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Incorporating Context Dependency of Species Interactions in Species Distribution Models

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Synopsis Species distribution models typically use correlative approaches that characterize the species–environment relationship using occurrence or abundance data for a single species. However, species distributions are determined by both abiotic conditions and biotic interactions with other species in the community. Therefore, climate change is expected to impact species through direct effects on their physiology and indirect effects propagated through their resources, predators, competitors, or mutualists. Furthermore, the sign and strength of species interactions can change according to abiotic conditions, resulting in context-dependent species interactions that may change across space or with climate change. Here, we incorporated the context dependency of species interactions into a dynamic species distribution model. We developed a multi-species model that uses a time-series of observational survey data to evaluate how abiotic conditions and species interactions affect the dynamics of three rocky intertidal species. The model further distinguishes between the direct effects of abiotic conditions on abundance and the indirect effects propagated through interactions with other species. We apply the model to keystone predation by the sea star *Pisaster ochraceus* on the mussel *Mytilus californianus* and the barnacle *Balanus glandula* in the rocky intertidal zone of the Pacific coast, USA. Our method indicated that biotic interactions between *P. ochraceus* and *B. glandula* affected *B. glandula* dynamics across >1000 km of coastline. Consistent with patterns from keystone predation, the growth rate of *B. glandula* varied according to the abundance of *P. ochraceus* in the previous year. The data and the model did not indicate that the strength of keystone predation by *P. ochraceus* varied with a mean annual upwelling index. *Balanus glandula* cover increased following years with high phytoplankton abundance measured as mean annual chlorophyll-a. *M. californianus* exhibited the same pattern to a lesser degree, although this pattern was not significant. This work bridges the disciplines of biogeography and community ecology to develop tools to better understand the direct and indirect effects of abiotic conditions on ecological communities.

Introduction

Species distribution models typically use correlative approaches that characterize the species–environment relationship using occurrence or abundance data for a single species (Guisan and Zimmermann 2000). These models are often used to forecast changes in species’ geographic distributions in response to climate change (Hijmans and Graham 2006). Such forecasts inform conservation and management decisions including reserve design, assisted migration, and adaptive

management. In essence, all species distribution models project the realized niche onto geographic space (Pulliam 2000; Soberón 2007; Peterson et al. 2011). As the realized niche reflects the range of abiotic conditions and biotic interactions under which a species can persist (Hutchinson 1957), it is essential that both abiotic conditions and species interactions be incorporated into species distribution models (Guisan and Thuiller 2005; Schurr et al. 2012; Warton et al. 2015; Thorson et al. 2016).

Species interactions such as competition, predation, and facilitation can be just as important as the environment in structuring communities across scales (Connell 1961b; Paine 1966; Leibold et al. 2004; Holyoak et al. 2005; Gross 2008). For example, in marine systems, consistent spatial patterns of community structure across rocky intertidal zones arise due to the joint effects of species interactions and the environment (Connell 1961b, 1970; Paine 1966, 1984; Dayton 1971; Menge and Sutherland 1976; Lubchenco and Menge 1978). Specifically, the distribution of species is limited by predation and competition in the lower intertidal (Connell 1961b; Paine 1966) and desiccation stress in the upper intertidal (Connell 1961a). Within the zone located between the lower and upper intertidal, competition (Connell 1961a, 1970; Dayton 1971; Menge and Sutherland 1976; Paine 1984), keystone predation (Paine 1966; Dayton 1971; Menge and Sutherland 1976; Lubchenco and Menge 1978), and disturbance (Dayton 1971; Sousa 1979) dictate community structure. Positive interactions can also affect community structure by ameliorating stressful abiotic conditions (Turner 1983; Menge 1976). If an inferior competitor facilitates recruitment by a superior competitor, the resulting refuges in space permit the inferior competitor to persist (Gouhier et al. 2011).

