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Title: **Pattern and scale: evaluating generalities in crab distributions and marsh dynamics from small plots to a national scale**

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Abstract

The generality of ecological patterns depends inextricably on the scale at which they are examined. We investigated patterns of crab distribution and the relationship between crabs and vegetation in salt marshes at multiple scales. By using consistent monitoring protocols across 15 US National Estuarine Research Reserves, we were able to synthesize patterns from the scale of quadrats to the entire marsh landscape to regional and national scales. Some generalities emerged across marshes from our overall models, and these are useful for informing broad coastal management policy. We found that crab burrow distribution within a marsh could be predicted by marsh elevation, distance to creek and soil compressibility. While these physical factors also

affected marsh vegetation cover, we did not find a strong or consistent overall effect of crabs at a broad scale in our multivariate model, though regressions conducted separately for each site revealed that crab burrows were negatively correlated with vegetation cover at 4/15 sites. This contrasts with recent smaller-scale studies and meta-analyses synthesizing such studies that detected strong negative effects of crabs on marshes, likely because we sampled across the entire marsh landscape, while targeted studies are typically limited to low-lying areas near creeks, where crab burrow densities are highest. Our results suggest that sea-level rise generally poses a bigger threat to marshes than crabs, but there will likely be interactions between these physical and biological factors. Beyond these generalities across marshes, we detected some regional differences in crab community composition, richness and abundance. However, we found striking differences among sites within regions, and within sites, in terms of crab abundance and relationships to marsh integrity. Although generalities are broadly useful, our findings indicate that local managers cannot rely on data from other nearby systems, but rather need local information for developing salt marsh management strategies.
Key words: consumer, conservation, decapod crustacean, long-term monitoring, National Estuarine Research Reserves, plant-herbivore interactions, salt marsh

Introduction

"The problem of pattern and scale is the fundamental problem in ecology, unifying population biology and ecosystems science, and marrying basic and applied ecology"

Simon Levin, MacArthur Award Lecture (Levin 1992)

Generality in ecology can be elusive, but is worth seeking (Lawton 1999). Compelling studies of particular systems are not necessarily representative, and patterns from single sites do not necessarily scale up to broader landscapes. This makes it difficult to evaluate the general importance of mechanisms to entire landscapes or ecosystems. Meta-analyses offer one effective tool for quantifying generality, by standardizing and analyzing groups of similar studies (Gurevitch et al. 2018). For instance, meta-analyses have been used to assess the general importance of herbivory across systems, revealing that the effect of herbivory is ubiquitous and often strong (Bigger and Marvier 1998; Gruner et al. 2008). However, the studies synthesized in a meta-analysis are not necessarily distributed randomly across systems, but rather may be biased towards systems where the factor of interest is conspicuous. Herbivore exclusion experiments,

for example, may be more likely conducted in areas where prior natural history observations have revealed conspicuous signs of herbivory.

Generality and scale matter not just for advancing ecological theory but for practice. Local decision-makers need to know how to prioritize among threats so they can invest limited resources in the best strategies for safeguarding habitats and species. If data are unavailable from the exact places they manage, can they use data from another similar area? How far away can that be? Regional or national decision-makers need to know whether and how to scale up from individual studies to broader policies. There is thus a pressing societal need to enhance understanding of ecological processes at regional to continental scales (Heffernan et al. 2014). The most powerful approach to generality across landscapes is from studies that span a range of conditions, and integrate data from multiple spatial scales, from single organisms to entire geographic regions (Borer et al. 2014, Anderson-Teixeira et al. 2015, Duffy et al. 2015).

Salt marshes provide an example of an ecosystem where there are conceptual debates about the relative importance of different driving forces, with concrete implications for conservation and management. Salt marshes are highly productive and provide numerous ecosystem services, including fish nursery habitat, shoreline protection, and water quality improvement (Gedan et al. 2009). Extensive salt marsh loss has occurred in the past century and continues today due to direct and indirect effects of human activities (Kennish 2001, Watson et al. 2017). Thus, coastal managers at local to national scales are interested in understanding factors that affect marsh resilience (Raposa et al. 2016).

Typical of all ecosystems, salt marshes are affected by both physical and biological factors, as well as human alterations to these factors. Tidal inundation strongly affects marsh distribution, so historically, academic and management emphasis has been placed on physical factors, such as sediment supply and marsh elevation, and how both can affect resilience to sea-level rise, another critical physical stressor (Kirwan and Murray 2007). Complementing this perspective, there has been an emerging focus on biological factors, especially consumers, such as mammals (Bakker et al. 1993), birds (Jefferies et al. 2006), and snails (Silliman et al. 2005). In particular, herbivory and bioturbation by crabs can exert strong negative effects on marshes (e.g. Holdredge et al. 2009, Smith and Tyrrell 2012, Bertness et al. 2014, Alberti et al. 2015). The scale of most crab studies is typically small (plots within a marsh), while the scale of studies assessing sea-level rise is typically larger (entire estuary or region). Conceptually, to advance

estuarine theory, as well as for applied management, there is a need to better understand the relative importance of different drivers of marsh sustainability, and how they vary across scales (Petengill et al. 2018).

The understanding of ecological phenomena at regional and broader scales lags behind understanding at smaller scales (Heffernan et al. 2014, Estes et al. 2018) for all systems, including salt marshes. A recent synthesis of consumer control of coastal vegetation (He and Silliman 2016) highlighted the need for studies in coastal systems that are located across multiple regions and at sites distributed at random, so bias towards areas with strong consumer effects is avoided. The US National Estuarine Research Reserve System (NERRS) implements consistent monitoring protocols across an extensive coastal network, and thus is well-suited as a platform for exploring generality in estuarine processes, (Apple et al. 2008, Raposa et al. 2016, Baumann and Smith 2018, Raposa et al. 2018a).

The goal of this study was to take advantage of consistent NERRS salt marsh monitoring to explore generalities in crab communities and abundance and their relationship to indicators of marsh integrity from small scale (square meter plots within marshes) to local scale (marshes within Reserves) to regional and national scales. Unlike most previous studies of crabs in marshes, sites were chosen to be representative of marsh health in the region, without regard to crab abundance (permanent marsh transects were established prior to our interest in crabs). Location of sampling plots within marshes was at random with regard to crabs, and occurred at uniform intervals spanning the marsh landscape, from landward to seaward edge. One focus was a characterization of crab communities and abundance across multiple scales. Previous studies (e.g. Holdredge et al. 2009, Coverdale et al. 2012) suggest crabs can be highly abundant in salt marshes: how general is this? which species dominate? are there latitudinal patterns or regional trends? A second focus was to examine whether the strong negative effects of crabs on salt marshes that have been demonstrated at the plot-scale at selected marshes (e.g. Bertness et al. 2014, Angelini et al. 2018) scale up to entire marsh landscapes or regions. We also compared the role of top-down vs. bottom-up effects, examining whether crabs or physical factors better predict marsh integrity. The NERRS monitoring network thus enabled us to explore generality and scale in both biological and physical factors that affect salt marsh resilience.

Methods

Study sites. We conducted this investigation in tidal marshes in 15 National Estuarine Research

Reserves located along the US East, West, and Gulf coasts, representing six major bioregions (Fig. 1; Appendix S1: Table S1). Most Reserves sampled in just one marsh; others included multiple marshes, or regions of a large marsh, resulting in a total of 30 marsh sites sampled. These marshes span a diverse range of landscape settings and environmental conditions. Nine Reserves sampled marshes located within estuarine embayments but others sampled marshes in open coast, back-barrier, or brackish settings. The marshes collectively encompassed wide ranges in mean salinity (11-34 ppt), water temperature (13-29 °C), and nitrate concentrations (2-626 ug l^{-1}), as revealed from nearby NERR water quality and nutrient monitoring stations. This wide diversity of marsh sites ensures that results of our study are representative of marsh crab communities across much of the conterminous US.

