

A new framework to understand context dependence of two-species population dynamics: A case study of rocky intertidal sessile assembly

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Abstract

How population dynamics depend on changes in the environment is a classic but important question in ecology. We propose a new framework to understand the context dependence of the mechanism driving two-species population dynamics, in which we use intrinsic growth rates as a proxy for environmental suitability, then assess how the strengths of intra- and interspecific density dependence in a two-species system change depending on environmental suitability. By using census data for pairwise sessile species on a rocky intertidal shore, collected over 18 years, we showed that the strength of both intra- and interspecific density dependence decreased as the environmental suitability of the focal species increased, but was scarcely affected by the environmental suitability of the other species. Combining this framework with modern coexistence theory could provide a deeper understanding of coexistence mechanisms and context-dependence in two-species systems.

INTRODUCTION

Both theoretical and empirical studies have pointed out that environmental factors can regulate population dynamics (Menge & Sutherland 1987; Cantrell & Cosner 1991), thus how population dynamics depends on environmental changes has attracted extensive attention of ecologists. To answer this question, many studies have examined how population parameters, such as intrinsic growth rate and strength of density dependence, vary spatially within a single species between the center and the margins of the species' range (e.g., Fukaya et al. 2014; Nielsen et al. 2014) and at different positions along a single environmental gradient (e.g., Agrawal et al. 2004; Jenkins et al. 2008; Armas et al. 2011; Street et al. 2015). These comparative studies revealed that population parameters may be interdependent: populations with higher intrinsic growth rates tend to exhibit stronger negative density dependence (Underwood 2007). This finding suggests that increasing environmental suitability (i.e., higher intrinsic growth rate) often increases the strength of density dependence (Maguire 1973; Weber et al. 2017). Unlike at the single population level, however, the context dependence of population dynamics is harder to predict at the community level, owing to the scarcity of empirical studies on the topic and the lack of a study framework to quantify the context dependence of the dynamics of multiple species.

Similar to single population dynamics, the dynamics of multiple species can be described by mathematical population models; therefore, context dependence might be clarified by examining how population parameters of all members of a community vary depending on the environment. To investigate this question, a two-species system is the most convenient, because mathematical population models of two-species systems (e.g., species i and j) consist of the smallest possible set of population parameters: intrinsic growth rates (r_i , r_j), strengths of intraspecific density dependence (α_{ii} , α_{jj}), and strengths of interspecific density dependence (α_{ij} , α_{ji}). Although most natural communities consist of more than two species and the behavior of systems comprising

three or more species can rarely be predicted from parameters obtained from two-species systems (Levine et al. 2017; Grilli et al. 2017; Broekman et al. 2019), such concision of parameters assures several advantages, such as ease of estimating population parameters from empirical data, simplicity of hypotheses, and ease of predicting the context dependence of population parameters. Indeed, both theoretical and empirical studies using two-species systems have greatly contributed to the progress in understanding various types of species interactions (Wootton & Emmerson 2005; Chesson & Kuang 2008) and to linking modern coexistence theory (Chesson 2000, 2003, 2018; Chesson & Kuang 2008; Barabás et al. 2018) to empirical testing (Adler et al. 2018; Ellner et al. 2019).

An effective approach to understanding the context dependence of the mechanisms driving two-species population dynamics is to examine how six population parameters (r_i , r_j , α_{ii} , α_{jj} , α_{ij} , and α_{ji}) vary among localities in which a certain two species co-occur. In this context, intrinsic growth rates at a certain locality might be considered as proxies of the time-averaged environmental suitability of each species at the locality, the intrinsic growth rate is the maximum instantaneous growth rate of a population under given physical and biological conditions, it can reflect the environmental suitability of the habitat in which the species resides. Here, we propose a new framework to understand the context dependence of the mechanism driving two-species population dynamics, in which we regard intrinsic growth rates as proxies for the environmental suitability of each species, and then assess how the strengths of intra- and interspecific density dependence change among localities on a coordinate plane constituted by intrinsic growth rates of the two species obtained from many localities. This study framework will provide critical information for understanding the relationship between population dynamics and environmental suitability in a two-species system.