The relative importance of competition, predation, and facilitation changes along abiotic gradients (Menge and Sutherland 1987; Bruno et al. 2003). As a result, species interactions could change in sign or magnitude along abiotic gradients, across a species' range or with climate change (Davis et al. 1998; Sanford 1999; Callaway et al. 2002; Tylianakis et al. 2008; Milazzo et al. 2013; Zarnetske et al. 2017). Furthermore, species may not exhibit the same response to abiotic conditions, and therefore climate change may have a distinct impact on each species and their interactions with the rest of the community (Gilman et al. 2010).

Here, we incorporate the context dependency of species interactions into a dynamic multi-species distribution model. We focus on how the strength of species interactions changes according to abiotic conditions for two reasons: (1) species interactions vary most along spatial and abiotic gradients (Chamberlain et al. 2014), and (2) we can use this variation to better understand the potential effects of climate change on ecological communities. We use a time series of observational survey data across a spatially extensive network of sites and a dynamic multi-species model to evaluate how abiotic conditions and species interactions affect the dynamics of three rocky intertidal species. These data and the

model are also used to distinguish between the direct effects of abiotic conditions on changes in abundance and the indirect effects propagated through interactions with other species.

A brief overview of species distribution models

A wide variety of methods have been used for species distribution modeling. At one end of the spectrum are mechanistic models, in which physiological processes such as metabolism, growth, and mortality give rise to the distribution of species (Kearney and Porter 2009). They can yield highly accurate distribution maps and allow us to understand the processes that give rise patterns of abundance (e.g., Chuine and Beaubien 2001). However, these methods can only be deployed for species whose biology and ecology have been extremely well studied. At the other end of the spectrum, machine learning techniques such as random forests and boosted regression trees can be used to model complex relationships for a wide variety of species (Cutler et al. 2007; Elith et al. 2008). Although these approaches can yield accurate predictions, they do not explicitly model the underlying ecological processes.

Statistical models can bridge the two ends of the spectrum (Dormann et al. 2012). These models describe the relationship between occurrence or abundance and covariates that quantify habitat characteristics, climate, or in some cases, the abundance of other species in the community. They quantify the species–environment relationship, and model parameters correspond to hypotheses about how environmental covariates determine distribution and abundance, albeit phenomenologically (Guisan and Zimmermann 2000; Elith and Leathwick 2009). Multivariate statistical models account for dependence among species in a community, which encompasses both species interactions and shared responses to unmeasured covariates (Kissling et al. 2012; Pollock et al. 2014).

Traditional species distribution models lack a temporal dimension that is often essential for detecting and incorporating species interactions (Wisze et al. 2013). In contrast to traditional static species distribution models, dynamic modeling approaches focus on the effect of abiotic conditions and species interactions on demographic rates (Dennis et al. 2006; Schurr et al. 2012). Therefore, they estimate the realized niche of a species (Schurr et al. 2012). In a multivariate setting, such models can also estimate pairwise species interactions from observational data

(Mutshinda et al. 2009, 2011). Model parameters correspond to the dynamic processes that determine species' niches, and structure populations and communities (Pagel and Schurr 2012). Thus, dynamic models further bridge the continuum between process-based models and traditional statistical approaches.

Incorporating the context dependency of species interactions

In the dynamic multivariate models described above, the sign and magnitude of species interactions are fixed and do not vary in space or time. However, species interactions are context dependent (Chamberlain et al. 2014). To address this limitation, we capture the spatial and temporal variability by relaxing the modeling assumption that species interaction coefficients are fixed, and instead allow the interaction coefficients to differ by location and time because the abiotic context differs. The model specifies an equation for each pairwise species interaction describing the process by which an abiotic covariate can affect the sign and magnitude of the interaction coefficient. An abiotic covariate (e.g., precipitation or temperature) can have a direct effect on population growth rate or an indirect effect propagated through interactions with other species in the community.

