Estuaries and Coasts (2022) 45:260–271
https://doi.org/10.1007/s12237-021-00953-y

Variation in Densities of the Salt Marsh Katydid *Orchelimum fidicinium* over Space and Time

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Received: 23 September 2020 / Revised: 11 May 2021 / Accepted: 13 May 2021 / Published online: 20 May 2021

Abstract

Densities of Orthoptera typically vary greatly over space and time. The most important salt marsh orthopteran on the East Coast of the US is *Orchelimum fidicinium*, an omnivore that feeds on cordgrass (*Spartina alterniflora*) and arthropods. We examined spatial (34 sites) and temporal (5 sites, 17 years) variation in *O. fidicinium* density in coastal Georgia. Sites with considerable adjacent upland habitat had higher densities of *O. fidicinium* than sites with little adjacent upland. Grasshoppers fed *S. alterniflora* from both types of sites did not differ in growth rates, ruling out food quality as an explanation. We speculate instead that *O. fidicinium* require terrestrial habitat for reproduction or escape from predators during extreme high tides. At five sites where *O. fidicinium* was common, densities varied greatly among years. Regression models indicated that current year plant biomass (three sites) or previous year plant biomass (one site) was the best predictor of *O. fidicinium* density. Relationships between *O. fidicinium* and current year plant biomass were typically negative (more grasshoppers in years with lower plant biomass). A possible explanation for this pattern is that plant nutrients may be diluted in years with high plant biomass. We found little evidence that density of animal prey (*Prokelisia* spp.) or abiotic factors affected *O. fidicinium* densities. Our study illustrates the value of examining population densities across multiple sites and years, because results from any one site or year would likely have mischaracterized the spatial and temporal distribution of this common salt marsh consumer.

Keywords Orchelimum, · Population dynamics, · Prokelisia, · Salt marsh, · Spartina, · Orthoptera

Introduction

All species vary in abundance over space and time. A major goal of ecology, and the primary goal of population ecology, is to gain a predictive understanding of this variation (Taylor 1984). This challenge is particularly acute for small species with high reproductive rates such as insects that at times can increase in density explosively and at other times crash to low levels (Wallner 1987). Population dynamics of Orthoptera are of particular interest because they can compete with livestock for plants in rangelands (Le Gall et al. 2019), many are occasional food items for humans (Francuski and Beukeboom 2020), and others are important pests of crops (Van Der Werf et al. 2005). In particular, periodic outbreaks of locusts in the genus *Schistocerca* have caused considerable harm to agriculture and human livelihood (Latchininsky 2013).

Despite considerable interest, we have a very limited understanding of factors that drive orthopteran abundance and richness. For example, in arid regions, high precipitation supports higher grasshopper abundance due to greener pastures (Hunter et al. 2001; Hao et al. 2015). In wetter areas, however, increased precipitation can decrease orthopteran richness by promoting plants that are not preferred foods of grasshoppers (Steck and Pautasso 2008). Warm temperatures can have opposite but important effects on grasshopper survival and fecundity (Laws and Belovsky 2010). Fire can favor grass-feeding grasshoppers in the short term but depress their abundance over the long term (Evans 1984). Biotic factors also affect orthopterans. For example, grazing by livestock can increase grasshopper abundance and richness by increasing plant heterogeneity and favoring species preferred by grasshoppers (Joern 2005; Hao et al. 2015; Zhu et al. 2020). Intense grazing and mowing can sometimes suppress grasshopper species through trampling of grasshopper eggs and displacing nymphs (Miller and Gardiner 2018). And there is also some evidence that predators can suppress grasshopper populations (Schmitz 2008). Similarly, there is a rich literature on spatial

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Communicated by Mark S. Peterson

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variation in orthopteran abundance, with different studies identifying precipitation (Rosetti and Remis 2018), dispersal limitation (Rominger et al. 2009), fire (Joern 2005), and micronutrients (Joern et al. 2012) as important controlling factors.

In contrast to the rich literature on orthopterans in terrestrial habitats, relatively little is known about orthopterans in salt marsh habitats, probably because salt marshes are not widely used for agriculture or as rangelands (Kennish 2001). In salt marshes along the Atlantic Coast of the US, the dominant orthopterans are tettigoniids in the genera *Conocephalus,* which is most common at higher latitudes, and *Orchelimum*, which is most common at lower latitudes (Wason and Pennings 2008). Species in both genera are omnivorous, feeding on salt marsh grasses, flowers and seed heads, and other arthropods such as abundant plant-hoppers in the genus *Prokelisia* (Bertness et al. 1987; Jiménez et al. 2012). In the extensive salt marshes of the south Atlantic Bight, which are dominated by monospecific stands of the grass *Spartina alterniflora*, the dominant salt marsh orthopteran is *Orchelimum fidicinium* (Smalley 1960). *Orchelimum fidicinium* serves as prey to an assortment of marsh bird and invertebrate species, and feeds on the dominant salt marsh grass *S. alterniflora* (Pfeiffer and Wiegert 1981). A handful of papers have examined the feeding preferences (Goranson et al. 2004), growth (Jiménez et al. 2012) and ecosystem role (Smalley 1960; Marples 1966) of this species, but none have explored variation in density among sites or over time.

The coastal salt marsh ecosystem along the US eastern seashore is typically divided into three habitat types (high-marsh, mid-marsh, and low-marsh). Each of these habitat types has its suite of dominant plant and invertebrate species and sometimes these invertebrates will move among locations based on their life history. Orthopteran species richness in the salt marsh is relatively low compare to rangelands, with one or two dominant species in each habitat type (Wason and Pennings 2008). The factors that control population abundances of orthopterans in salt marshes may be somewhat different than the factors that are important in terrestrial habitats. For example, in Florida, orthopteran species richness in salt marshes is comparatively low with around 11 species compared to over 30 species in typical rangelands (Squitier and Capinera 2002). Therefore, there may be less interspecific competition between orthopteran species in salt marshes than in terrestrial habitats. Instead, salt marshes are intertidal so both invertebrates and plants may be affected by tides and salinity. Heavy precipitation usually results in high river discharge, which lowers salinity in the marsh and promotes plant growth (Li and Pennings 2017). Because *O. fidicinium* is an important consumer of plants and arthropods, and they serve as an important food source for other salt marsh faunas, a better understanding of the temporal and spatial variation in their abundance may help us better understanding variation in marsh function.

We examined spatial and temporal variation in the density of the dominant salt marsh katydid *O. fidicinium* in Georgia, USA, salt marshes. We compared densities across sites to test the hypothesis that density would vary depending on the proximity of terrestrial habitat adjacent to the marsh. We compared densities among years to test the hypotheses that abiotic factors (precipitation, temperature, sea level, and river discharge) or dietary factors (plant biomass, flower abundance, and *Prokelisia* spp. density) might explain annual variation in *O. fidicinium* density. Due to the powerful gradients in abiotic factors such as sea level and river discharge that structure estuarine communities, we expected abiotic factors to influence salt marsh orthopterans as much as biotic factors.