Vegetation and crab sampling methods. Field sampling was built into ongoing long-term system-wide marsh biomonitoring as part of the NERR Sentinel Sites program, whereby percent cover of all vegetation species, and stem density and height of dominant species were quantified (Moore 2013; NERRS 2012). Transects were established specifically to track health of emergent vegetation consistently across Reserves. Sampling crabs was not originally part of the study design, so transects were established at random with respect to crab distribution and abundance. The results thus are representative of emergent marsh communities, but do not capture maximum crab abundance or diversity in each estuary, which is often greatest in mudflats or subtidal areas.

Crab sampling occurred in 1-m^2 monitoring plots spaced uniformly at intervals along multiple transects (at least 3 per Reserve) in each marsh following the protocols outlined in Roman et al. (2001). All plots were located on the marsh platform (vegetated or unvegetated); no plots were located in water features such as creeks, pools, or ditches. Most transects spanned the full elevational range of each marsh from the marsh/water edge to the marsh/upland edge, with plots spaced uniformly across this gradient, but a few Reserves were committed to an alternate pre-existing design and sampled plots along truncated transects near the water's edge. Mean transect length at individual sites therefore varied widely, from 10 to 1134 m. The number of plots at each marsh site ranged from 6 to 35, for a total of 466 sampling plots included in our study. All sampling occurred between June 7 and November 2, 2017 with sampling dates at each Reserve generally coinciding with the timing of peak vegetation biomass.

Crabs were sampled at each site once with pitfall traps to quantify abundance (as catch-per-unit-effort, CPUE), community composition, richness, and size. At most plots (438 total;

SFB could not conduct pitfall trap sampling due to permitting issues and samples could not be collected at two plots at NIW), a small pitfall trap (21 cm deep, 6.5 cm wide) constructed from a plastic tennis ball can with five 1-cm holes drilled in the bottom was sunk into the marsh peat so that the top of the trap was flush with the surface of the marsh. Traps (not baited) were placed in close proximity to, but not within, each monitoring plot for 24 hours. All crabs caught were identified to species (or genus if species could not be identified), measured for carapace width (mm), and returned live to the field (with the exception of a few difficult to identify specimens that were brought to the laboratory).

We also quantified indicators, or proxies, of crab impacts at each plot. Crab burrow counts were conducted in a 0.5 x 0.5 m quadrat nested inside the larger plot. Within this subplot, all crab burrows were counted by close visual examination and converted to density (burrows m^{-2}). No effort was made to excavate any burrows to identify crab occupants. As other indicators, any live crabs seen in the plot prior to or during burrow counts were counted and identified (when possible), and any sign of direct above-ground herbivory on marsh vegetation in the plot from crabs was noted (leaf damage, cropped stems). We did not assess below-ground herbivory. For each plot we also summarized whether there had been any sign of crabs or crab indicators (i.e. sign of herbivory, crabs observed or trapped, burrows counted, or presence of bare ground). We thus could quantify the proportion of plots at a site or overall with these indicators.

We used vegetation community patterns to relate to and help describe patterns in crab communities, and used percent unvegetated cover as an indicator of marsh integrity to test for potential crab impacts on marsh integrity across diverse marsh communities. While cover is only one indicator, it is the most common one used in GIS analyses of salt marsh trends over past decades (e.g. Watson et. al. 2017), or in models of future marsh resilience to sea-level rise (e.g. Kirwan and Murray 2007). The percent cover of all plant species present in each plot was also quantified using either a point-intercept or visual assessment method. For the most common species at each site, we also quantified canopy height and stem density. Ground was only considered as unvegetated if no live vegetation was observed directly above it (for the visual method) or if no live vegetation hit the intercept rod at a point (point-intercept).

Additional plot information. While sampling crabs and vegetation, we also assessed soil compressibility at each plot, using an index based on rough estimates (1 = very firm: researcher foot sinks < 2.5 cm; 2 = moderately firm, foot sinks 2.5-7 cm; 3 = soft, foot sinks 7-13 cm; 4 =

very squishy, foot sinks >13 cm). We also determined where each plot was located vertically and horizontally within the marsh landscape to explore within-marsh crab distribution patterns. Mean plot elevation was obtained from the most recent survey at each site using standard field methods associated with NERR Sentinel Sites monitoring (e.g. levelling from permanent benchmarks or RTK-GPS). Plot elevation was then related to local mean high water (MHW) and tidal range at each site to standardize elevation to the same tidal datum for data comparability among all sites. Elevation of each plot was expressed in the following currency: ((elevation of plot in NAVD88)-(elevation of MHW in NAVD88))/(tidal range) x 100. The proximity of each plot to the nearest tidal creek at least 1 m wide and at least as deep as MLLW was also determined using GIS.

Data analysis. To characterize crab communities within and across marshes we focused on the pitfall catch data, conducting primarily descriptive analyses and summary statistics. We examined geographic patterns, size distributions, and frequency as a function of elevation and distance from tidal creek and conducted linear regressions of latitude vs. species richness, CPUE, and burrow density. To examine patterns of community composition, we used a suite of multivariate analyses provided by PRIMER version 7.0.13 (Clarke and Gorley 2015). These included: 1) a one-way Analysis of Similarity (ANOSIM) to compere marsh crab community composition among all sites with pitfall trapping data, with a global test across all sites followed by individual pairwise tests to compare communities between each pair of sites; 2) a one-way Similarity Percentages (SIMPER) test to quantify the contribution of each species to overall % community similarity between paired sites; 3) a LINKREE analysis with SIMPROF procedure to naturally arrange sites into progressively smaller groupings based on crab community similarity, and; 4) a RELATE analysis across all sites to determine if patterns in crab community data, summarized at the site level, were related to patterns in vegetation community data, also summarized at the site level. All PRIMER analyses were run using Bray-Curtis similarity matrices and untransformed data except for the vegetation community data in the RELATE analysis, which were square-root transformed to downweight very abundant species.

To investigate the broadscale factors that might predict burrow density and CPUE across all sites, we constructed a generalized additive mixed-model (GAMM) for each response. GAMMs use a non-linear smoothing function to determine the relationship between the response and predictor variables. This is similar to using a general linear model, but a Bayesian function is applied to better fit non-linear relationships described in the data. Including the intercept-only

random effect of Reserve (site) in the mixed model utilizes all data points regardless of imbalanced sampling efforts, while accounting for within-site dependence and variation. Burrow density or CPUE were the response variables, and we examined how they related to elevation (standardized tidal elevation as described above), distance to nearest creek, and compressibility of the marsh soil. Due to its low number of discrete values, the soil compressibility index had to be estimated as a linear parametric term rather than with the Bayesian smoothing function. Models were developed with the gam function of the mgcv package in R version 3.5, using a poisson distribution (Wood 2004). The smoothing function used was the default thin plate regression splines (Wood 2003). Mission-Aransas Reserve was omitted from this modeling because it lacked elevation data.

We constructed another GAMM to examine factors that might predict marsh integrity. Percent unvegetated cover (a critical indicator of marsh integrity) was modeled with predictor variables of burrow density, CPUE, elevation, distance to nearest creek, and soil compressibility of the marsh platform. Modeling was conducted as described above using a Gaussian distribution. Two Reserves were analyzed separately using generalized linear models: Wells NERR because soil compressibility did not vary within this marsh, and San Francisco NERR because no CPUE data were available.

GAMMs are useful for pooling data to determine the strength of any universal relationships with response and multiple predictor variables. To complement this broad analysis, we also conducted simple linear regressions for each Reserve individually, to explore the relationship between unvegetated cover and two potential drivers of interest, burrow density (as a proxy for crab effect) and relative elevation (as a proxy for sea-level rise effects). We report the coefficient of determination and significance of the slope parameters for each Reserve, arranged in a geographic order to visualize any potential spatial patterns in the relationships.