We modified the dynamic multivariate model described by Mutshinda et al. (2011) that contains a multi-species population dynamics kernel as well as terms describing how abiotic variables affect population growth rate. Our modification extends the Mutshinda et al. (2011) model to accommodate multiple sites, and a hierarchical process is specified to capture possible interactions that may vary based on abiotic conditions. Let $n_{i,t,s}$ denote the natural logarithm of the observed abundance for each species $i=1 \dots N$ at time t and site s . The log-abundance of species i at time t and site s is

$$n_{i,t,s} = n_{i,t-1,s} + r_i \left(1 - \sum_{j=1}^N \alpha_{i,j} n_{j,t-1,s} / k_i \right) + \beta_{i,1} X_{1,t,s} + \beta_{i,2} X_{2,t,s} + \tau_{i,t,s}$$

where r_i is the intrinsic growth rate and k_i is the natural logarithm of the carrying capacity of species i . $\alpha_{i,j}$ is the interaction coefficient quantifying the effect of species j on species i .

$X_{1,t,s}$ and $X_{2,t,s}$ represent abiotic covariates specific to time t and site s . $\beta_{i,1}$ and $\beta_{i,2}$ are species-specific coefficients describing the effect of the abiotic covariates on the growth rate of species i . The residual error $\tau_{i,t,s}$ is modeled with a multivariate normal

distribution with mean vector 0 and variance–covariance matrix Σ .

To model the context dependence of species interactions, we allow each pairwise interaction coefficient to vary by site and time and include a linear term describing how an abiotic covariate $X_{3,t,s}$ may affect the interaction strength. Therefore, $\alpha_{t,i,j,s} = b_{i,j}^0 + b_{i,j}^1 X_{3,t,s}$ for all $j \neq i$. There are $N(N-1)$ possible pairwise species interactions, and we set $\alpha_{t,i,i,s} = 1$. Each $b_{i,j}^0$ is a pairwise species interaction coefficient because the covariates are mean-centered and standardized to unit variance. Each $b_{i,j}^1$ captures the variability of the effect of species j due to the abiotic covariate $X_{3,t,s}$.

Case study: keystone predation in rocky intertidal ecosystems of the California current large marine ecosystem

Study system

The rocky intertidal ecosystem comprises an ideal case study to illustrate this model because species interactions are strong in this system (Paine 1966, 1974) and depend on the abiotic context (Menge and others 1994, 2004). Preferential predation by the sea star *Pisaster ochraceus* on the mussel *Mytilus californianus* is known to promote coexistence between *M. californianus* and subordinate competitors (e.g., Paine 1966, 1974). Experimental work has shown that the strength of keystone predation by *P. ochraceus* on *M. californianus* changes according to abiotic conditions (Menge et al. 1994; Sanford 1999). For example, in field and laboratory studies Sanford (1999) showed that during periods of upwelling that were accompanied by cooler sea surface temperatures (SSTs) individual *P. ochraceus* consumed fewer *M. californianus*, and there were fewer *P. ochraceus* present. Abiotic conditions are also known to have direct effects on *M. californianus* and their barnacle competitors. *Mytilus californianus* grew faster in the warmer, more productive areas of their distribution that experienced intermittent upwelling (Menge et al. 2008). SST, upwelling, and phytoplankton abundance (measured as chlorophyll-a concentration) are also known to affect mussels and barnacles at different spatial and temporal scales (Gouhier et al. 2010; Menge et al. 2015).

Data

To illustrate the method for incorporating the context dependency of biotic interactions into species distribution models, we focused on a three-species community module: keystone predation by *P. ochraceus* on the mussel *M. californianus* and the barnacle

Balanus glandula (Fig. 1). Data were gathered in the lower intertidal zone at 32 study sites in the California current large marine ecosystem. The study sites spanned approximately 12.5 degrees latitude (>1000 km) from Cape Flattery, WA to Point Piedras Blancas, CA (Fig. 2). Sites were surveyed annually during the summer months using a transect-quadrat method (Schoch et al. 2006; Gouhier et al.



