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1   **Latitude, temperature and habitat complexity predict predation pressure in eelgrass beds**

2   **across the Northern Hemisphere**

3

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28

29   **ABSTRACT**

30   Latitudinal gradients in species interactions are widely cited as potential causes or

31   consequences of global patterns of biodiversity. However, mechanistic studies documenting

32   changes in interactions across broad geographic ranges are limited. We surveyed predation

33   intensity on common prey (live amphipods and gastropods) in communities of eelgrass (*Zostera*

34   *marina*) at 48 sites across its Northern Hemisphere range, encompassing over 37^0 of latitude and

35   four continental coastlines. Predation on amphipods declined with latitude on all coasts but

36   declined more strongly along western ocean margins where temperature gradients are steeper.

37   Whereas *in situ* water temperature at the time of the experiments was uncorrelated with

38   predation, mean annual temperature strongly positively predicted predation, suggesting a more

39   complex mechanism than simple increased metabolic activity at the time of predation. This

40   large-scale biogeographic pattern was modified by local habitat characteristics; predation

41   declined with higher shoot density both among and within sites. Predation rates on gastropods,

42   by contrast, were uniformly low and varied little among sites. The high replication and

43   geographic extent of our study not only provides additional evidence to support biogeographic

44   variation in intensity, but also insight into the mechanisms that relate temperature and

45   biogeographic gradients in species interactions.

46   ***Key words***: biogeography, latitude, *Zostera*, seagrass, species interactions, predation,

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47   temperature, mesograzer

48   **INTRODUCTION**

49   Predation pressure is greater at lower than higher latitudes for many taxa, from fishes to

50   marine invertebrates, ants, and birds (Vermeij 1987; Schemske et al. 2009; Freestone and Osman

51   2011). Declines in the strength of predation and other interactions with latitude have been

52   implicated as either a cause or consequence of latitudinal gradients in biodiversity (Dobzhansky

53   1950). However, despite a long history of investigation, the extent to which these gradients

54   represent a monotonic decline with latitude versus a simple difference between higher and lower

55   latitudes remains unresolved because most studies rely on extreme differences between tropical

56   and extra-tropical or temperate regions (Novotny et al. 2006; Pennings et al. 2009; Freestone et

57   al. 2011). Many factors co-vary between high and low latitudes, and most studies offer relatively

58   sparse geographic coverage of intermediate latitudes (but see Harper and Peck 2016; Roslin et al.

59   2017). Thus, it can be difficult to infer the underlying causes of ecological variation correlated

60   with latitude and whether they result from discrete differences between environments versus

61   factors that change continuously with latitude.

62   While numerous processes may drive latitudinal gradients in species interactions, perhaps

63   the most fundamental is temperature, which generally declines with latitude and affects

64   metabolic rates, demography, and ecological and evolutionary processes (Sanford 2002;

65   O'Connor et al. 2011; Dell et al. 2014; Schluter 2016; Edwards et al. 2010; Manyak-Davis et al.

66   2013). While a wealth of data is available on biogeographic patterns in population abundance,

67   traits, and diversity, standardized comparisons of communities and species interactions are much

68   rarer. Geographic variation in predation strength may be an important driver of community

69   assembly and evolutionary adaptation, but testing this requires rigorous quantification of species

70   interactions across wide latitudinal gradients (Moles et. al 2016). Thus, understanding the drivers

71   of predation risk at multiple scales remains an important challenge for understanding variability

72   in the strength of biotic interactions.

73   Eelgrass (*Zostera marina*) is a key foundation species in estuaries and coastal seas across

74   the northern hemisphere (30° to 67° latitude), and thus provides a unique opportunity to test

75   latitudinal gradients in ecological processes within communities of a single habitat-forming

76   species, minimizing potential confounding factors in prior biogeographic studies. Like other

77   seagrasses, eelgrass provides many important functions and services in coastal ecosystems,

78   forming complex, productive habitats for abundant and diverse organisms (Duffy et al. 2014;

79   Cullen-Unsworth et al. 2014) as well as model systems for testing community interactions across

80   spatial scales (Nelson 1980; Virnstein et al. 1984; Orth et al. 1984; Heck and Wilson 1987; Heck

81   and Crowder 1991). Small invertebrate mesograzers are key trophic links in these communities,

82   and often act as mutualists, facilitating seagrasses via selective grazing of their algal competitors

83   (Valentine and Duffy 2006; Duffy et al. 2015). Thus, understanding and predicting global drivers

84   of top-down pressure on these epifauna may have strong implications for seagrass ecosystems.