Methods

We sampled salt marsh orthopterans at seven of the permanent sampling sites of the Georgia Coastal Ecosystems Long-Term Ecological Research program (GCE-LTER) that are dominated by the grass *Spartina alterniflora* (Bortolus et al. 2019) (Fig. 1). The marshes at each site consisted of a relatively extensive "platform" over which surface elevation varied little. If the marsh bordered terrestrial habitats, the platform sloped upward rapidly to the terrestrial border; this "high marsh" was typically dominated by the rush *Juncus roemerianus* or the shrub *Borrichia frutescens.* At the water's edge, the platform sloped down abruptly to a creek.

We sampled orthopterans in late July or early August every year from 2003 to 2019. Even though *O. fidicinium* densities are higher earlier in the season (Smalley 1960), we sampled later in the year when almost all individuals encountered were reproductive adults and easily observed. At each site, we walked eight transects that were 2 m wide and 10 m long in the marsh platform, avoiding high marsh and creek habitats. We used a 120-cm-long PVC pipe to beat the vegetation along each transect in a 2 m wide swath while walking at a moderate pace. This disturbance caused the orthopterans to jump or fly, making them easier to count. Presumably some grasshoppers remained stationary and were not observed; therefore, these counts are under-estimates of the true number present. Our interest, however, is in trends of population density rather than the exact density, and we believe that this method was reasonable for estimating how relative density of orthopterans varied among sites and years.

Orchelimum fidicinium is an omnivore that eats both *S. alterniflora* (leaves, flowers and seeds) and small arthropods (Jiménez et al. 2012). To estimate the density of potential arthropod food sources for *O. fidicinium*, we measured the density of common marsh planthoppers, at the same time as we counted orthopterans, and we estimated end of season biomass and flower abundance of *S. alterniflora* in October of each year. The sampling for both *O. fidicinium* and

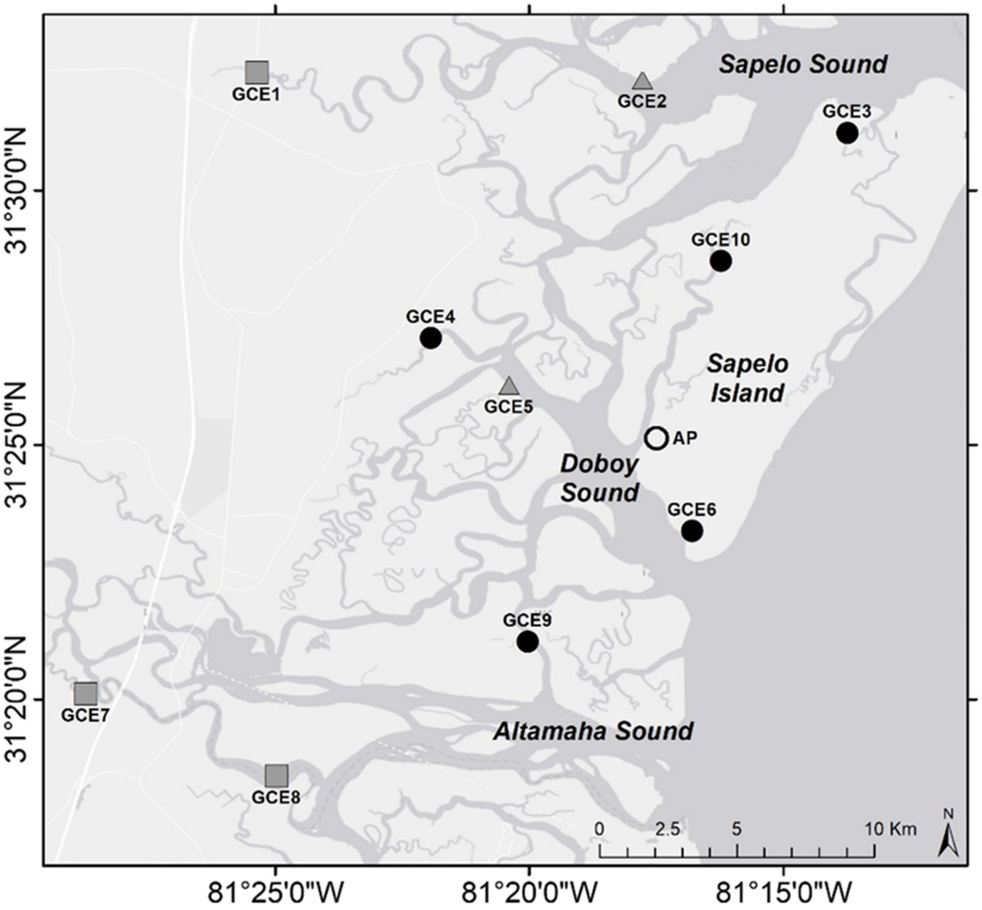


Fig. 1 GCE study sites. *Orchelimum fidicinium* were counted in salt marsh sites (2, 3, 4, 5, 6, 9, and 10) and were abundant only at sites 3, 4, 6, 9, and 10 (represented by solid circles). Sites represented by squares (1, 7, and 8) were not included in the analysis because the dominant vegetation is not *Spartina alterniflora*. Sites represented by triangles (2 and 5) were not included in the analysis due to very low *Orchelimum fidicinium* densities. In addition, site 3, 4, 6, 9, 10 had high upland influence, while site 2 and 5 had low upland influence

planthoppers was done by the same person (SCP) each year to minimize observer bias.

There are two common species of *Prokelisia* (*P. marginata* and *P. dolus*) that feed on *S. alterniflora* and can reach high densities (thousands per square meter) in Atlantic coast salt marshes (Denno 1977). We scored the density of *Prokelisia* spp. at each site on a five-point scale, from absent (0) to extremely abundant (4), at the same time as we counted orthopterans.

We measured the number of *S. alterniflora* shoots, and the height (cm) and flowering status (flowering or not) of each shoot, in eight permanent plots on the marsh platform at each site in October of each year from 2002 to 2019. These data were converted to dry biomass (g/m^2) using a site and zone-specific allometric equation based on shoot height and flowering status generated from a harvest of ~30 measured stems adjacent to the plots (Wieski and Pennings 2013; Li and Pennings 2017).