Fig. 1 Sea stars *Pisaster ochraceus* feeding on mussels *Mytilus californianus* and gooseneck barnacles *Pollicipes polymerus* at Strawberry Hill, OR. Acorn barnacles (*Semibalanus cariosus*, *Balanus glandula*, *Chthamalus dalli*) can be seen attached to some of the mussel shells. Sea stars are ~20–30 cm in diameter.

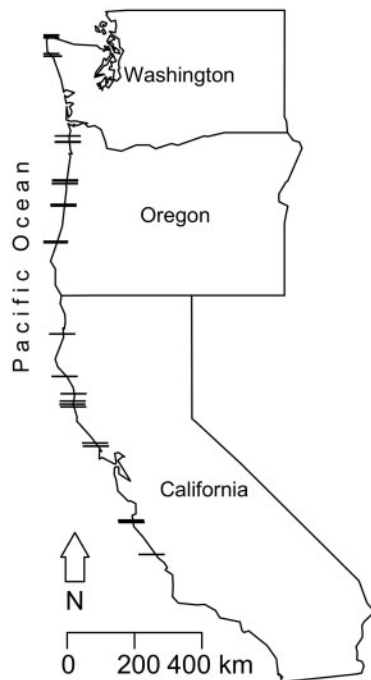


Fig. 2 Thirty-two sites located in the California current large marine ecosystem (Washington, Oregon and California, USA) were surveyed in 2000–2004.

2010) from 2000 to 2004. Counts of *P. ochraceus* and cover of *M. californianus* and *B. glandula* were recorded in 10 haphazardly placed 0.25 m² quadrats along each of three 50 m transects in the lower intertidal zone. Counts of *P. ochraceus* and % cover of *M. californianus* and *B. glandula* in each site-year were summed across all quadrats and $\ln(x+1)$ transformed prior to analysis.

Abiotic covariates were obtained for each site-year and validated as in Gouhier et al. (2010). Mean annual SST (°C) was obtained from the advanced very high resolution radiometer (National Oceanic and Atmospheric Administration), chlorophyll-a concentration (chl, mg/m³) from the sea-viewing wide field-of-view sensor (National Aeronautics and Space Administration), and upwelling index (upw, m³/s/100 m of coastline) from sea level pressure maps (Pacific Fisheries Environmental Laboratory) (Gouhier et al. 2010). Data on SST and chlorophyll-a concentration occurred within a 0.2° radius of each study site, and upwelling data occurred within a 1° radius of each site. Mean annual upwelling and mean annual SST were weakly, positively correlated ($r=0.31$), and both tended to decrease with latitude (Fig. 3). Chlorophyll-a tended to increase with latitude (Fig. 3), and was negatively correlated with both mean annual upwelling ($r=-0.33$) and mean annual SST ($r=-0.50$). Abiotic covariates were mean centered and standardized to unit variance prior to analysis.

Model

The following model captures the effects of abiotic covariates and species interactions on the dynamics of each species, as well as the way the strength of species interactions may vary with upwelling. Let $n_{i,t,s}$ denote the $\ln(x+1)$ transformed abundance for each species i at time t and site s . Here, $i=1$ for *M. californianus*, $i=2$ for *B. glandula*, and $i=3$ for *P. ochraceus*. The abundance of species i at time t and site s on a logarithmic scale is

$$n_{i,t,s} = n_{i,t-1,s} + r_i \left(1 - \sum_{j=1}^3 \alpha_{t,i,j,s} n_{j,t-1,s} / k_i \right) + \beta_{i,1} \text{sst}_{t-1,s} + \beta_{i,2} \text{chl}_{t-1,s} + \tau_{i,t,s},$$

