interact, with precipitation affecting plant communities differently in the presence of grazers (Miller et al. 2005). We found declines in plant diversity at low latitudes where herbivores typically exert the strongest effects over plant communities. Many studies have found positive impacts of grazing on plant community diversity when competitively dominant species experience the greatest losses to herbivores (Daleo et al. 2014, Borer et al. 2014). However, grazing can also have negative effects on plant species richness (Hillebrand et al. 2007). Thus, biotic factors may also contribute to community-level differences among geographic regions, but further work will be necessary to determine how they affect large-scale patterns in community dynamics.

These results advance our knowledge of determinants of salt marsh community diversity and stability in important ways. They suggest that precipitation may be an important driver of community dynamics. This has been shown in some salt marshes (Allison 1992, Callaway and Sabraw 1994, Charles and Dukes 2009, Canepuccia et al. 2013), but its importance in driving large-scale geographical patterns in salt marshes is somewhat surprising as salt marshes are often thought to be relatively unaffected by precipitation due to frequent tidal inundation. Other environmental conditions not included here such as tidal elevation, salinity, and soil nutrients may also be important (García et al. 1993, Deegan et al. 2012, Canepuccia et al. 2013, Janousek and Folger 2014), and more widespread collection of those

data would assist in further efforts to understand their role in driving large-scale patterns. This work also highlights the need for continued and expanded long-term monitoring of salt marsh vegetation following consistent methods. Very few studies have previously attempted to understand stability in salt marshes, and more data from more geographical locations are necessary to better understand the causes of geographical differences in salt marsh stability. As climate change becomes a more eminent threat, it will be necessary to understand how those changes will affect these critical and endangered ecosystems.

Our study provides evidence that long-term means of temperature and precipitation are closely related to community diversity and stability. These results suggest that despite predicted changes in the degree of environmental variability, changes in community dynamics are most likely to be related to changing mean conditions. Thus, as rainfall patterns change (IPCC 2014), communities may become less diverse with lower turnover in places where precipitation increases while becoming more diverse with more turnover where precipitation decreases. Environmental variability is also predicted to increase, and if it increases sufficiently to depart from current bounds, it may become an additional driver of community dynamics whose influence will be difficult to predict if conditions are unlike any encountered in present-day salt marshes. Nevertheless, under current conditions, communities with low temperatures and rainfall may be the most resilient to future changes due to naturally high species turnover and richness.

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Supplementary material (available online as Appendix oik-04056 at <www.oikosjournal.org/appendix/oik-04056>). Appendix 1.

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