To determine if orthopteran density was influenced by abiotic factors, we compiled data on precipitation (mm), mean annual temperature (°C), mean sea level (m) and daily discharge (m^3/s) to the coast of the Altamaha River from 2002-2019. Sea level data were downloaded from the National Oceanographic and Atmospheric Administration with daily readings from a single station (8670870 Fort Pulaski, Georgia, http://www.noaa.gov/). The other abiotic data were downloaded from the GCE-LTER data portal (http://gce-lter.marsci.uga.edu/portal/monitoring.htm). Daily temperature and precipitation measurements were collected from a weather station on Sapelo Island, and daily river discharge data were collected from the USGS gaging station on the Altamaha River at Doctortown. Abiotic data, data on orthopteran and *Prokelisia* density, and data on *S. alterniflora* abundance are all publicly available (Appendix Table 1).

Our observations suggested that *O. fidicinium* density was greater at sites close to upland habitat than at sites without adjacent upland. To test this, we grouped the GCE sites into two categories, those with high upland influence (3, 4, 6, 9, and 10) and those with low upland influence (2 and 5) and tested the difference between these categories using a Mann-Whitney Rank Sum Test in Sigmaplot V.14 (Systat Software, Inc.). To determine whether the observed pattern held with a larger number of sites, we sampled orthopterans at 34 sites within the GCE domain in June 2003. We used the same sampling methodology as with the GCE sites, but with only 4 transects per site. We categorized each site as having high (*n*=21) or low (*n*=13) upland influence and compared the groups with a Mann-Whitney Rank Sum Test using Sigmaplot V.14 (Systat Software, Inc.).

Finally, to test the hypothesis that different numbers of *O. fidicinium* at sites with high versus low upland influence was caused by differences in plant quality among these sites, we conducted a greenhouse growth experiment in June 2010. Individual *O. fidicinium* were housed in 946 ml glass containers with a mesh top and fed *S. alterniflora* from sites with either high (n=3 sites) or low (n=2 sites) upland influence. Plants were replaced every 7 days. We weighed *O. fidicinium* to the nearest 0.00001 g at the start of the experiment and after 21 days and calculated the relative growth rate of each individual using the formula $\log_{10}$(final weight – initial weight)/21 days. Since the data from site 10 and the airport did not meet normality assumption of one-way ANOVA (Shapiro-Wilk normality test: site 10: P = 0.03; airport: P =0.02), we compared site means using Kruskal-Wallis one-way ANOVA on ranks using Sigmaplot V.14 (Systat Software, Inc.)

The density of *Orchelimum fidicinium* varied among the long-term sampling sites. We focused on five sites where *O. fidicinium* was common (3, 4, 6, 9, and 10) for analyses of variation over time (Appendix Table 2). We standardized the dataset into Z scores in order to better compare between variables of different unit and distribution. To determine whether the five GCE sites should be analyzed separately, we conducted cross-correlations with the package "synchrony" 0.3.8 version in R 3.6.1 (Gouhier and Guichard 2014; R core team 2019). After transforming data to Z scores, we cross-correlated *O. fidicinium* density, current plant biomass, and flower abundance between the GCE sites. Because the sites were not highly correlated with each other (Table 1), we first analyzed each site separately. To determine which factors predicted *O. fidicinium* density, we regressed density versus potential predictors using best subset regression procedure in the R package leaps (Lumley 2015). This procedure tests all possible models using a given set of predictors and identifies the best linear regression models. We included potential food sources (plant biomass, flower abundance, and *Prokelisia* density rank) and abiotic factors that might affect either plants or grasshoppers (precipitation, river discharge, sea level, and temperature). Because *O. fidicinium* overwinters as eggs, we also examined all these predictor variables from the previous year, reasoning that they might have affected egg production. Fourteen models were generated by the best subset regression, but none of them were satisfactory. Many of the variables were correlated with each other (e.g., precipitation increases river discharge), and most models were over-fitted. Since we had 14 variables and only 17 data points (years), we decided to reduce the dimensionality of the dataset with principal component analysis (PCA) using Primer 6 (Primer-E Ltd V.6; United Kingdom).

During the PCA analysis, plant and abiotic variables were analyzed separately, and current year and previous year data were also analyzed separately, resulting in a total of 4 analyses (Table 2). Then we conducted a best subset regression analysis using only the first two principal components (PCs) scores from each PCA analysis. We did not conduct a principal component analyses on the *Prokelisia* dataset because there was only a single variable for this dataset, therefore, we used Z-score transformed *Prokelisia* density from current and previous year in all analyses. We examined all possible regression models for each site with best subset regression (R package leaps) using the eight PC variables (first two PCs from each of the 4 analyses) and two *Prokelisia* variables as predictors and identified the best linear regression model for each site based on the lowest Mallow's CP value and highest R^2 value.

Based on the result of the best subset regression using PC axes, we conducted a multiple linear regression model for each site to determine the relationship between specific predictors and *O. fidicinium* density at each site. For example, if

Table 1 Cross-correlation table of *Orchelimum fidicinium* density, *Spartina alterniflora* biomass and flower abundance at five GCE sites. Numbers are r values with P values in parentheses. Correlations with r>0.5 and P<0.05 are bolded

		GCE-3	GCE-4	GCE-6	GCE-9
O. fidicinium density (count/20m^2)	GCE-4	0.39 (0.11)			
	GCE-6	0.27 (0.29)	0.42 (0.1)		
	GCE-9	0.47 (0.06)	0.25 (0.34)	0.2 (0.44)	
	GCE-10	**0.65 (0.01)**	**0.53 (0.03)**	0.43 (0.08)	0.45 (0.07)
S. alterniflora biomass (g/m^2)	GCE-4	0.39 (0.13)			
	GCE-6	0.27 (0.29)	0.42 (0.1)		
	GCE-9	0.47 (0.06)	0.25 (0.33)	0.2 (0.45)	
	GCE-10	**0.65 (0.007)**	**0.53 (0.03)**	0.43 (0.08)	0.45 (0.08)
S. alterniflora flower abundance (count/m^2)	GCE-4	0.39 (0.13)			
	GCE-6	0.27 (0.27)	0.42 (0.09)		
	GCE-9	0.47 (0.06)	0.25 (0.33)	0.2 (0.44)	
	GCE-10	**0.65 (0.01)**	**0.53 (0.03)**	0.42 (0.09)	0.45 (0.07)

Table 2 Principal Component analyses. A) Eigenvector scores of variables related to *Orchelimum fidicinium* food abundance at five GCE sites. Current year and previous year data were analyzed separately. Cumulative percent variation explained by the PCA axes is denoted by the percentage in parenthesis. B) Eigenvector scores of abiotic variables affecting the GCE study area. Current year and previous year data were analyzed separately. Sites were not analyzed separately because we had only a single measurement of each abiotic variable for the entire GCE domain. The percent variation explained by each PCA axis is denoted by the percentage in parenthesis. In both cases, results for previous year (2002–2018) differ slightly from those for the current year (2003-2019) because they consider different time ranges