Some independent variables and the fixed effects of the independent variables on unvegetated cover may be related at spatial scales greater than the local site scale but smaller than the global scale used in our GAMM analysis. To determine if there are regional similarities in mean independent variables and the effects of independent variables on unvegetated cover, we looked for natural groupings among sites using spatial constraints in ArcGIS 10.3.1 using the Group Analysis tool. We used Delaunay triangulation to identify natural neighbors between sites and we set the group parameter to six for the natural geographic regions in which the sites are

located. Because the Mission-Aransas (MAR) NERR site was missing relevant tidal elevation data, it was excluded from the group analysis of the fixed effect of tidal elevation on unvegetated cover. The exclusion of this site removed a geographic region from the data so the group parameter was constrained to five.

To examine the relationship between sea-level rise and crabs, we used data from 8 Reserves (WQB, NAR, DEL, CBV, NIW, SFB, ELK, TJR) where we had previously conducted a multi-metric assessment of marsh resilience to sea-level rise (Raposa et al. 2016). (The other 7 sites either had not been included in this earlier analysis, or had used substantially different marsh locations.) We correlated the score for sea-level risk of each marsh to the percent of plots in that marsh with any sign of crabs.

Results

Broad-scale patterns in crab communities, species, and burrows

Tidal marshes at NERR sites across the US generally supported very simple crab communities comprised of a small number of species. A total of 575 individuals from 20 species (including 28 individuals that could not be identified beyond the genus level) were captured in 438 pitfall trap samples collected across all sites (Table 1). Nine species comprised approximately 90% of all captured crabs and all of these were found at multiple Reserves. The remaining 11 species each made up approximately 2% or less of all crabs and were found at only one Reserve each. In general, West Coast sites were dominated by *Pachygrapsus crassipes* and East Coast sites by multiple *Uca* spp. A gradient in the composition of secondary species also occurred while moving north to south along the East coast, from *Carcinus maenas*, to *Sesarma reticulatum*, to *Eurytium limosum*/*Panopeus* spp., to *Rhithropanopeus harrisii* at GTM where the intermixing of mangroves and marshes resulted in a relatively rich crab assemblage. All twelve of the most abundant species (98% of all individuals) excavate burrows directly into marsh peat, whereas only two species (*S. reticulatum* and *Armases cinereum*; 8% of all individuals) have been documented to graze directly on marsh vegetation (Appendix S1: Table S2). Crabs in US marshes are generally small; median carapace width of all crabs was 21 mm, and 83% of all crabs were less than 30 mm wide (Table 1; Appendix S1: Fig. S1). The largest species included *C. maenas* (in New England) and *Panopeus* spp. (in North Carolina and Georgia), comprising only 5.7%; *Callinectes* spp. were larger still, but only two individuals were captured.

CPUE, burrow density, and species richness varied across sites (Fig. 2A-C). Cursory

examination of these patterns suggested a latitudinal effect on the East Coast, so we examined this relationship with linear regressions. Indeed, burrows and species richness decreased significantly with increasing latitude, and CPUE showed a non-significant but similar pattern (Fig. 2D-F). Species richness was not only low at the plot scale but at the scale of sites. Two or three crab species were captured at most sites; GTM had the highest richness (8 species), NIW had 5, and CBV and SAP each had 4 (Table 1). Only one species was caught in northern New England (*C. maenas*) and in California (*P. crassipes*).

Marsh crab community composition differed significantly among the Reserves (ANOSIM, global R = 0.23, P = 0.001). Crab communities were similar between regional pairs of sites (i.e. non-significant pairwise tests between sites; P>0.05) within northern New England (WEL and GRB; *C. maenas* contributed 100% to site similarity from SIMPER), southern New England (WQB and NAR; *U. pugnax* 79% and *C. maenas* 11%), the mid-Atlantic (DEL and CBV; *Uca minax* 89% and *S. reticulatum* 10%), and across the West Coast (SOS, ELK, and TJR; *P. crassipes* >99%). Crab communities were also similar between MAR and GRB (likely to most traps being empty at both sites); communities at all other sites were not similar to any other site. These results are supported by a complementary LINKTREE analysis, which shows West Coast sites with high *P. crassipes* CPUE grouping together and apart from East Coast sites at the broadest scale (Fig. 3). Other notable groupings include the four New England sites with high *C. maenas* CPUE separating from the remaining East Coast sites, and southern New England sites with high *U. pugnax* CPUE separating from northern New England sites. At the national scale using data that were summarized across all plots within each site, patterns in crab community data were significantly related to patterns in vegetation community data (RELATE, Rho = 0.52, P = 0.001).

Patterns in crab indicators across sites and regions

Burrow densities, the most conspicuous of crab indicators, were low on average but many Reserves had at least some plots, often on the creek edge, with high densities, such as >100 per m^2 (Fig. 4). Burrow density and CPUE were not well correlated in a regression using Reserve as replicate (R^2 = -0.11, P = 0.73). Examined within each of the 14 Reserves that collected both types of data (San Francisco Bay did not collect CPUE), three of these had a significant positive relationships with $R^2 > 0.1$ and $P < 0.05$.

Considering all indicators combined, about half of all plots across the Reserves had

burrows, and about half had a catch of at least one crab (Fig. 5). At about a third of plots, crabs were seen by observers. Very few plots showed any conspicuous signs of herbivory (such as freshly cropped vegetation or leaf damage). At almost 70% of plots, there was some sign of crab activity (one of the above).

Clear geographic patterns emerged when considering these indicators. For example, the percentage of plots with burrows, crabs caught, and crabs seen steadily increased while moving south along the East Coast, and was much lower in Gulf and West Coast marshes (Fig. 5). The percentage of plots with visible crab herbivory was low; at NAR and CBV it was likely associated with the direct *Spartina* spp. herbivore *S. reticulatum*. The percentage of plots with bare ground was high at almost all East Coast sites, MAR, and TJR, and low in northern New England and the Pacific northwest. Taken together, these results show that the percentage of plots with any indication of crabs was consistently high from southern New England to Florida, and relatively low everywhere else.

Within-marsh distributions relative to elevation and distance from creek

At the within-marsh scale, the distribution of many species was related to how far plots were from the nearest tidal creek and/or their elevation relative to the tidal frame. For example, *C. meanas* was consistently found close to creeks and at low elevations (relative to MHW), whereas *A. cinereum* was mostly found far from creeks and at higher elevations (Fig. 6). *Uca* spp. were found more broadly distributed across the marsh platform, and *P. crassipes* on the West Coast were most often found close to creeks but at intermediate elevations, because the marsh dominant, *Salicornia pacifica*, occurs at higher elevations than *Spartina alterniflora*, which dominates many East Coast marshes.

Across all marshes combined, mean burrow density was highest within 50 m of a tidal creek, dropped off dramatically as distance increased, and approached zero at distances beyond 250 m. In stark contrast, mean crab CPUE steadily increased with distance to the nearest tidal creek and peaked between 200-250 m; CPUE also approached zero at distances beyond 250 m. Burrow density peaked at elevations 20-59 cm below local MHW and dropped off quickly and dramatically at higher and lower elevations. The pattern for CPUE with elevation was similar to that for distance to creek; CPUE steadily increased with elevation, and peaked at 40-59 cm above local MHW. (See Appendix S1: Fig. S2 for details on all of the above patterns).

Modeling factors related to burrow density and CPUE at a broad scale

The general additive mixed model was able to effectively predict burrow density (adjusted $R^2 = 0.63$), with highly significant ($P < 0.0001$) contributions to explaining the variation provided by elevation, distance to tidal creek, and soil compressibility, with strong differences among sites (random effects). Burrow density peaked at elevations near MHW (Fig. 7a), declined with distance from creek (Fig. 7b), and increased with soil compressibility (Fig. 7c).

The general additive model was less strong for CPUE (adjusted $R^2 = 0.31$), with highly significant contributions by elevation ($P < 0.001$) and distance to tidal creek ($P < 0.01$), and no significant ($P = 0.869$) contribution by soil compressibility, as well as strong differences among sites (random effects). CPUE peaked near MHW (Fig. 7d) and decreased in the first 100 m from creeks then increased again (Fig. 7e), and has slight and insignificant decrease with soil compressibility (Fig. 7f).