SST ($\text{sst}_{t-1,s}$) and mean annual chlorophyll-a concentration ($\text{chl}_{t-1,s}$) in the previous year could directly affect the population growth rate of each species (Gouhier et al. 2010). The hierarchical process $\alpha_{t,i,j,s} = b_{i,j}^0 + b_{i,j}^1 \text{upw}_{t-1,s}$ for all $j \neq i$ represented species interactions. Each of the six $b_{i,j}^0$ estimate a pairwise interaction strength because the covariates

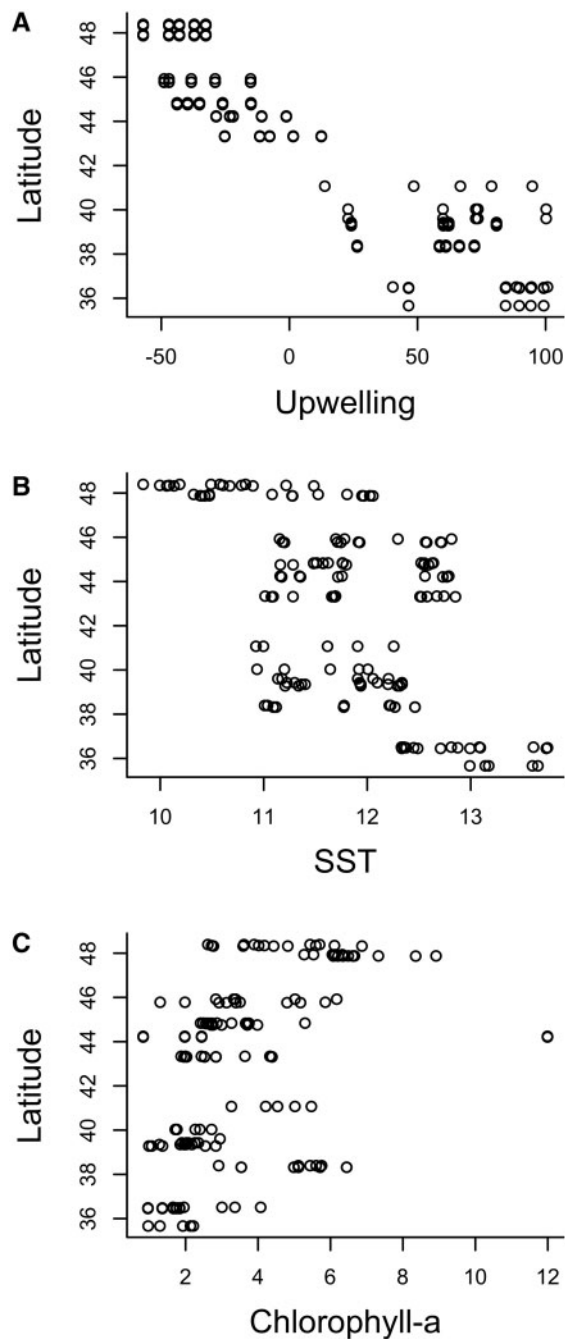


Fig. 3 Mean annual upwelling index (A, $\text{m}^3/\text{s}/100$ m of coastline), mean annual sea surface temperature (B, SST, $^{\circ}\text{C}$), and mean annual chlorophyll-a concentration (C, mg/m^3) at each of 32 rocky intertidal sites in Washington, Oregon and California, USA, overall years of study (2000–2004).

were mean-centered. Each of the six $b_{i,j}^1$ describe the slope of the linear relationship between interaction strength and mean annual upwelling, $\text{upw}_{t-1,s}$.

We obtained inference in a Bayesian framework using the statistical software JAGS (Plummer 2003) and R (R Development Core Team 2015). Vague priors were assigned as in Mutshinda et al. (2011).

We placed a Wishart prior with degrees of freedom equal to the number of species and $N \times N$ identity matrix as scale on the inverse of the covariance matrix Σ .