85   To quantify and mechanistically explore variation in predation pressure on seagrass

86   epifauna with latitude, we used a comparative-experimental approach of standardized field

87   surveys and predation assays in 48 eelgrass communities across the species' range. We measured

88   predation pressure on the two major types of common seagrass-associated mesograzers

89   (amphipods and gastropods) across latitudinal gradients, and explored the potential role of local

90   and global environmental factors on predation. These taxa represent two distinct functional

91   groups (amphipods are generally more mobile and less defended than their shelled gastropod

92   counterparts), and may respond differently to predation, with consequences for the strength of

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93   top-down control (Östman et al. 2016).

94   **METHODS**

95   To assess biogeographic patterns in predation in *Zostera marina* habitats, in the summer

96   of 2014 we conducted a series of surveys and assays of epifaunal predation within 48 eelgrass

97   beds across the Northern Hemisphere (see Appendix S1). All eelgrass beds were in shallow

98   water (0 – 3 m water depth at low tide), and were typically monospecific *Zostera marina*. We

99   measured the intensity of predation on two live, locally abundant mesograzers species (1 species

100   in the Order Amphipoda, 1 shelled species in the Class Gastropoda) by tethering one individual

101   of each locally abundant species within each of twenty 1 m^2 plots per site and recording presence

102   or absence of these prey after 24 hours. We also quantified habitat structure (plant biomass,

103   shoot density, morphology), and characteristics of the epifaunal community (abundance, species

104   richness, body sizes) within each plot using standardized methods, described below. Most sites

105   were surveyed in mid-summer; exact sampling times were based on local site logistics and

106   known system dynamics to target peak productivity.

107   **Predation assays:** Locally collected live prey were tethered and deployed within each

108   experimental plot for 24 hours to quantify predation intensity. We glued individual prey to a 10

109   cm piece of monofilament (Fireline™; dia. 0.13 mm) tied to a stake (Fig. S1). One prey stake per

110   individual prey (a replicate) was deployed adjacent to a live *Zostera marina* shoot within field

111   plots. While the species tethered at each location varied (Table S1), individuals within and across

112   sites were similar in size (mean = 10.7±4.6 S.D. mm for 773 amphipods and 6.5±3.40 S.D. mm

113   for 711 gastropods measured from field deployments), were commonly found in surveys, and are

114   known to be eaten by local mesopredators. All stakes were retrieved after 24 hours and prey

115   were scored as present or absent. Partially consumed prey were considered eaten; molted prey

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116   were removed from the analysis. To test whether missing prey might result from failure of the

117   glue binding the prey to the tether, we held a subset of 5-10 prey per site in a flow-through

118   mesocosm, bucket of seawater, or predator exclusion field cage for 24 hours. Water flow did not

119   vary appreciably among sites (see Duffy et al. 2015) and no prey detached from tethers in the

120   control trials; thus all missing prey were assumed to be due to predation. Missing stakes were

121   rare and were not included in the analysis.

122   **Environmental surveys:** In conjunction with the predation assays, we also surveyed

123   characteristics of the eelgrass community and recorded *in situ* temperature and salinity

124   measurements. We quantified seagrass shoot density within each plot by counting all shoots per

125   1 m^2 plot for sites with low seagrass density (less than 50 shoots/plot), or all shoots within a

126   haphazardly placed smaller quadrat (314 cm^2) for sites with higher seagrass density. We assessed

127   seagrass biomass from two cores (20 cm diameter, 20 cm deep) per plot. Cores were cleaned of

128   sediment, separated into below-ground (root, rhizome) and above-ground (shoot, leaf) tissues,

129   and dried in an oven at 60°C until there was no change in mass. We collected a 3-cm length from

130   one healthy inner leaf from each of five randomly distributed *Zostera marina* shoots per plot and

131   processed these samples for tissue nitrogen as a proxy for site-level nutrient status

132   (Burkholder et al. 2007) using a CHN analyzer (Thermo Fisher Scientific Inc., Waltham, MA).