A) Plant variables	Current year		Previous year	
GCE-3	PC1 (60%)	PC2 (40%)	PC1 (61%)	PC2 (39%)
Plant biomass (g/m^2)	0.71	0. 71	0.71	0.71
Flower abundance (count/m^2)	0.71	−0. 71	0.71	−0.71
GCE-4	PC1 (75%)	PC2 (25%)	PC1 (75%)	PC2 (25%)
Plant biomass (g/m^2)	0.71	0. 71	0.71	0.71
Flower abundance (count/m^2)	0. 71	−0. 71	0.71	−0.71
GCE-6	PC1 (88%)	PC2 (12%)	PC1 (85%)	PC2 (15%)
Plant biomass (g/m^2)	0. 71	0. 71	0.71	−0.71
Flower abundance (count/m^2)	0. 71	−0. 71	0.71	0.71
GCE-9	PC1 (72%)	PC2 (28%)	PC1 (81%)	PC2 (19%)
Plant biomass (g/m^2)	0. 71	−0. 71	0.71	0.71
Flower abundance (count/m^2)	0. 71	0.71	0.71	−0.71
GCE-10	PC1 (74%)	PC2 (26%)	PC1 (77%)	PC2 (23%)
Plant biomass (g/m^2)	0. 71	0. 71	0.71	−0.71
Flower abundance (count/m^2)	0. 71	−0. 71	0.71	0.71
B) Abiotic variables	Current year		Previous year	
	PC1 (53%)	PC2 (20%)	PC1 (56%)	PC2 (16%)
River discharge (m^3/s)	0.55	−0.18	−0.48	0.81
Air Temperature (°C)	−0.5	0.45	0.51	−0.06
Precipitation (mm)	0.54	−0.04	−0.51	−0.38
Tide height (m)	0.39	0.88	−0.5	−0.45

the best linear regression model generated by the best subset regression for site 3 was current year plant PC1, then we would have conducted a multiple linear regression using *O. fidicinium* density as the dependent variable with plant biomass and flower abundance as the independent variables.

The site by site analyses suggested that the predictor variables had different relationships with *O. fidicinium* density at different sites. To determine whether data from all the sites could instead be represented with a single model, we used a stepwise procedure to select the single best ANCOVA model for the entire dataset. Specifically, we first conducted the analysis using sites as factors, *O. fidicinium* density as the dependent variable and a single predictor out of the following covariates: four plant PC scores, four abiotic PC scores and both current and previous year *Prokelisia* densities. We kept the predictor in the model if the interaction between site and the predictor had $P < 0.1$ (e.g., if the slopes were not homogeneous). Then we added an additional predictor into the model, conducted the analysis again, and retained the predictors only if interaction between site and the predictors achieved $P < 0.1$. We repeated this process until all predictor combinations were analyzed to result in a final ANCOVA model. Assumptions of normality and equal variance were all met. We were only interested in the interaction and not the main effect because the goal of this analysis was to determine whether predictor variables had different relationships with *O. fidicinium* density at different sites.

There is widespread recent interest in the possibility that insect populations are declining over time (Hallmann et al. 2017; Welti et al. 2020). To address this with our data, we conducted linear regression models for each site using *O. fidicinium* density as the dependent variable and year as the independent variable to examine whether *O. fidicinium* density declined over time.

Results

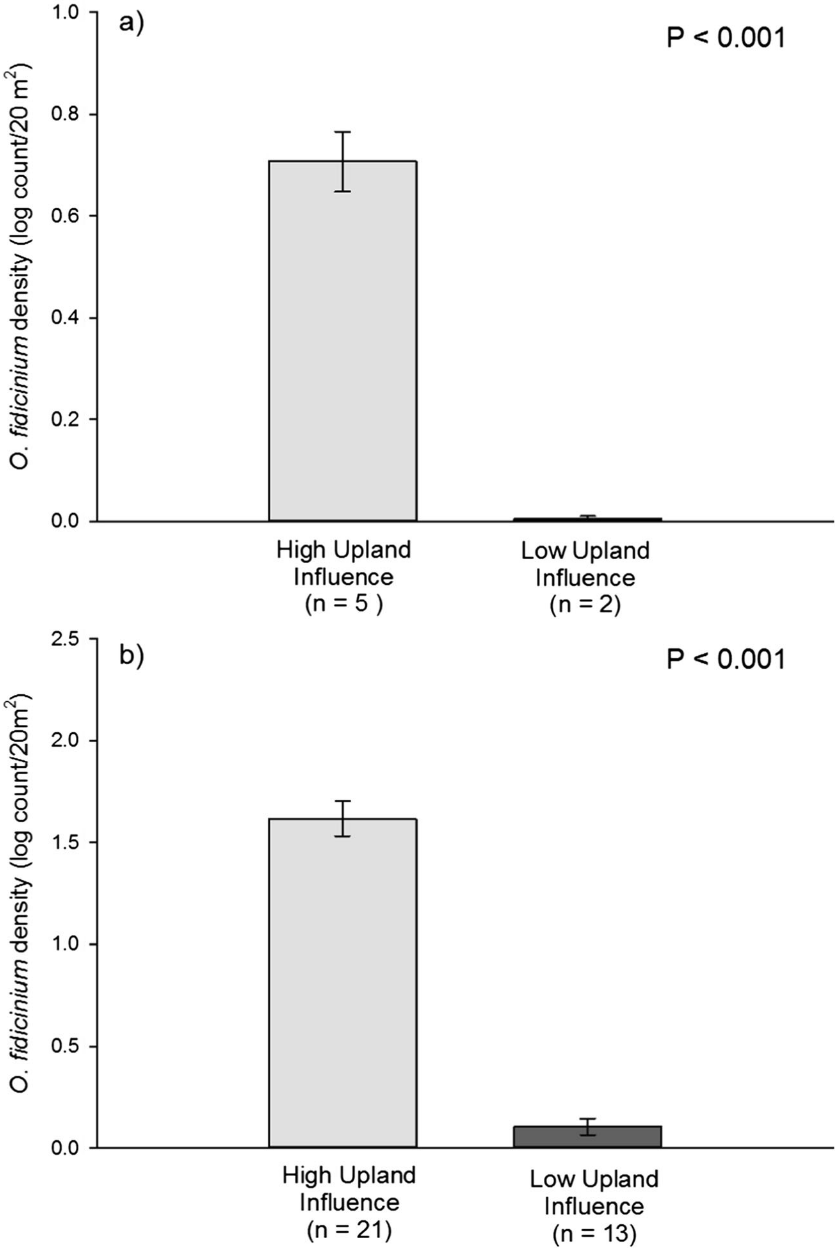
The number of orthopterans observed per transect ranged from 0 to 58. Most (96.7%) of the orthopterans counted were the seaside meadow katydid, *O. fidicinium*, and we limited our analyses to this species because it is the only resident orthopteran in Georgia salt marshes that are dominated by *S. alterniflora*. Other species that we observed (*Paroxya clavuliger*, *Mermiria intertexta*, *Orphulella pelidna, Schistocerca obscura* and *Romalea guttatus*) are transients that are resident in terrestrial or high marsh habitats rather than resident on the marsh platform.