We assigned r_i and k_i independent normal priors $N(0,1)$ and $N(0,10)$, respectively, truncated to be positive. Each β_i was independently assigned a $N(0,100)$ prior. Each $b_{i,j}^0$ and $b_{i,j}^1$ was independently assigned a $N(0,1)$ prior. The model was run for 60,000 iterations, and the first 10,000 were discarded as burn in. Diagnostics indicated model convergence (Gelman–Rubin convergence diagnostics <1.01).

Results and discussion

Our method indicated that interactions between *P. ochraceus* and *B. glandula* affected their dynamics across the study area. The growth rate of *B. glandula* varied according to the abundance of *P. ochraceus* in the previous year. The coefficient describing this interaction ($b_{2,3}^0$) was negative (Fig. 4), which indicates that *B. glandula* increased in abundance (cover) following a year with higher *P. ochraceus* abundance due to the negative sign in Equation (2). One explanation for this pattern is that *P. ochraceus* preferentially fed on *M. californianus*, releasing *B. glandula* from competition with *M. californianus* (Paine 1966, 1974).

The model indicated that mean annual upwelling did not have a significant effect on the strength of the effect of *P. ochraceus* on *B. glandula* ($b_{2,3}^1$, Fig. 4). In fact, the mean annual upwelling index did not have a strong effect on any of the species interactions included in this model (Table 1). However, fine-scale field and laboratory studies have shown that the strength of keystone predation varies according to conditions associated with upwelling (Menge et al. 1994) and species interactions are highly context dependent in this system (Menge et al. 1994, 2004). The coarse resolution of the abiotic variables used in this study likely led to discrepancy between the remotely sensed, broad scale data, and the local conditions actually experienced by individual organisms at each site. Error in predictor variables is a common source of uncertainty in species distribution models (Stoklosa et al. 2015) and highlights the importance of gathering fine-scale data on the environmental conditions experienced by organisms. Methods for incorporating uncertainty in predictor variables interpolated from coarse resolution, gridded environmental data are discussed in Stoklosa et al. (2015). Even so, the effect of *M. californianus* on the growth rate of *B. glandula* tended to get weaker as upwelling decreased,

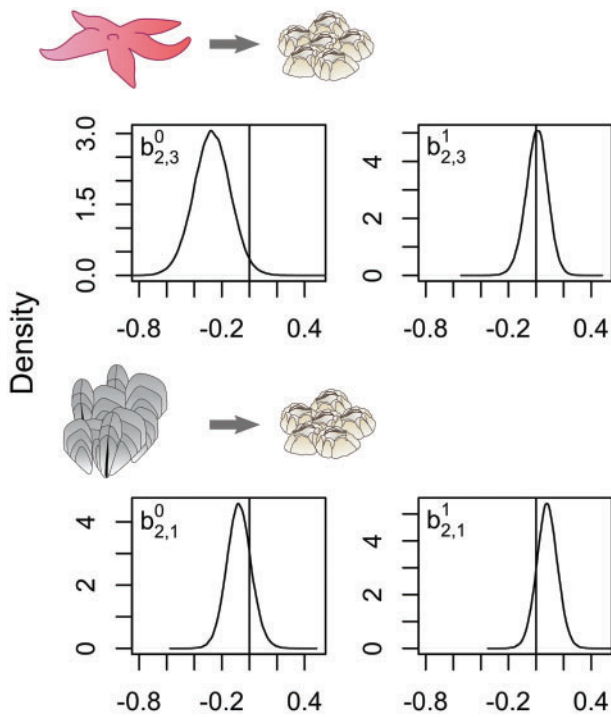


Fig. 4 Posterior distribution of coefficients describing the interaction strength between each predator–prey pair (left column) and the variability of interaction strength due to mean annual upwelling (right column). The top row shows the effect of *Pisaster ochraceus* on *Balanus glandula*, and the second row shows the effect of the *Mytilus californianus* on *Balanus glandula*. Images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

although this was not significant based on the 95% credible interval (Fig. 4, Table 1). This posterior estimate ($b_{2,1}^1$) indicates that the model can distinguish the indirect effects of upwelling on growth rate, propagated through interactions with other species in the community.