133   We also removed and sorted to species all macroalgae from each plot, and dried these to constant

134   weight. We collected epifauna from *Zostera marina* shoots in the center of each plot by placing a

135   fine mesh bag over the seagrass and cutting it at the sediment surface (see Reynolds et al. 2014).

136   Epifauna were preserved (in 70% ethanol or frozen), identified to species or lowest taxonomic

137   resolution, and counted. We determined size class (a proxy for body size) for all specimens using

138   a series of stacking sieves (Edgar 1990). To sample potential predators of seagrass-associated

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139   epifauna, we deployed Gee-style minnow traps for 24 hours at 13 of our study sites and

140   determined catch-per-unit-effort (CPUE, Appendix Table S1). In addition to water temperature

141   measured during field work at each site, we retrieved estimates of annual mean sea surface

142   temperature (SST) from the surrounding region provided by NASA and made available in the

143   Bio-ORACLE dataset (Tyberghein et al. 2012, 9.6 km^2 resolution, 2002-2009). We used the

144   raster package in R to extract the annual mean temperature and temperature range from all cells

145   within 10 km of each site, and averaged these estimates to generate site-level predictors.

146   **Analyses:** We tested the influence of latitude and environmental drivers on predation

147   intensity on amphipods using two sets of generalized linear models at (1) the broad site scale and

148   (2) local scale (up to 20 plots per site) in R (R Core Team 2016). Due to the consistently low

149   predation rates on gastropods (see Results), we constructed models only to predict predation on

150   amphipods, which were sufficiently abundant to tether at 42 of our sites.

151   We first modeled amphipod predation at a given site (N = 42 sites) as a matrix of total

152   successes (prey missing) and failures (prey remaining) with a quasibinomial error distribution

153   and logit link using the lme4 package. This allowed us to weight by sample size per site and to

154   address overdispersion of the data. The following models were constructed *a priori* (Table 1)

155   using site-level means of environmental variables and compared to predict predation pressure on

156   tethered prey: biogeography (latitude, ocean and ocean margin; models 1-5), abiotic environment

157   (*in situ* temperature, salinity, and leaf percent nitrogen as a proxy for site-level eutrophication;

158   model 6), temperature regime (regional mean annual water temperature and temperature range;

159   models 7-9), animal community (mobile crustacean density and median body size; model 10),

160   biodiversity (richness of total or crustacean mobile epifauna; models 11-12), and habitat

161   complexity (seagrass aboveground biomass, density and canopy height, and biomass of

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162   macroalgae; model 13). Based on findings from the hypothesis-driven model set, we then

163   constructed two composite models with shoot density and either the interaction of latitude and

164   ocean margin (model 14), or mean annual water temperature (model 15). Salinity and seagrass

165   biomass correlated strongly with latitude and moderately with mean annual temperature, and

166   were thus removed from the composite model set. We compared models using quasi Akaike

167   information criteria (qAICc) values, calculated using the bbmle package in R. A second, plot-

168   level analysis used each individual plot (N = 960) as a replicate in a hierarchical mixed model on

169   the plot-level binomial data with site as a random factor to compare the role of local community

170   and habitat characteristics on predation intensity. Data were transformed as necessary to meet

171   model assumptions. The limited predator trap sampling (Table S1) precluded the formal

172   inclusion of secondary consumers in our broader statistical analyses and correlations between

173   predation and CPUEs were evaluated separately.