Modeling factors related to marsh integrity at a broad scale

The general additive mixed model was able to effectively predict percent unvegetated cover (adjusted $R^2 = 0.64$), with highly significant ($P < 0.0001$) contributions to explaining the variation provided by elevation and soil compressibility, weakly significant ($P = 0.04$) contribution by burrow density, marginal ($P = 0.06$) contribution by CPUE, no significant effect of distance to tidal creek, and strong differences among sites. Unvegetated cover decreased with elevation (more vegetated cover in higher areas) (Fig. 8a) and increased with compressibility (Fig. 8e) and burrow density (Fig. 8c).

The results of linear regressions for individual sites showed strong differences among sites in the relationship of unvegetated cover with two potential drivers, burrow density and elevation (Fig. 9). Four sites had significant positive relationships between unvegetated cover and burrow density (vegetation cover declines with increasing burrow density). Nine sites had significant relationships between unvegetated cover and elevation, one positive and eight negative (vegetation cover declines with decreasing elevation).

Geographic and sea-level rise analyses

Results of the grouping analysis indicated geographic correlations in burrow density, and the modeled fixed effects of elevation and burrow density on unvegetated cover. Interestingly,

these similarities did not strictly align with geographic regions. High burrow densities linked sites in the Southeast region, but also led to groupings across coasts, as both Northeast and West Coast sites had low densities (Appendix S1: Fig. S3). The effects of elevation on unvegetated cover were more explicitly spatially grouped by East and West Coast (Appendix S1: Fig. S4). Burrow density as an effect on unvegetated cover showed strong geographic regional divisions (Appendix S1: Fig. S5). Since only four of the site effect values were statistically significantly different than zero ($P < 0.05$), the burrow density effect groups should be interpreted with caution.

In our exploration of the relationship between sea level rise resilience and crabs, we found a strong relationship ($R^2 = 0.77$, $P = 0.02$) between the risk sea-level rise poses to a marsh (from Raposa et al. 2016 assessment) and the percent of plots with evidence of crabs in that marsh (summarized in Fig. 5).

Discussion

Generality of distribution and abundance patterns

Broadly, across the nation, our synthesis revealed crabs to be common but not ubiquitous in marshes: about 50% of plots distributed uniformly across the marsh elevational gradient had burrow holes or crabs caught in traps. So crabs, whether considered a concern as potential drivers of marsh degradation (e.g. Alberti et al. 2015) or as a benefit as prey for consumers (e.g. clapper rails, Rush et al. 2010), are not everywhere in the marsh. Conspicuous signs of herbivory, such as leaf damage or cropped stems, were extremely rare (4% of plots) across these marsh landscapes.

The general additive model we employed revealed significant predictors of crab distribution across all marshes combined, with burrow density and crab abundance peaking around Mean High Water, and with burrow density decreasing with distance to tidal creeks and increasing with soil compressibility. These outcomes provide some generality as to crab patterns at a broad geographic scale. However, site was a highly significant factor in the models, and there were strong differences in the relationships of crab abundance to the physical variables even among neighboring sites, resulting in only weak regional groupings in these relationships. We also found differences among crab species in distribution relative to creek distance and elevation.

Elkhorn Slough estuary in California provides a good case study illustrating our findings

at different scales. There were dramatic differences in burrow density among plots within a single marsh. There were also differences among marshes within the estuary -- three of the four marshes assessed had many plots with burrow holes, but one marsh had none at all. Comparison of patterns at Elkhorn Slough and nearby San Francisco Bay also revealed stark contrasts: while burrow holes were common at Elkhorn, they were virtually absent in San Francisco. Yet, despite all these contrasts, a unifying theme emerges from the patterns: elevation is a very important predictor of the patterns, at the plot, marsh, and estuary scale. The plots without burrow holes are at high elevation at Elkhorn, the marsh with no burrows is one of Elkhorn's highest, and the marsh assessed in San Francisco is a similarly high one.

Previous studies have identified patterns of crab abundance in marshes at smaller scales. Luk and Zajac (2013) found *Uca pugnax* in the northeastern US to be most common in low marsh, but not eroding seaward edges. Coverdale et al. (2012) found that *Sesarma reticulatum* in the northeastern US needs sediment soft enough to burrow into, but firm enough to avoid burrow collapse. Vu et al. (2017) found that the same species had predictable patterns of distribution in the southeastern US, with highest abundance near creek heads, but three other species showed no clear patterns. Li et al. (2018) working on *Helice tientsinensis* in the Yellow River Delta of China found crab abundance to be linked to sediment moisture and soil compressibility. Overall, our broadscale assessment and species-level characterizations match these individual studies: elevation, creek proximity and sediment conditions affect crab distribution and abundance, but there are differences among sites and crab species.

Characterization of crab community composition across different scales

Some clear generalities about crab communities emerged at the broadest spatial scale from this first national synthesis of crabs in US marshes. For the most part, only a few crab species are common in marshes, and most of these are small, burrowing species, with only a few species known to cause conspicuous above-ground herbivory of marsh vegetation. Almost all species we caught are also native species; only *C. maenas* and *H. sanguineus* are invasive in US marshes. The species we detected in marshes are certainly not the only crabs in these estuaries: all have more diverse crab communities and include larger species. For instance Elkhorn Slough has about 30 crab species documented for the estuary (Wasson et al. 2002), but only one species found in the marsh; North Inlet has 32 crab species documented, and six in the marsh (Allen et al. 2014).

In addition to these broad generalities, we detected regional patterns. In particular, crab richness and burrow density in marshes decreased significantly with increasing latitude on the East Coast. Community composition also showed regional groupings that separate the West from East Coast, and on the latter, the Northeast from Southeast.

Relationship between crabs and marsh integrity at different scales

Impacts by consumers on plants are common across all ecosystems (Bigger and Marvier 1998), and are increasingly recognized for coastal habitats (He and Silliman 2016). There have been many studies in the past decade identifying the potential for strong negative effects of crabs on salt marshes (e.g. Holdredge et al. 2009, Wilson et al. 2012, Smith and Tyrrell 2012, Bertness et al. 2014, Alberti et al. 2015). So one goal of our study was to seek generality about the relationship between crabs and indicators of marsh integrity, and to compare the strength of the crab effect with that of physical drivers.

Across all 15 US sites, we detected a fairly weak relationship between a key indicator of marsh integrity (unvegetated cover) and crab burrow density, and no relationship with CPUE (Fig. 8). Within individual sites, we found that unvegetated cover increased significantly with burrow density at 4/15 sites (Fig. 9), with site-to-site variation swamping any regional patterns. In terms of physical signs of above-ground herbivory, such as leaf damage or cropping, we found very little evidence anywhere: 5% of plots on the East coast, 1% on the West.

Why did our synthesis reveal a weaker negative effect of crabs on marshes than many recent studies? We suspect that the main reason is because we examined crab effects throughout the entire marsh landscape. Our transect locations were selected without consideration of crab dynamics (they were established to track vegetation long before this study was conducted), and they spanned the entire marsh elevation, from landward to seaward edge. Studies that have demonstrated very strong negative effects of crabs are often focused on particular marshes, or parts of marshes, with very high crab densities, which our sampling suggests are not typical for coastal vegetation communities. For instance Coverdale et al. (2012) showed strong negative effects, but average burrow densities were above 100 per m^2; we only had such high burrow densities at 2/15 sites, and only at a few plots at those two sites. Altieri et al. (2012) sampled along creekbanks in vegetated marshes across Cape Cod MA, including in Waquoit Bay, and reported *Sesarma* CPUE of approximately 0.25 per pitfall and about 40% of stems were grazed. In our study, at Waquoit Bay across the entire marsh, *Sesarma* CPUE was zero and 9% of stems

were grazed. Angelini et al. (2018) found crabs can convert marsh to mudflat only at the highest experimental densities, 32 crabs stocked in 1-m^2 plots. Such studies in high density areas are well suited for detecting the maximum potential of consumers to affect marshes, but not for generalizing about average effects across the entire marsh landscape. Caution must be taken not to assume that crab effects observed in the highest density parts of the marsh system (such as low lying areas near creeks) scale up to the entire marsh landscape. Indeed, negative effects at a small scale may scale up to positive effects at the landscape scale: crab burrowing can lead to erosion of creek banks, but this can increase marsh drainage (Vu et al. 2017). Burrowing at the marsh edge might also increase sediment availability and thus resilience of the marsh interior, if net sediment transport is landward.