The dynamics of the filter feeding species were related to phytoplankton abundance, measured as remotely sensed chlorophyll-a. The growth rate of *B. glandula* was greater following years with high mean annual chlorophyll-a (Fig. 5). *Mytilus californianus* exhibited the same pattern to a lesser degree, although this was not significant based on the 95% credible interval (Fig. 5). However, mean annual chlorophyll-a did not have a significant effect on the growth rate of *P. ochraceus* (Fig. 5). These results align with the ecology of each species. Mean annual SST did not have a significant effect on the dynamics of any of the three species (Table 1). The posterior mean estimates and 95% credible intervals for all model parameters are given in Table 1.

The growth rates of all three species exhibited synchrony that was not explained by the processes

Table 1 Posterior mean estimates and 95% credible intervals for the model parameters in the keystone predation model

Parameter	Mean	Credible interval
<i>Abiotic covariates</i>		
$\beta_{1,1}$	0.013	(−0.211, 0.238)
$\beta_{2,1}$	−0.005	(−0.188, 0.177)
$\beta_{3,1}$	0.008	(−0.163, 0.175)
$\beta_{1,2}$	0.082	(−0.030, 0.210)
$\beta_{2,2}$	0.216	(0.115, 0.345)
$\beta_{3,2}$	−0.028	(−0.114, 0.056)
<i>Population dynamics</i>		
<i>Interaction coefficients</i>		
$b_{2,1}^0$	−0.075	(−0.249, 0.107)
$b_{3,1}^0$	0.106	(−0.348, 0.919)
$b_{1,2}^0$	0.213	(−0.549, 1.140)
$b_{3,2}^0$	−0.206	(−0.736, 0.458)
$b_{1,3}^0$	−0.030	(−0.930, 1.029)
$b_{2,3}^0$	−0.272	(−0.535, −0.012)
<i>Context dependence of interactions</i>		
$b_{2,1}^1$	−0.081	(−0.069, 0.232)
$b_{3,1}^1$	0.001	(−0.450, 0.479)
$b_{1,2}^1$	0.079	(−0.640, 0.829)
$b_{3,2}^1$	−0.004	(−0.482, 0.376)
$b_{1,3}^1$	−0.319	(−1.133, 0.518)
$b_{2,3}^1$	0.005	(−0.158, 0.158)
<i>Other</i>		
r_1	0.568	(0.136, 1.062)
r_2	1.579	(1.130, 2.024)
r_3	0.519	(0.095, 0.940)
k_1	2.789	(0.807, 5.719)
k_2	2.282	(1.684, 2.917)
k_3	2.034	(0.770, 4.537)
<i>Residual</i>		
<i>Variance</i>		
$\Sigma_{1,1}$	1.38	(1.06, 1.78)
$\Sigma_{2,2}$	0.84	(0.65, 1.09)
$\Sigma_{3,3}$	0.75	(0.57, 0.97)
<i>Covariance</i>		
$\Sigma_{1,2}$	0.21	(0.02, 0.42)
$\Sigma_{1,3}$	0.33	(0.15, 0.54)
$\Sigma_{2,3}$	0.35	(0.21, 0.53)

Notes: Species 1 is *Mytilus californianus*, species 2 is *Balanus glandula*, and species 3 is *Pisaster ochraceus*. Parameters are defined in the case study.

included in the model. Residual covariance was positive for all three species pairs (Table 1). This covariance could be caused by synchronous responses to unmeasured covariates. For example,