We applied 18-year intertidal sessile assemblage census data obtained from 33 quadrats located on 4 sites along the Pacific coast of Japan, where *Chthamalus dalli* (a barnacle) and *Gloiopeltis furcata* (a perennial red alga) are the first and second most dominant species at high shore of rocky intertidal zone (Munroe et al. 2010). Rocky intertidal sessile assemblages are ideal for studying the relationship between population dynamics and environmental suitability because they share a common resource: space (Dayton 1971). They can therefore provide insight into the general processes affecting community structure and how these vary between environments. In addition, both the amount of the shared resource (space) utilized, and the population size of all species can be measured easily, precisely, and simultaneously, as coverage (Menge 2000). Furthermore, because physical environmental stress and predation pressure vary within small spatial scales (Menge & Farrell 1989), intrinsic growth rates and strengths of intra- and interspecific density dependence will vary spatially, depending on the variation of these environmental conditions.

MATERIAL AND METHODS

Census design

We used a hierarchical sampling design (Noda 2004) to examine the context dependence of population dynamics of *C. dalli* and *G. furcata*. We performed an 18-year intertidal sessile assemblage census in the rocky intertidal zone at five sites (Sites 1–5) along the Pacific coast of eastern Hokkaido, Japan (Fig. 1). Within each site, five 4000-cm² sampling plots ($n = 25$) were established on near-vertical rock walls at semi-exposed locations. Each plot was 50 cm wide by 80 cm high, and the vertical midpoint corresponded to the mean tidal level. The vertical range of each plot was divided into four equal quadrats (upper, upper middle, lower middle, and lower). In each quadrat, 40 grid points were placed on the rock surface at 5-cm intervals in both the vertical and horizontal directions excluding the edges, and the sessile species occupying each grid point were identified at a fixed observation point and recorded. Coverage data were collected annually in summer (July or August) from 2002 to 2019.

Quadrats in which *C. dalli* and *G. furcata* were observed continuously during the census period were used for further analyses. A total of 33 quadrats at four different heights (9 upper, 14 in upper middle, 7 lower middle, and 3 lower) from 15 rocks (4 in Site 1, 4 in Site 2, 2 in Site 3, and 5 in Site 4; Fig. 1) met the above conditions. The median coverage of *C. dalli* and *G. furcata*, average coverage of other species, and total coverage of other species for all quadrats in each year during the census period were 32.5%, 15%, 0.1%, and

5% respectively (Fig. 2).

State-space modeling of population dynamics

We used a state-space model that includes a data model that represents an observational process and a process model that represents the underlying population dynamics. This approach allowed us to separate observational and process errors.

Data model. The observed data vector $Y_{t,j}$ contains the number of observed grid points for *C. dalli* ($Y_{C,t,j}$) and *G. furcata* ($Y_{G,t,j}$), and those that were bare or occupied by other species ($Y_{other,t,j}$) at quadrat j and census year t :

$$Y_{t,j} = (Y_{C,t,j}, Y_{G,t,j}, Y_{other,t,j}). \quad (1)$$

Population size (cm² coverage) of *C. dalli* and *G. furcata* and the remaining plot area, including bare area and that occupied by other species, are denoted as $N_{G,t,j}$, $N_{C,t,j}$, and $N_{other,t,j}$, respectively. Note that the sum of these terms equals the total area of each quadrat (1000 cm²). We assumed that the observed data Y follow a multinomial distribution (Multi), in which the cell probabilities are the proportional coverage of each element:

$$Y_{t,j} \sim \text{Multi}(40, N_{t,j} / 1000), \quad (2)$$

where $N_{t,j} = (N_{C,t,j}, N_{G,t,j}, N_{other,t,j})$ and the number of trials is equal to the number of grid points (40).

Process model. For a logarithmic Gompertz population model (Ives et al. 2003), a normally distributed stochastic term with variance σ^2 was applied as the population dynamics for each species in each quadrat:

$$\ln(N_{C,t,j}) \sim N(r_{C,j} + (1 - \alpha_{CC,j}) \times \ln(N_{C,t-1,j}) - \alpha_{CG,j} \times \ln(N_{G,t-1,j}), \sigma_C^2) \quad (3a)$$

$$\ln(N_{G,t,j}) \sim N(r_{G,j} + (1 - \alpha_{GG,j}) \times \ln(N_{G,t-1,j}) - \alpha_{GC,j} \times \ln(N_{C,t-1,j}), \sigma_G^2), \quad (3b)$$

where r_C and r_G represent the intrinsic growth rate of *C. dalli* and *G. furcata*, respectively. α_{CC} and α_{GG} are the strength of intraspecific density dependence for *C. dalli* and *G. furcata*, respectively; α_{CG} is the strength of interspecific density dependence of *G. furcata* on *C. dalli*, and vice versa for α_{GC} .