174

175   **RESULTS**

176   We found a strong biogeographic signal in predation intensity on amphipods across 42

177   seagrass beds in the Northern Hemisphere, with predation declining monotonically with latitude

178   from 100% consumption at the southernmost sites to ~20% in the north (Fig. 1A). Few

179   gastropods were consumed at most sites (average of $14 \pm 16\%$ S.D. loss) relative to amphipods

180   (average of $68 \pm 35\%$ S.D. loss; Fig. 1B). Predation on amphipods did not correlate with

181   predation on gastropods (hierarchical binomial mixed model with plot nested within site, p =

182   0.232) due largely to a lack of variation in predation in gastropods among sites. Although

183   predation on amphipods declined with latitude along all four coasts, it declined more sharply

184   along western ocean basin margins (Fig. 1C), potentially reflecting steeper thermal gradients

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185   along those coasts. Indeed, mean annual water temperature best predicted predation intensity on

186   amphipods (Table 1; Fig 1D). Characteristics of the mobile epifaunal community did not predict

187   predation on amphipods, nor did ambient water temperature at the time the assays were

188   conducted (Table 1). Predation on amphipods decreased with increasing seagrass shoot density

189   (Fig. 1E), and the model that best described our data included both shoot density and mean

190   annual temperature (model 15). The across-site results were consistent with those at the plot-

191   scale where shoot density also correlated with reduced odds of predation (Table 2). Unlike many

192   of the other variables, shoot density was uncorrelated with latitude ($F_{1,40} = 2.616$, $p = 0.1136$, R^2

193    $= 0.61$). While total secondary consumer species richness was generally low, the CPUE of fishes

194   (Pearson's $r = 0.42$), but not invertebrates (Pearson's $r < 0.01$), positively correlated with

195   predation intensity on amphipods (Table S1).

196

197   **DISCUSSION**

198   Using a comparative-experimental approach within the habitat formed by a single species

199   of seagrass (*Zostera marina*) across its range, we found a strong latitudinal signal in the intensity

200   of predation on epifaunal amphipods (Fig. 1, Table 1). Latitudinal gradients in species'

201   abundances and diversity are a general and consistent pattern across many communities (e.g.,

202   Dobzhansky 1950; Pianka 1966; Hillebrand 2004). Limited data suggest that species interactions

203   increase in intensity at low compared to high latitudes, but whether this trend is a contributor to

204   the diversity gradient, a consequence of it, or simply driven by the same environmental variables

205   is poorly understood (Schemske et al. 2009). Here, we found a latitudinal signal in predation

206   intensity on a vulnerable prey type (amphipods) compared to an armored prey (gastropods) that

207   was likely driven by biogeographic variation in temperature regime and habitat structure.

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208   Predation on amphipods followed a strong latitudinal cline with high predation at low

209   latitudes on both coasts, but a sharper decline with latitude on western compared to eastern ocean

210   margins (Fig. 1C). This correlated with annual mean temperature, whereby thermal gradients are

211   generally steeper on western than eastern ocean margins due to western boundary currents,

212   which move warm tropical waters offshore as they flow poleward and deliver it to the higher

213   latitudes of eastern margins. The importance of ocean circulation and latitude-driven effects of

214   temperature is supported by our modeling results, where the strongest model predicting the

215   strength of predation included mean annual water temperature (Table 1, Fig. 1D). Although a

216   difference in the slope of the predation effect with latitude varied across continental coastlines,

217   statistical confidence in the interaction between latitude and ocean margin was marginal ($P <$

218   0.10), possibly due to non-linear relationships between latitude and temperature regime and/or

219   our comparatively more limited geographic sampling on western margins.

220   Our results suggest that temperature, or factors related to temperature, may drive

221   increased predation on seagrass epifauna. The failure of ambient water temperature at the time of

222   sampling to explain this variation suggests that the relationship is not simply a direct metabolic

223   correlate, but instead may be related to variation in plant (habitat), epifauna, or consumer

224   assemblage characteristics influenced by the long-term temperature regime. In addition to the

225   influence of regional temperature, we found that increasing shoot density decreased predation on

226   amphipods both across and within sites (Table 1, 2; Fig. 1E), likely because increasing shoot

227   density can reduce detection and capture of mobile prey by active fish and crab predators

228   (Lannin and Hovel 2011; Carroll et al. 2015; Hovel et al. 2016; but see Mattila et al. 2008).

229   Shoot density was independent of both latitude and mean annual water temperature, and thus

230   may be a useful predictor of predation intensity on amphipods at both broad (site) and fine (plot)

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231   scales. In contrast, plant biomass negatively correlated with latitude, suggesting that its greater

232   potential to serve as prey refuge in low-latitude sites was not strong enough to overcome a

233   latitudinal signal of predation pressure. Thus, a clear prediction of predation intensity at a

234   particular site requires understanding the combined influence of multiple biogeographic (latitude,

235   temperature) and local (shoot density) drivers.