Orchelimum fidicinium densities were much higher in five of the long-term GCE sampling sites with high upland influence than at two sites with low upland influence, where *O. fidicinium* numbers were almost zero (Fig. 2A). Similarly, the 34 sites sampled in 2003 also showed much higher *O. fidicinium* density at sites with high (n=21) versus low (n=13) upland influence (Fig. 2B). Again, densities at the sites with low upland influence were almost zero. The greenhouse growth experiment showed that orthopterans did not differ in relative growth rate when fed plants from sites with high or low upland influence ($H_3 = 3.78$, $P = 0.44$, Fig. S1), indicating that the spatial distribution pattern of *O. fidicinium* was probably not due to variation in plant quality.

The density of *O. fidicinium* fluctuated dramatically (up to 100-fold) among years at the five study sites where *O. fidicinium* was most common (Fig. 3). Site 9 had the greatest fluctuations in *O. fidicinium* density and the highest density, with a maximum of 35 individuals /20m^2 in 2011. Fluctuations in *O. fidicinium* density over time showed some similarities across sites. For example, densities peaked compared to long term averages in 2011 at four of the five sites. Overall, however, cross-correlation procedure indicates that densities at the sites were not highly correlated (Table 1), so variation over time at each site was analyzed separately.

The first PC axis for the plant variables explained 60-88% of the variation, depending on site, with the second PC axis explaining the remaining variation (Table 2). The first PC axis for the abiotic variables explained 53% (current year) to 56% (previous year) of the variation, with the second PC axis explaining an additional 17–21% (Table 2). All the abiotic variables loaded strongly onto PC1, whereas the

Fig. 2 a) Mean *Orchelimum fidicinium* density ($\log_{10}$ count/20m^2) across five GCE sites with high upland influence versus two GCE sites with low upland influence. Error bars represent one standard error; data are averages for each site for 2003-2019; b) mean *Orchelimum fidicinium* density across 21 sites with high upland influence versus 13 sites with low upland influence; data are from one sampling period at each site in 2003; in each case error bars represent one standard error



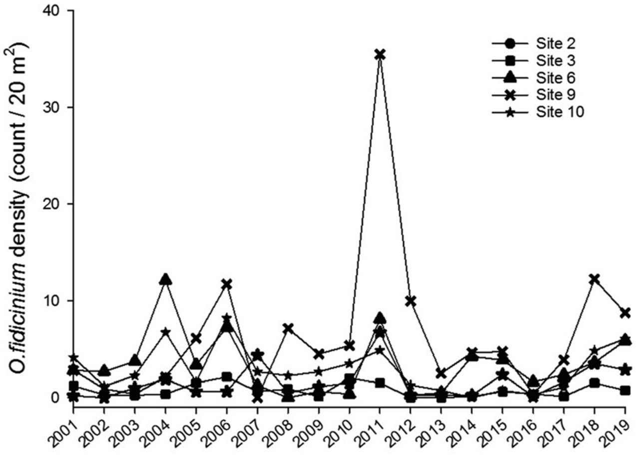


Fig. 3 Density of *Orchelimum fidicinium* at five sites from 2001 to 2019

variable loading most strongly onto PC2 was tide height (current year) or river discharge (previous year).

Best subset regressions using the PC scores and *Prokelisia* density indicated that plant variables had the highest influence on *O. fidicinium* density compared to abiotic variables in four of the five sites (3, 4, 6, and 9); however, predictive power was low to modest, with model R^2 values ranging from 0.18 to 0.64 (Table 3). Current year plant PC1 entered into regression models for sites 3, 6, and 9, and current year plant PC2 entered into the model for site 4. Previous year plant PC1 and PC2 entered into the model for site 6, as did previous year *Prokelisia* density. In contrast, an abiotic PC only entered weakly into two models for sites 3 and 10. Scatter plots showing the bivariate relationship between *O. fidicinium* density and the best overall plant PC predictor (current year PC1) illustrate these relationships (Fig. 4). Similarly, a ANCOVA model using principal component scores, including the interaction of all five sites and current year plant variables (PC1 and PC2) also indicated that the effect of the PCs differed among sites (Table 4).

Table 3 Summary of multiple linear regression analyses of *Orchelimum fidicinium* density at five GCE sites using PCA scores and *Prokelisia* spp. density as predictor variables. *P*-values $\leq$ 0.05 are indicated in bold

Site	Coefficient and variable	*P*-value
GCE-3	−0.48 Current year plant PC1	**0.04**
	0.52 Previous year abiotic PC2	0.08
Model adjusted R^2=0.24, $F_{2,14}$=3.58, *P*=0.056		
GCE-4	−0.0001 Current year plant PC2	**0.02**
Model adjusted R^2=0.27, $F_{1,15}$=6.83, *P*=**0.02**		
GCE-6	0.22 Current year plant PC1	0.10
	0.49 Previous year plant PC1	**0.002**
	−0.67 Previous year plant PC2	**0.03**
	0.32 Previous year *Prokelisia*	0.07
Model adjusted R^2=0.64, $F_{4,12}$=7.97, *P*=**0.002**		
GCE-9	−0.4 Current year plant PC1	**0.05**
Model adjusted R^2=0.18, $F_{1,15}$=4.46, *P*=**0.05**		
GCE-10	−0.27 Previous year abiotic PC1	0.12
Model adjusted R^2=0.1, $F_{1,15}$=2.75, *P*=0.12		

When we performed regressions using the individual plant variables that contributed to the plant PC axes, we found that current year plant biomass was negatively related to *O. fidicinium* density at three sites (Site 3, 4, and 9; Table 5). Predictive power was low, however, with model R^2 values ranging from 0.10 to 0.44. Current year flower abundance was negatively related to *O. fidicinium* density at sites 3 and 9, and positively at site 4, but none of these relationships were strong. At site 6, previous year plant biomass was positively related to *O. fidicinium* density. Scatter plots showing the bivariate relationship between *O. fidicinium* density and current year plant biomass illustrate the negative relationships at site 3, 4, and 9, the positive relationship at site 6, and no relationship at site 10 (Fig. 5).