Another potential reason why we failed to detect a strong negative relationship between marsh integrity and crabs could be because we were using an observational, rather than experimental design. However, a recent meta-analysis of consumer control in coastal vegetation (He and Silliman 2016) found that similarly strong consumer effects were detected with observational studies vs. consumer-addition experiments, and a stronger negative effect size in observational studies vs. consumer-exclusion experiments.

Still another reason for our detection of diminished crab effects relative to other studies could lie with our choice of marsh integrity indicator. We focused on unvegetated cover as an indicator of marsh integrity. The complete loss of vegetation on a formerly vegetated marsh platform is an indicator of severe degradation. Many experimental studies used more subtle indicators, such as decreased biomass or growth rate. A recent meta-analysis (He and Silliman 2016) found that on average, herbivores had no effect on vegetation cover, while they detected strong effects on survival, above-ground biomass, and height. Thus our results may be partly explained by choice of indicator. However, we also looked for visible signs of herbivory and found very little, in contrast for instance with a broad survey in the southwest Atlantic, which found on average 20% of marsh leaves were damaged (Alberti et al. 2007). So crab effects do appear to be lower in our broadscale synthesis than in previous focused studies.

The contrasting results we found across the marsh landscape and among sites and regions highlights the need for a thorough understanding of local factors that affect the marsh-crab relationship, including marsh structure and dominance by different crab species. For instance, the geographically broadest study prior to ours (Alberti et al. 2007) detected dramatically higher

herbivory rates at lower elevations of marshes from Brazil to Argentina. He and Silliman (2016) found that the effect of herbivory on coastal vegetation varied with latitude and with nutrient-loading. Shultz et al. (2016) contrasted recent die-off at two sites in Long Island Sound, attributing one to a physical driver, excessive inundation, and another to a biological driver, crab herbivory. Vu et al. (2017) detected strong effects of herbivory by one crab species in a marsh system, but no effects by three others. Clearly, context-dependence is critical for understanding of the effect of crabs on salt marsh functioning (Alberti et al. 2015).

Crabs and sea-level rise

Overall, our analysis suggests that projected sea-level rise (SLR) poses a greater threat to marshes than do crabs. Tidal elevation, which directly affects inundation time and serves as a proxy for SLR, was a stronger predictor of marsh integrity than crab abundance or burrow density across all sites combined (Fig.8), and at a greater number of sites in individual site-level analyses (Fig. 9). Compressibility of marsh soils also had a highly significant relationship with marsh cover. So in general, the physical drivers we assessed had a stronger relationship than biological ones, when assessed across the marsh landscape at multiple marshes. However, there is likely an interaction between the threat to marsh vegetation posed by SLR and crabs. Our analyses suggest that crabs will become more abundant with SLR, since many common species are more abundant in low elevation areas that are more frequently inundated, which will expand with rising seas. We also found a strong relationship between the risk sea-level rise poses to a marsh (using the Raposa et al. 2016 assessment) and the percent of plots with evidence of crabs in that marsh. The monitoring data provided here may provide an important baseline to which to compare future changes when crabs become more abundant at some of these study sites.

Our prediction of increasing crab abundance and distribution with SLR complement findings of a recent review that suggests consumer effects in coastal vegetation can intensify in the face of physical stress (Silliman and He 2018). Luk and Zajac (2013) suggested that landward expansion of low marsh vegetation species may facilitate increased distribution of fiddler crabs. Szura et al. (2017) found stronger effects of *Sesarma reticulatum* with increased inundation. Likewise, Crotty et al. (2017) indicated the potential interaction between future SLR and *Sesarma reticulatum* impacts on marshes, as did Raposa et al. (2018b) based on increases in crab burrows during recent periods of higher water levels. Vu et al. (2017) noted that crab

burrowing that increases creek size may actually have a positive effect on marsh integrity in the face of SLR, by increasing drainage. Our synthesis combined with these earlier studies suggests crabs and their burrows will play an increasing role, whether positive or negative, in marshes with accelerated SLR.

Conclusions

The concepts of pattern and scale are linked (Hutchinson 1953). Taking a macroecological perspective to seek broadscale patterns can be valuable (Lawton 1999, Estes et al. 2018), and such a perspective is needed to better understand the role of crabs in salt marshes (Alberti et al. 2015). Our study uncovered some important generalities at a national scale: crab distribution is broadly predictable with marsh attributes (tidal elevation, creek distance and soil compressibility), and such physical factors better predict marsh vegetation cover than crab abundance or burrow density. We also detected some some regional trends, with sites within the US West Coast, Northeast and Southeast regions showing generally similar crab communities and burrow density. Such generalities are useful for broadly informing coastal management policy about the distribution and effects of crabs.

However, our spatial analyses of crab burrow densities and their effects on marsh integrity revealed low predictability at regional scales, and we detected striking contrasts both within and among sites, suggesting that local managers must rely on local data to develop the most effective management strategies. Networks of protected sites such as the NERRS can serve as platforms for examining patterns at scales from quadrats to entire landscapes to regions to nations. Ideally, monitoring data can be complemented with coordinated experiments across sites (Heffernan et al. 2014). By collecting data consistently across sites, we can identify the appropriate scale at which to seek generality for different ecological processes.

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Table 1. Summary table of crab abundance (as catch-per-unit-effort, CPUE) from pitfall trapping across the NERRS. B/H indicates if a species in a marsh is a burrower and/or a herbivore on live marsh vegetation (see Appendix S1: Table S2 for the basis of these assessments). Genus level identifications are marked with "n/a", as this assessment could not be made (since some species within the genus may display a behavior that others do not). NERR biogeographic regions are labelled above each site. 'P' indicates species that were observed in one or more plots at a site but not captured in pitfall traps. Blank cells indicate zero CPUE. Total=average CPUE across all sites. Cum %= cumulative percentage of all crabs caught represented by this species plus those listed above it, up to a 90% cut-off. Freq and Freq % = the number and percentage of sites where each species was found. Carapace widths are in mm.

		Acadian		Virginian				Carolinian				Louisian ian	Columb ian	Californi an						
Species	B/ H	WE L	GR B	WQ B	NA R	DE L	CB V	NO C	NI W	SA P	GT M	MAR	SOS	EL K	TR J	Tot al	%	Cu m %	Fre q	Fre q %	Carap ace width (mm)
Uca minax	B					1.9 3	1.2 8	P	0.1 1							0.28	21. 6	21. 6	3	21. 4	23 (2-36)
Pachygraps us crassipes	B/ H												0.18	1.3 8	0.8 3	0.20	15. 5	37. 0	3	21. 4	25 (11-37)
Uca pugnax	B			0.63	1.4 3		0.2 4		1.2 6	0.0 3						0.20	15. 5	52. 5	5	35. 7	14 (3-23)
Eurytium limosum	B								0.4 7	1.4 3						0.12	9.0	61. 6	2	14. 3	26 (8-38)
Uca	B			0.49		0.1	P		1.0	P						0.10	7.3	68.	3	21.	12 (4-

pugilator						7			5								9		4	17)
Rhithropanopeus harrisii	B										1.10	0.06			0.08	5.9	74.8	2	14.3	19 (4-33)
Carcinus maenas	B	0.75	0.17	0.34	0.10										0.07	5.6	80.3	4	28.6	32 (9-48)
Sesarma reticulatum	B/H				0.29	0.10	0.46								0.07	5.6	85.9	3	21.4	21 (11-30)
Uca spp.	n/a			0.06					0.74		0.13				0.05	3.5	89.4	3	21.4	4 (1-7)
Armases cinereum	B/H						0.06	0.04	0.53	0.03					0.03	2.6	92.0	4	28.6	11 (7-17)
Panopeus herbstii	B									0.43					0.03	2.3		1	7.1	34 (24-47)
Panopeus obesus	B							0.46							0.03	1.9		1	7.1	28 (9-43)
Sesarma spp.	n/a										0.20				0.01	1.0		1	7.1	4 (3-5)
Hemigrapsus oregonensis	B												0.04		0.01	0.5		1	7.1	12 (11-13)
Armases benedicti											0.10				0.01	0.5		1	7.1	8 (4-11)
Hemigrapsus nudus													0.03		<0.01	0.4		1	7.1	25 (24-25)