236   Whereas rates of predation on amphipods were generally high and varied with latitude,

237   temperature and shoot density, predation on similarly sized gastropods was consistently very low

238   (Fig. 1B). Similarly, a meta-analysis of experiments in North Atlantic seagrass and seaweed

239   systems concluded that crustacean populations respond more strongly to predation than

240   gastropods and that cascading top-down effects are primarily mediated through crustacean

241   grazers (Östman et al. 2016). The higher predation we observed on amphipods vs. gastropods

242   may arise, in part, due to a preponderance of browsing fishes and fewer crushing crustacean

243   predators in temperate to boreal grass beds. Indeed, surveys of secondary consumer abundance at

244   13 of our sites found over 6.5 times more fish than invertebrate consumers. Additionally,

245   reduced prey value of gastropods versus amphipods, or more rapid consumption by vertebrate

246   than invertebrate predators, may mean that our standardized 24 hour deployment interval was

247   insufficient to capture variability in lower predation rates on gastropods. As a corollary,

248   temperate seagrass beds may provide sufficient refuge to gastropods as to obscure a more general

249   effect of latitudinal variation in predation found in our and other studies. However, the greater

250   abundance of crushing fish predators in the tropics may restore a latitudinal gradient in predation

251   on gastropods across a broader range of habitats (Palmer 1979).

252   In summary, we find consistent latitudinal declines in predation on a common type of

253   crustacean across four coasts and two oceans, with variation in predation closely linked to annual

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254   mean temperature. These strong global gradients in predation pressure can nevertheless be

255   modified by local habitat factors (e.g., shoot density), demonstrating that large sample sizes

256   across continuous environmental and biological variation are needed to adequately capture

257   drivers of latitudinal gradients in ecological patterns and processes. Although we avoided

258   working in degraded seagrass beds, anthropogenic stressors in these habitats (including

259   overfishing, eutrophication, and habitat destruction) are known to strongly influence ecological

260   linkages and should be accounted for when making biogeographic comparisons that inform

261   conservation and management. Because our sites are within temperate communities based on the

262   same foundation species (*Zostera marina*) and with similar food web structure (eelgrass and

263   microalgae, invertebrate mesograzers, fish and invertebrate predators), our results are less

264   influenced by the biological differences in comparisons between temperate and tropical systems.

265   Thus we suggest that the latitudinal gradient in predation is likely robust, and determined more

266   by thermally-associated community differences than metabolically influenced direct effects of

267   temperature. Whether this mechanistic connection is robust awaits intensive studies like ours,

268   conducted in a range of other systems.

269

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274

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370   **Table 1.** Comparisons of candidate quasibinomial (logit link) models estimating components of site-level variation in predation intensity on

371   amphipods across the Northern Hemisphere. Bold italicized numbers are regression coefficients for significant (black, P < 0.05; grey 0.10 > P >

372   0.05) effects of predictor variables. Coefficients are standardized for continuous variables. Based on comparing quasi Akaike information criteria

373   (qAICc) values, the composite II (Model 15) best describes the data.