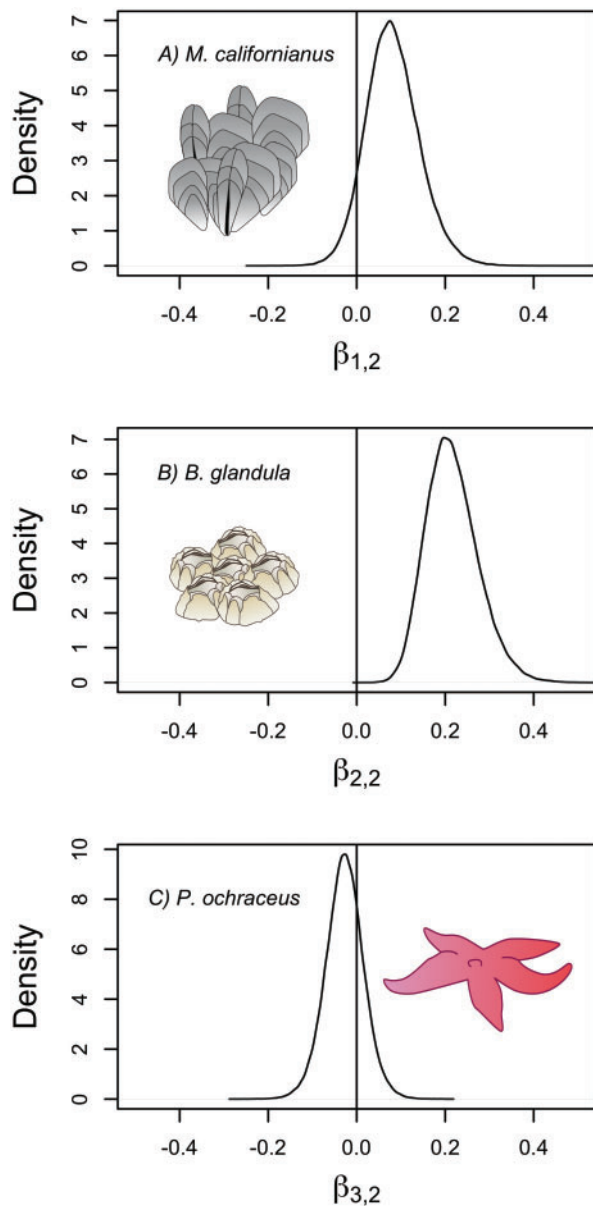


Fig. 5 Posterior distribution of coefficients describing the direct effects of mean annual chlorophyll-*a* (mg/m^3) on the growth rate of *Mytilus californianus* (A), *Balanus glandula* (B), and *Pisaster ochraceus* (C) in the lower intertidal zone at 32 sites in Washington, Oregon, and California, USA (2000–2004). Images courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

variability in abiotic conditions is not reflected in the annual averages used in this analysis, but is known to affect species dynamics (Menge et al. 2004; Menge and Menge 2013). Residual dependence between species could also arise from shared responses to habitat characteristics that were not modeled (Pollock et al. 2014). Using a multi-species modeling approach that accounts for residual dependence between species improves prediction accuracy (Clark et al. 2014).

Additionally, dispersal affects the population dynamics of *M. californianus*, and can synchronize dynamics across large spatial scales (Gouhier et al. 2010), but was not included in the model.

Conclusion

This proposed method for incorporating the context dependency of species interactions into dynamic species distribution models has several applications. It permits estimation of the way abiotic conditions affect the sign and magnitude of species interactions using a time series of abundance observations made at a spatially extensive network of sites. Abiotic covariates can affect abundance directly and indirectly via species interactions. Distinguishing the direct and indirect effects of abiotic conditions will improve understanding of the potential effects of global change on ecological communities (Gilman et al. 2010). Long-term data collected across spatial or abiotic gradients using standardized methods are essential for understanding the direct and indirect effects of global change. Coordinated inventory and monitoring programs are an important source of data. Using these methods, results from observational data gathered at broad spatial scales can complement fine-scale field and laboratory experiments. This work bridges the disciplines of community ecology and biogeography to develop tools to better understand the indirect effects of abiotic conditions, and therefore of climate change, on the distribution and abundance of organisms.

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