Callinectes sapidus											0.06			<0.01	0.2	1	7.1	35 (n/a)
Callinectes similis										0.03				<0.01	0.2	1	7.1	69 (n/a)
Dyspanopeus sayi										0.03				<0.01	0.2	1	7.1	25 (n/a)
Hemigrapsus sanguineus	B						0.04							<0.01	0.2	1	7.1	17 (n/a)
Panopeus spp.	n/a									0.03				<0.01	0.2	1	7.1	28 (n/a)
Uca panacea	B									0.03				<0.01	0.2	1	7.1	5 (n/a)
Uca rapax	B									0.03				<0.01	0.2	1	7.1	12 (n/a)
Xanthoidea spp.	n/a									0.03				<0.01	0.2	1	7.1	4 (n/a)
Total		0.75	0.17	1.51	1.81	2.20	2.04	0.54	4.16	1.93	1.73	0.11	0.24	1.38	0.83	1.31		

FIGURE LEGENDS

(all figure uploaded separately)

Figure 1. Map of NERR sites participating in this study. Sites are coded to correspond with Table 1. Refer to Appendix S1: Table S1 for descriptive information for each site.

Figure 2. Variation in crab indicators across sites. A) catch-per-unit-effort (CPUE); the number of crabs caught in a single pitfall trap per plot across sites (no data for SFB); B) burrow density (per m^2) per plot across sites; C) species richness per plot across sites; D-F) relationship between latitude and CPUE, burrow density, and plot species richness across East Coast sites.

Figure 3. Results from LINKTREE analysis comparing linkages among sites based on crab community similarity. Species responsible for identified groups of sites are listed below.

Figure 4. Crab burrows near marsh edges at four Reserves. These images represent the high end of burrow density detected in this study; most plots were more vegetated and had fewer burrows. Upper left = NAR; upper right = CBV; lower left = ELK; lower right = GTM.

Figure 5. Summary of crab indicators across all participating NERR sites. All data are percentages of the total number of sampling plots per site and are conditionally formatted so that reds are high levels of each indicator and greens are low levels (each indicator was formatted separate from all the others; thus the color distribution for each indicator depends on its corresponding overall range of values).

Figure 6. Distributions of common crab species relative to (A) plot distance to the nearest tidal creek and (B) elevation relative to mean high water (MHW). All data are from pitfall trapping and for each species are pooled across all marshes. For each species in each plot, the dots represent 5% and 95% ranges. CARMAE=*Carcinus maenas*; PACCRA=*Pachygrapsus crassipes*; SESRET=*Sesarma reticulatum*; EURLIM=*Eurytium limosum*; UCAPUG=*Uca pugnax*; UCAMIN=*Uca minax*; UCAPUL=*Uca pugilator*; ARMCIN=*Armases cinereum*.

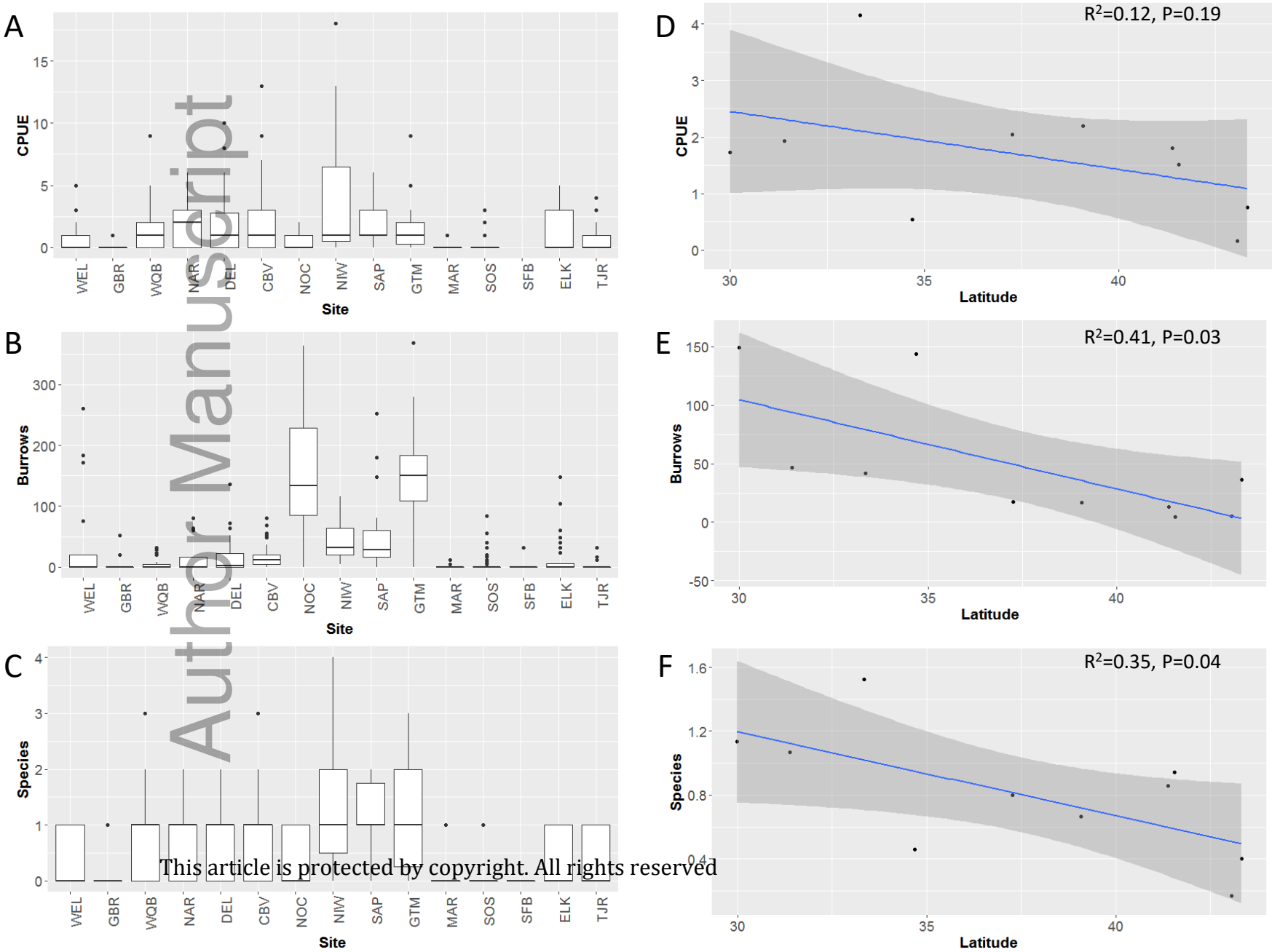
Figure 7. Relationships from generalized additive model examining factors predicting burrow density (a-c) and cpue (d-f). Y-axis is log of the smoothed response (burrow density). a,d) elevation expressed as the difference from MHW as a percentage of the tidal range at that site. b,e) creek distance is the number of meters to the nearest creek at least 1-m wide and below MLLW. c,f) soil compressibility is rated from 1-4.