	Site-Level Models	df	Pseudo R2	qAICc	delta qAICc	Weight	Latitude	Margin	Ocean	Latitude*Margin	Latitude*Ocean	In situ temperature	In situ salinity	Leaf % nitrogen	Mean annual temperature	Mean annual temperature range	Mean annual temperature*Range	Log crustacean epifauna density	Median gammarid body size	Log epifaunal richness	Crustacean richness	Log aboveground seagrass biomass	Log macroalgae biomass	Log shoot density	Log canopy height
1	Biogeography	2	0.31	85.40	10.59	0.00	***-0.73***																		
2	Biogeography	4	0.43	81.80	6.99	0.02	***-0.97***	***-1.14***	0.08																
3	Biogeography	4	0.46	79.55	4.75	0.06	***-0.88***	***-1.50***		-0.90															
4	Biogeography	5	0.46	82.24	7.43	0.02	***-0.86***	***-1.48***	0.09	-0.90															
5	Biogeography	6	0.46	85.13	10.32	0.00	***-0.86***	***-1.49***	0.09	-0.91	0.02														
6	Abiotic environment	4	0.32	89.52	14.71	0.00						0.23	***0.62***	-0.19											
7	Temperature regime	2	0.41	77.88	3.07	0.14									***0.92***										
8	Temperature regime	2	0.04	105.10	30.28	0.00										-0.27									
9	Temperature regime	4	0.45	80.34	5.52	0.04									***0.99***	-0.19	-0.29								
10	Community	3	0.02	109.01	34.19	0.00												0.20	0.00						
11	Total biodiversity	2	0.04	105.47	30.65	0.00														0.25					
12	Biodiversity	2	0.07	103.13	28.31	0.00															*0.34*				
13	Seagrass habitat	5	0.25	96.63	21.81	0.00																***0.73***	-0.09	***-0.95***	*-0.68*
14	Composite I	5	0.49	79.48	4.67	0.06	***-0.77***	***-1.41***	-1.00															*-0.31*	
15	***Composite II***	3	0.49	74.81	0.00	0.65									***0.85***									***-0.41***	

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374   **Table 2.** Hierarchical mixed binomial model of local (plot-scale) variation in predation intensity

375   on amphipods with site as a random term. (Marginal $R^2 = 0.112$, conditional $R^2 = 0.403$.) N = 42

376   sites and 809 plots.

Predictors	Coefficient	Pr (>|z|)	CI (2.5, 97.5%)
Log crustacean epifaunal density	0.203	0.271	-0.167, 0.569
Log aboveground seagrass biomass	0.284	0.072	-0.031, 0.598
Log macroalgae biomass	0.087	0.667	-0.315, 0.508
Log shoot density	-0.737	< 0.001	-1.118, -0.371
Log canopy height	-0.054	0.807	-0.487, 0.393

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377   **Figure 1.** (A) Map of field sites and predation intensity on amphipods from distributed experimental field assays at 42 sites across the

378   Northern Hemisphere with mean annual sea surface water temperature (SST). Adjacent circles represent sites in close geographic

379   proximity. Warmer colors (closer to red) indicate greater predation intensity. (B) Mean predation intensity across sites was greater on

380   amphipod compared to gastropod prey. (C) Predation on amphipods declines more steeply with latitude along western (unfilled

381   symbols) than eastern (filled symbols) ocean margins and (D) increases with annual mean water temperature. Regressions (solid lines)

382   and 95% confidence intervals (dashed line) are fit from model 15, Table 1. (E) Predation on amphipods was negatively correlated with

383   seagrass shoot density after accounting for effects of mean annual temperature.