Orchelimum fidicinium density did not decline over time during the period of record (Regression of *O.fidicinium* density vs. year, Site 3: $R^2 = 0.02$, $P = 0.56$; $R^2 = 0.07$, Site 5: $P = 0.29$; Site 7: $R^2 = 0.02$, $P = 0.60$; Site 9: $R^2 = 0.04$, $P = 0.40$; Site 10: $R^2 = 0.03$, $P = 0.46$).

Discussion

There was a striking spatial pattern in *O. fidicinium* density during the course of this study. Sites close to upland habitat had variable but positive *O. fidicinium* densities, whereas sites far away from upland habitat had densities close to zero. This suggests upland is critically important to this salt marsh orthopteran at some point in its life cycle. We tested the hypothesis that plant quality might vary among these types of sites and ruled it out as a causal explanation for differences in densities—orthopteran growth rates were identical when fed plants from sites with and without adjacent upland. At least three alternative possibilities remain unexamined. First, species in the genus *Orchelimum* tend to oviposit their eggs in plant leaves and stems, and *O. fidicinium* is known to deposited eggs into the leaf sheath of *S. alterniflora* (Stiling and Strong 1982). It is possible that survival of eggs is highest in high marsh habitats where plants are not routinely flooded by the tides. If so, adults might rarely travel far enough from their birthplace to reach sites that lack significant upland influence. Second, *O. fidicinium* adults might require upland habitat as a refuge from predation during especially high tides. *Spartina alterniflora* is mostly or completely inundated during extreme high tides, and at these times orthopterans are exposed to aquatic predators such as fish. We have observed that *O. fidicinium* often retreat to uplands in high numbers during such extreme high tides, suggesting that individuals at sites which lack adjacent upland might be exposed to significant

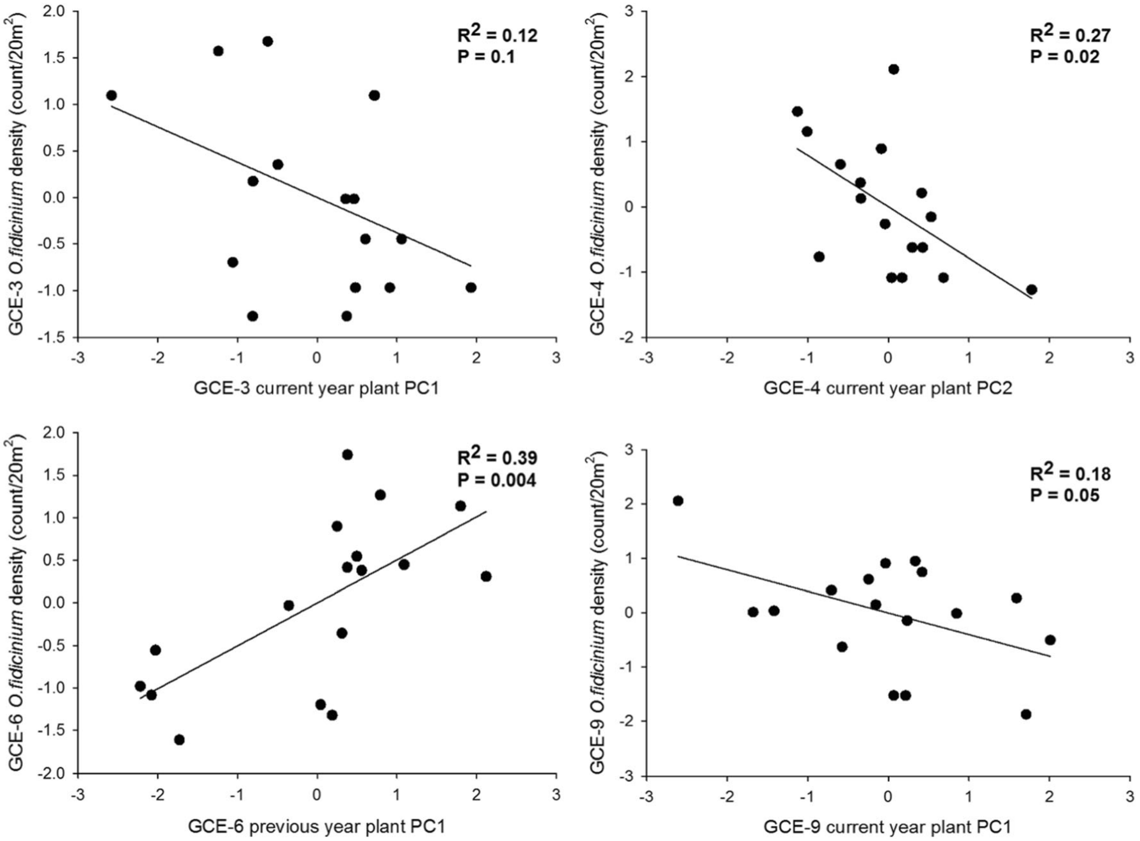


Fig. 4 Bivariate regressions between *Orchelimum fidicinium* densities at four sites illustrating the effect of the most important predictor variable at that site. There was not significant predictor variable for site 10, therefore no relationship is shown for that site. R^2 and *P*-values are for the bivariate relationships shown, and so may differ from the multiple regression relationships reported in Table 3

risks. Third, *O. fidicinium* may follow the phenology of perennial plants and migrate between upland and lowland habitats while consuming flowers and seeds. For example, in New England, *Juncus gerardii* flowers during early summer, *Spartina patens* flowers during mid-summer, and *S. alterniflora* flowers during late summer, and the grasshopper *Conocephalus spartinae* migrate from the high to the low marsh accordingly (Bertness et al. 1987). A similar dynamic might occur in Georgia, with *J. roemerianus* flowering earlier in the year than *S. alterniflora*, but only sites with adjacent upland would have both species available. Other salt marsh arthropods also move among habitats during their life cycle. For example, the endangered maritime ringlet butterfly *Coenonympha nipisiquit* spends its larval stage in the low

Table 4 Summary of final ANCOVA model of *O. fidicinium* density at the five GCE sites. *F* and *P* values for the main effects should be interpreted with caution because interaction terms had $P < 0.1$

Variable	DF	F	P
Site	4	< 0.001	1
Current plant PC1	1	3.26	0.08
Current plant PC2	1	0.01	0.91
Site x current plant PC1	4	2.94	0.03
Site x current plant PC2	4	2.41	0.06
Residual	70		

Table 5 Summary of multiple regression analyses of *O. fidicinium* density at four GCE sites using plant variables only (current or previous year as suggested by Table 3). Site 10 was not included in this table because plant variables were not included as predictors for this site. *P*-values ≤ 0.05 are indicated in bold