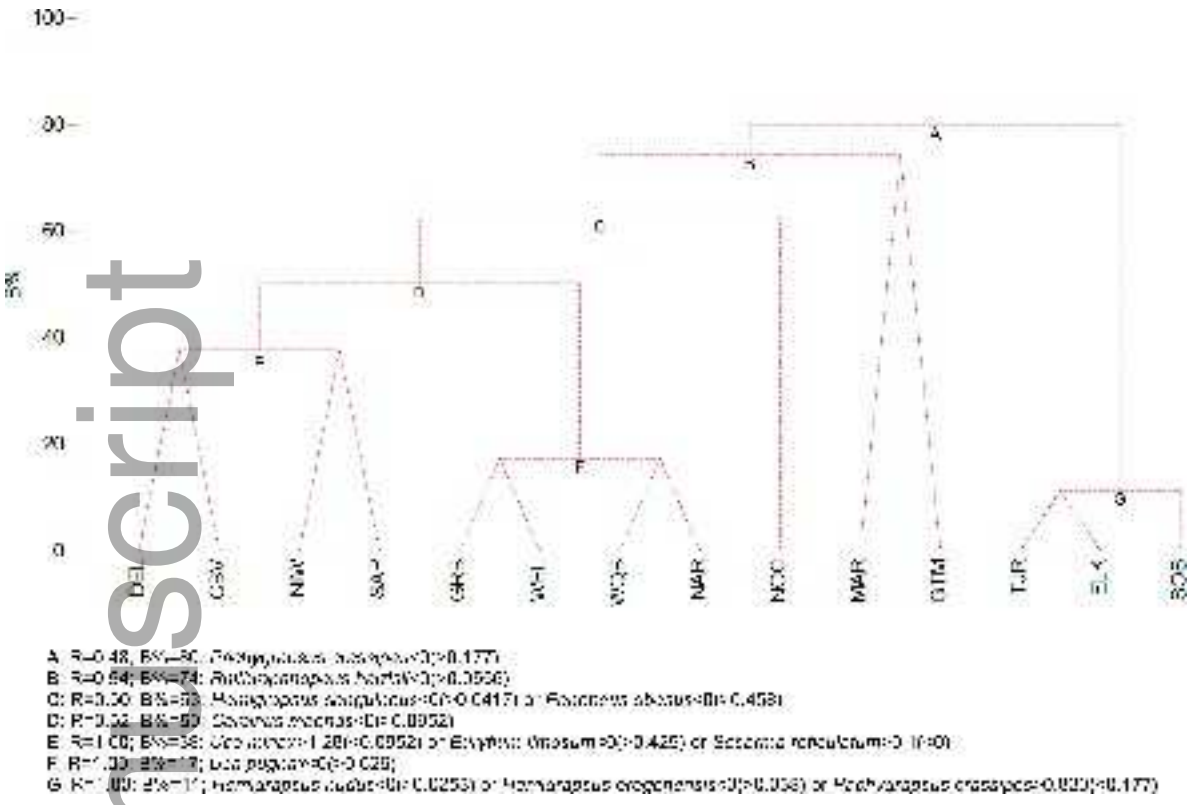
Figure 8. Relationships from generalized additive model examining factors predicting unvegetated cover. Y-axis is the log of the smoothed response (percent unvegetated cover). a) elevation expressed as the difference from MHW as a percentage of the tidal range at that site. b) creek distance is the number of meters to the nearest creek at least 1-m wide and below MLLW. c) burrow density. d) catch-per-unit-effort (number of crabs per pitfall trap). e) soil compressibility is rated from 1-4.

Figure 9. Relationship between unvegetated cover and two potential drivers across sites. Linear regressions were conducted to examine the relationship between unvegetated cover (%) and burrow density (per m2) (left) and unvegetated cover (%) and elevation (relative to MHW, as explained in Methods) (right). No elevation data were available for MAR. The colored bars show the magnitude of the coefficient of determination (adjusted R^2), red and to the left if the relationship was negative; green and to the right if the relationship was positive. Significance values are shown to the right: ***<0.001; **<0.01; *<0.05.

ecy_2813_f1.tif

Fig 2





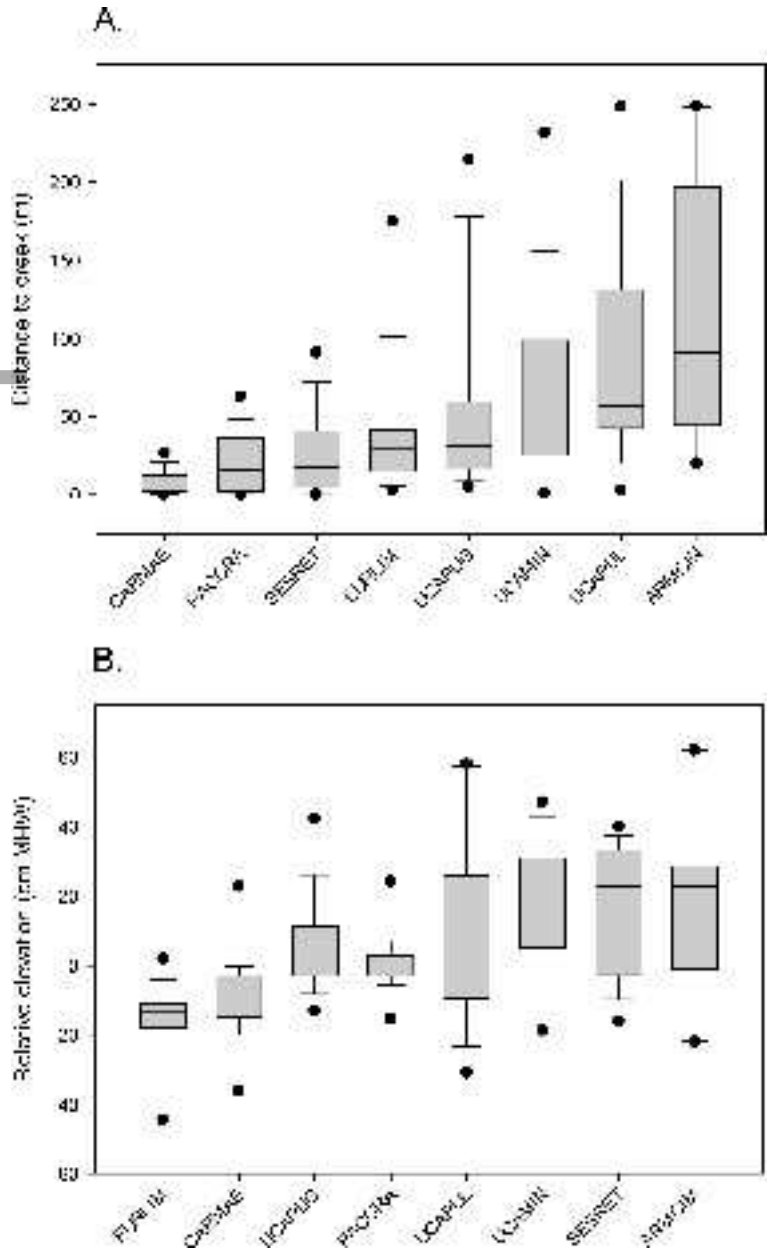
ecy_2813_f3.tif

ecy_2813_f4.pdf

Fig 4

Fig 5

Biogeographic province	**Acadian**		**Virginian**				**Carolinian**				**Louis-ianian**	**Colu m-bian**	**Californian**			***Means***		
SITE	WEL	GBR	WQB	NAR	DEL	CBV	NOC	NIW	SAP	GTM	MAR	SOS	SFB	ELK	TJR	*East*	*West*	*overall*
Total sampling plots	*20*	*18*	*47*	*21*	*30*	*50*	*24*	*19*	*30*	*30*	*18*	*79*	*26*	*40*	*24*	*29*	*42*	*32*
% with burrows	30	17	37	48	50	84	88	100	93	63	11	22	4	25	21	61	18	46
% with crabs caught	40	17	60	71	63	56	46	74	80	73	11	20	n/a	45	46	58	37	50
% with crabs seen	5	11	23	52	10	86	83	68	43	70	6	4	8	0	0	45	3	31
% with herbivory	15	0	9	10	0	18	0	0	0	0	0	3	0	0	0	5	1	4
% with any crab sign	55	28	80	90	77	98	88	100	100	100	17	35	8	50	63	82	39	66
% with bare ground	30	17	100	100	97	100	100	63	100	100	89	6	88	35	96	81	56	75