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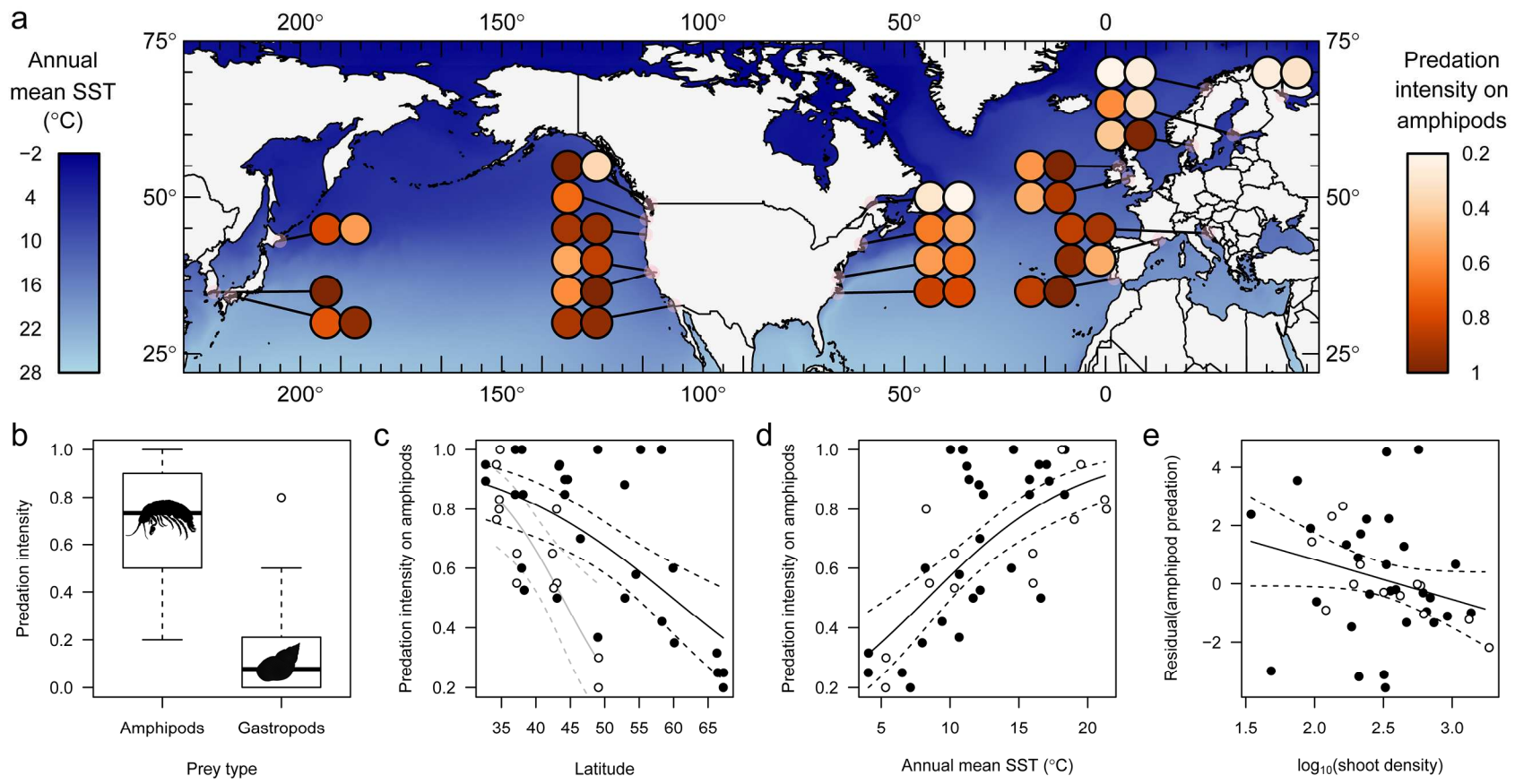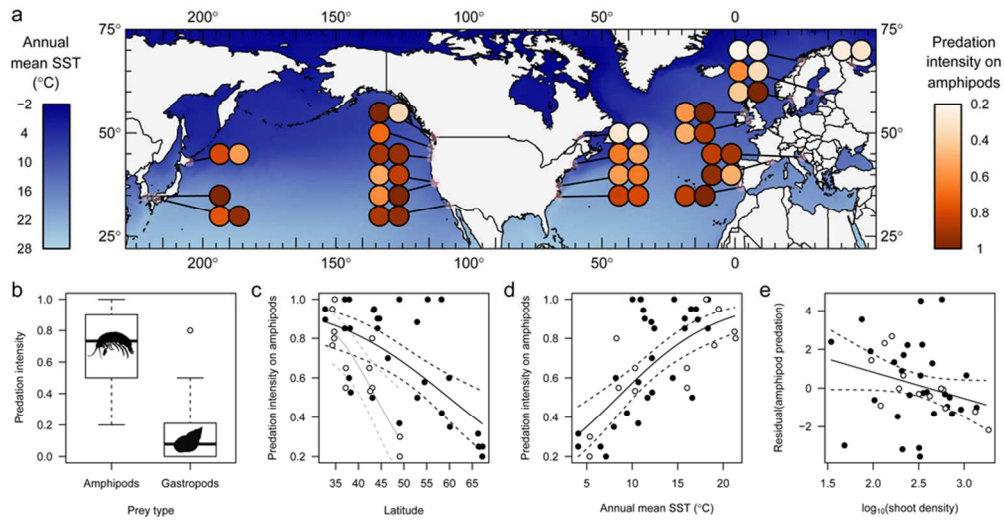
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