Site	Coefficient	P
GCE-3	−0.12 Plant biomass	0.64
	−0.42 Flower abundance	0.10
Model adjusted R^2=0.10, $F_{2,14}$=1.85, *P*=0.19		
GCE-4	−0.73 Plant biomass	**0.009**
	0.39 Flower abundance	0.13
Model adjusted R^2=0.31, $F_{2,14}$=4.63, ***P*=0.03**		
GCE-6	0.72 Previous year plant biomass	**0.02**
	−0.003 Previous year flower abundance	0.99
Model adjusted R^2=0.44, $F_{4,12}$=7.30, *P*=**0.007**		
GCE-9	−0.52 Plant biomass	0.06
	−0.05 Flower abundance	0.85
Model adjusted R^2=0.19, $F_{1,15}$=2.85, *P*=0.09		

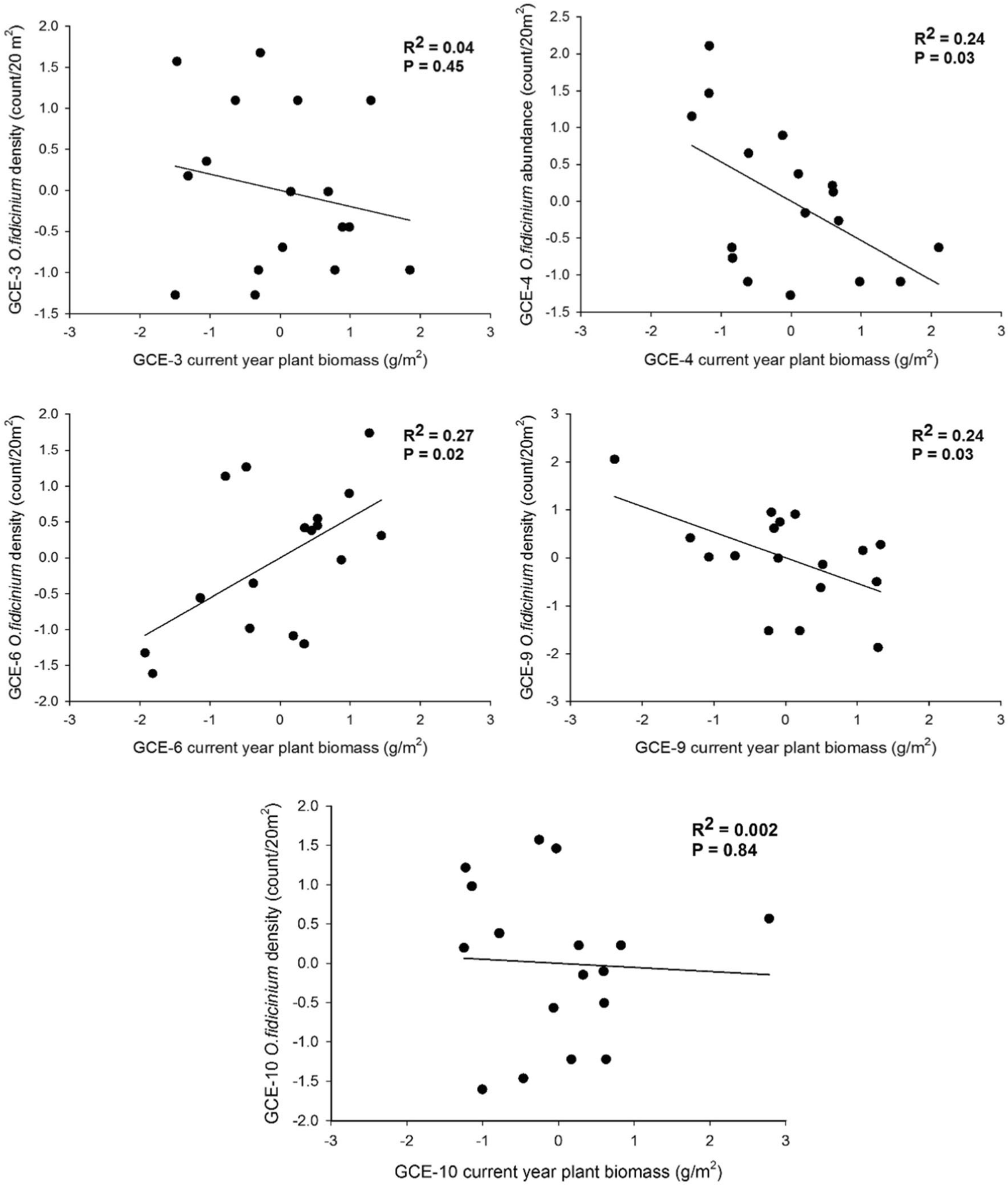


Fig. 5 Regression between *Orchelimum fidicinium* densities at five sites and current year plant biomass. R^2 and *P*-values are for the bivariate relationships shown, and so may differ from those in Table 4

marsh, tolerating periodic tidal inundation, while the adults are found entirely at higher elevations where their host plant *Limonium nashii* is abundant (Sei and Porter 2003). If *O. fidicinium* lacked an important food source early in the growing season at sites without adjacent upland, this might explain the low density of *O. fidicinium* at these sites. Testing between these possibilities and others will require future work.

A previous study of energy flow through the *O. fidicinium* population reported that the spatial distribution of *O. fidicinium* was affected by the height of its food plant, *S. alterniflora* (Smalley 1960). Our results similarly indicate that annual variation in vegetation is the primary driver of annual variation in abundance of *O. fidicinium.* This result is consistent with findings from many inland grasshopper species. For example, the density of locusts is highly influenced by the quality and abundance of their food plants (Despland et al. 2000; Cisse et al. 2013). To our surprise, however, the relationship was negative: at three of the five study sites, variation in the density of *O. fidicinium* over time was negatively related to plant abundance. One obvious possibility is that dense populations of *O. fidicinium* suppressed the abundance of their food plant; however, we consider this unlikely. The highest density of *O. fidicinium* that we observed in late summer was 1.75/m^2, which is low compared to grasshopper densities (~6/m^2) commonly found in terrestrial grasslands (Kemp and Dennis 1993). Similarly, Smalley (1960) found high densities of nymphs early in the season (May), but densities dropped to 10/m^2 in July and below 5/m^2 in August. At these modest densities, it is unlikely that *O. fidicinium* strongly suppresses *S. alterniflora* biomass. Smalley (1960) also estimated that *O. fidicinium* was consuming around 2% of the production of *S. alterniflora*, which again is not likely enough to strongly affect plant biomass. Similarly, Johnson and Jessen (2008) showed two *Melanoplus* species were also unable to strongly affect *S. alterniflora* biomass even at a grasshopper density of 34/m^2.