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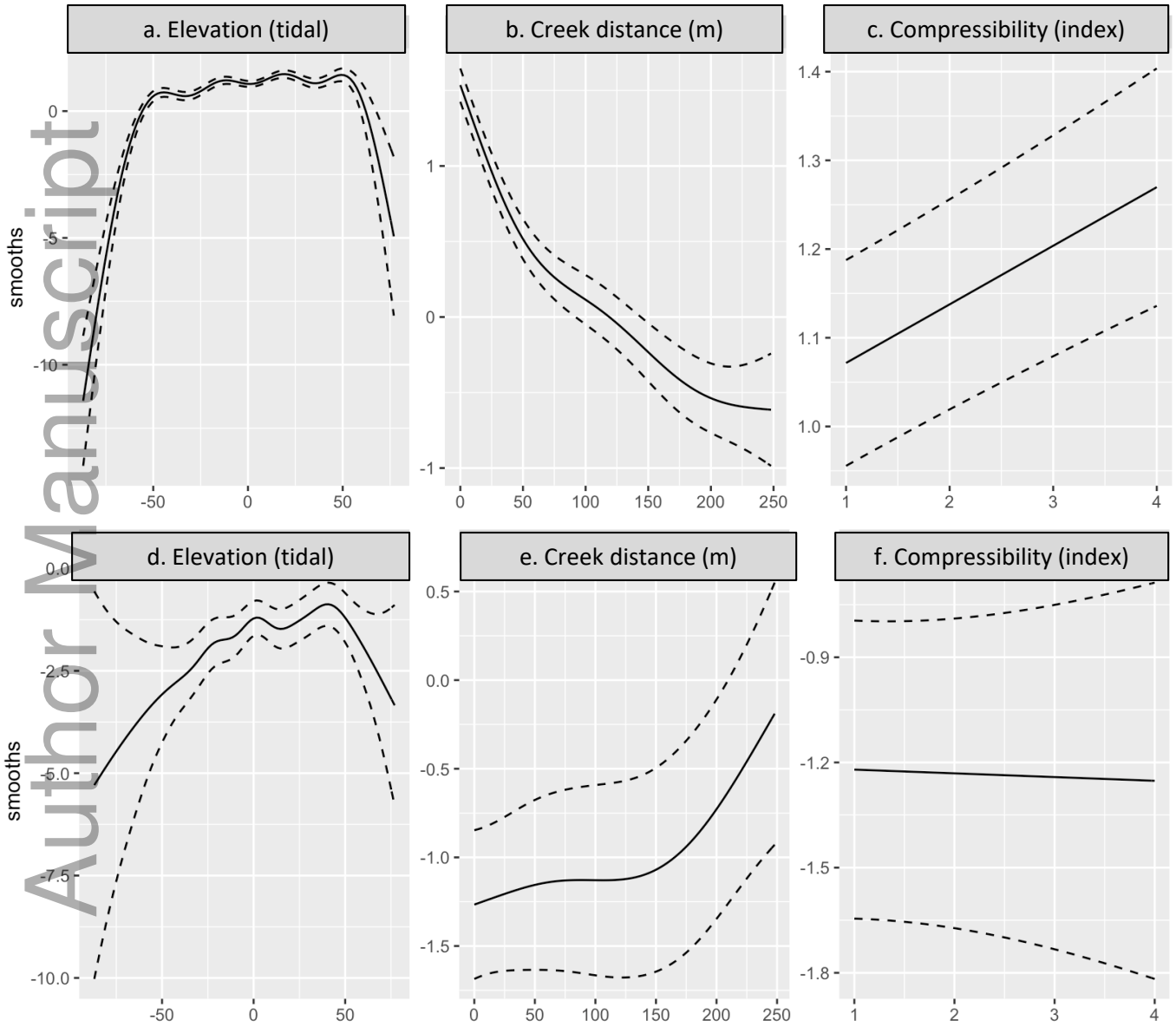

Fig 8

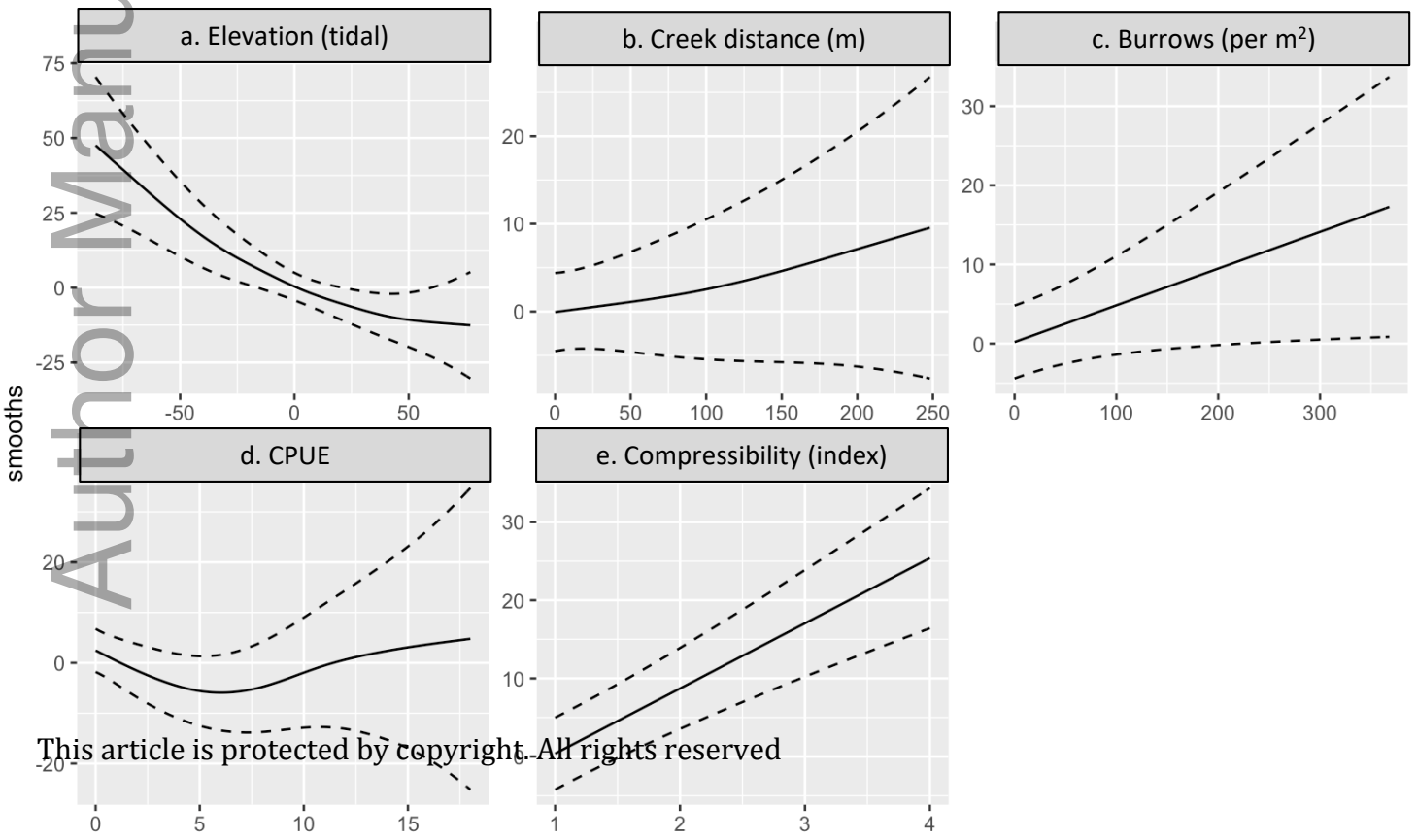

Fig 9