An alternative possibility is that plants are less nutritious when highly productive. In some terrestrial grasslands, grasshopper abundance among years is also negatively correlated with plant biomass, and a likely explanation is that concentrations of plant nutrients, such as N, P, K, and Na, are diluted in years with vigorous plant growth (Welti et al. 2020). We do not have plant nutrient data that would allow us to test this hypothesis for our study sites, but it seems more plausible than the possibility that *O. fidicinium* would be suppressing plant biomass. Finally, it is possible that plants are better defended against herbivores in years when they are less stressed, and that better defenses reduce herbivore population densities.

At site 6, *O. fidicinium* density was positively correlated with the previous year's plant biomass. One possible explanation for this is that it relates to over-wintering success. Katydids in the genus *Orchelimum* typically oviposit eggs within stems of their host plants, and *O. fidicinium* is known to oviposit in *S. alterniflora* (Stiling and Strong 1982); whether it also oviposits in other plant species is unknown. Assuming that *O. fidicinium* primarily lays eggs in *S. alterniflora* plants, taller plant stems may be more robust and survive the winter better, leading to greater *O. fidicinium* density the next year.

We were surprised not to find relationships between abiotic factors and *O. fidicinium* density. In terrestrial grasslands, grasshopper populations are often heavily influenced by precipitation, because high precipitation, particularly in spring, can dilute plant nutrients, damage nymphs, and promote parasitic fungal growth (Lockwood and Lockwood 2008). In addition, high temperatures tend to reduce survival of terrestrial grasshoppers due to increased metabolism and physiological stress which reduces nutrient intake relative to nutrient requirements (Laws and Belovsky 2010). It is likely, however, that *O. fidicinium*, being a wetland species exposed to both rain and tidal inundation, is adapted to constant wetness. Adults, in particular, actually will enter the water and swim to avoid terrestrial predators (Smalley 1960). Even if abiotic factors do not directly affect *O. fidicinium* density, precipitation, river discharge, and temperature are all important factors influencing *S. alterniflora* productivity (Wieski and Pennings 2013; Li and Pennings 2017), and so likely affect *O. fidicinium* indirectly. Moreover, because abiotic factors are strongly correlated with plant productivity, any direct effects on *O. fidicinium* density might be hard to statistically disentangle.

Like many tettigoniids, *O. fidicinium* is an omnivore, eating small arthropods in addition to plants Stiling and Strong (1991). Jiménez et al. (2012) noted that *O. fidicinium* grew best on a diet consisting of both *Prokelisia* planthoppers and *S. alterniflora*. However, we did not find any positive relationships between *O. fidicinium* and *Prokelisia* relative density. This may be because *Prokelisia* populations are highly dynamic on short time scales (Denno 1977) and we only estimated their density on a single date. As a result, we may not have a very good estimate of how dense *Prokelisia* was at each site over the several-month lifespan of the tettigoniids. The density of *Prokelisia* is a function of plant nitrogen content Stiling and Strong (1991), and so if *S. alterniflora* plants were low in nitrogen during years when plant biomass was high, as suggested above, the density of *Prokelisia* might also have been low in those years. If *Prokelisa* abundance did in fact drop during years when plant biomass was high, it would provide a second reason why *O. fidicinium* numbers would drop during those years.

We documented relationships between *O. fidicinium* abundance and plant PCs, but the overall R^2 values for the relationships were low. There may be several reasons for this. First, we only measured *O. fidicinium* density on a single day at each site in each year, and measuring on multiple dates might have given better estimates of orthopteran density. Second, we did not measure the abundance of predators such as spiders and birds that could have influenced *O. fidicinium* density (Marples 1966). Third, we had only one set of abiotic data that we applied to all the study sites; however, it is possible that each site experienced a different microclimate due to aspect or fetch that might have explained the different results between the four sites. Fourth, plant biomass was estimated later (October) in the growing season than *O. fidicinium* density (August) which could have obscured relationships, if, for example, plants had growth spurts late in the season in some years but not others. Having said this, almost all studies of grasshopper population variation among years have relationships with a poor predictive ability (Branson 2011; Welti et al. 2019), and our study, therefore, is not unique in this regard.

Because we examined five study sites, we were able to evaluate whether the factors determining *O. fidicinium* density were similar at each site. They were not: at three sites *O. fidicinium* density decreased as plant biomass increased, whereas, at a fourth site, *O. fidicinium* density increased with plant biomass in the previous year, and no relationship between *O. fidicinium* and plant biomass at a fifth site. Although more detailed studies will be needed to determine why we obtained different results at different sites, the lack of repeatability illustrates the value of studying multiple sites. If we had studied *O. fidicinium* density at only one or another of the five sites, we could have come to very different conclusions. Instead, by comparing results among five sites, we came to the more nuanced conclusion that controls on density may differ among sites. Although the five sites were fairly close to each other, all saline, and all dominated by the same plant species, they differed in proximity to upland habitat, in marsh size, in aspect and fetch, and in many other factors. Given the low R^2 values typical of other grasshopper population studies, it is likely that similar site-to-site variation in results would be common if it had been looked for. This suggests that we should be cautious about uncritically accepting the conclusions of results from any single site. For example, migratory locust (*Locusta migratoria*) oviposition rates vary from site to site and is highly dependent on vegetation cover, aspect, soil moisture, and salinity (Rong et al. 2006). Therefore, limited sampling may yield misleading or incomplete results.

Recent syntheses of insect time series have raised the possibility that insect populations are declining worldwide (Dirzo et al. 2014; Hallmann et al. 2017). This conclusion, however, has been challenged on multiple grounds (Macgregor et al. 2019; Klink et al. 2020). We conducted regressions of *O. fidicinium* density versus year for each of the five high-density sites, and in no case was there a strong relationship. Thus, whatever the merits of the global synthesis, we see no evidence of a population decline in *O. fidicinium* in Georgia over the past two decades.

In summary, our results indicate that the density of the dominant katydid species *O. fidicinium* in Georgia salt marshes varies dramatically among sites and years. A large part of the spatial variation is explained by having terrestrial habitat adjacent to the marsh, although the reason that the terrestrial habitat is essential remains a matter of speculation. A large part of the temporal variation appears to be linked to the productivity and flowering of *S. alterniflora*, the dominant plant in the habitat, although the relationship between *O. fidicinium* and *S. alterniflora* was different among sites, for reasons that are not yet clear, despite 17 years of data. Our study highlights the value of having multiple sites for long-term studies of orthopteran population dynamics, because average population densities and controls on populations may differ among sites, such that results from any one site would be misleading.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-021-00953-y.

Acknowledgements This material is based upon work supported by the National Science Foundation through the Georgia Coastal Ecosystems Long-Term Ecological Research program under grant numbers OCE-9982133, OCE-0620959, OCE-1237140, and OCE-1832178. We thank everyone who helped collect grasshopper density data, and especially J. Shalack for assistance in the field. This is contribution number 1094 from the University of Georgia Marine Institute.

Declarations

Conflict of Interest The authors declare no competing interests.

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