Parameter estimation. The Markov chain Monte Carlo (MCMC) method was used to jointly estimate all parameters in all quadrats for the census period 2002–2019, using the software JAGS through the R package *rjags* and *R2jags* (Plummer 2015) in R v3.6.2 (R Core Team 2013). We used independent and uninformative prior distributions for the parameters. Priors for σ_C and σ_G were specified as the uniform distribution (U), U(0, 100). Priors for intrinsic growth rates and strengths of density dependence were specified as the normal distribution (N), N(μ, s), where μ is the mean of the parameter that was specified as the normal distribution N(0, 0.0001) and s is the variance of the parameter that was specified as the uniform distribution U(0, 100).

We used four independent chains with 100,000 iterations each, and the first 50,000 iterations were used as burn-in iterations to ensure that the chains had converged. In addition, we thinned the chains by a factor of 10 to reduce autocorrelation in the posterior samples and to produce a reasonable amount of output. We used the Gelman and Rubin convergence diagnostics (Gelman & Rubin 1992) and visual inspection of the chains to ensure convergence. The value of \hat{R} of all parameters was between 1.001 and 1.036, indicating that the posterior distribution of all parameters in all quadrats adequately converged ($1.000 < \hat{R} < 1.050$; Gelman & Rubin 1992).

The JAGS code of the model is given in the Supporting Information.

Statistical analysis

Posterior medians were used as appropriate point estimates in the following statistical analysis. To examine how the strengths of intra- and interspecific density dependence of *C. dalli* and *G. furcata* change depending on intrinsic growth rates, the posterior median of each parameter obtained from the state-space model was used for regression analysis. We used the intrinsic growth rates of the two species as explanatory variables,

and the parameters of the four strengths of density dependence were treated as response variables. Without knowing whether the strength of density dependence changes linearly or nonlinearly with environmental suitability, we used a generalized linear model (GLM) and a generalized additive model (GAM) simultaneously and selected the optimal model based on the Akaike information criterion (AIC).

Model selection. To determine how the environmental suitability of *C. dalli* (r_{sC}) and *G. furcata* (r_{sG}) affect the strength of density dependence and whether the effect is linear or nonlinear, we started by modelling all possible covariate combinations and specifications for the relationship between strength of density dependence and environmental suitability. For each of α_{ii} , α_{jj} , α_{ij} , and α_{ji} , a total of four candidate GLMs and six candidate GAMs were defined (Table 1). Then, we screened for optimal models based on AIC.

All GLMs were fitted with the R function *lm* (R Core Team 2013), and all GAMs were fitted with the function *gam* in the R package *mgcv* v1.8 (Wood 2017) in R v3.6.2. Model selection was conducted using the R function *AIC* in R v3.6.2 (R Core Team 2013).

RESULTS

Posterior distribution of parameters

The intrinsic growth rates of *C. dalli* and *G. furcata* were approximately 4.8 and 3.8 (Fig. 3a), respectively. For both species, the strengths of intraspecific (α_{CC} and α_{GG}) and interspecific density dependence (α_{CG} and α_{GC}) were > 0 , indicating that both intra- and interspecific interactions were competitive (Fig. 3b). Furthermore, for both species, the strength of intraspecific density dependence significantly exceeded that of interspecific density dependence (i.e., $\alpha_{CC} > \alpha_{CG}$ and $\alpha_{GG} > \alpha_{GC}$, Fig. 3b).

Intraspecific density dependence

For both α_{CC} and α_{GG} , the combination GAM was optimal (Table 2). Among the α_{GG} candidate models, two had ΔAIC scores < 2 (Table 2).

For both *C. dalli* and *G. furcata*, while the strength of intraspecific density dependence decreased as their own intrinsic growth rate increased, the intrinsic growth rate of the opposite species exerted only a weak influence (Fig. 4a, b; Fig. S1, Supporting Information). For both species, the strength of intraspecific density dependence showed a similar trend in response to variations in the intrinsic growth rate. For α_{CC} , the isoline interval decreased as r_C increased (Fig. 4a), whereas for α_{GG} the isoline interval was nearly uniform and parallel (Fig. 4b).

Interspecific density dependence

According to the AIC score, the optimal models for α_{CG} and α_{GC} were the GAM parametric term (G. f) model and the GAM interaction model, respectively (Table 2). Among the α_{CG} candidate models, five had ΔAIC scores < 2 , and among the α_{GC} candidate models, one had a ΔAIC score < 2 (Table 2).

Similar to intraspecific density dependence (Fig. 4c, d; Figs. S2, S3, Supporting Information), the strength of interspecific density dependence decreased as the intrinsic growth rate of each species increased, whereas the intrinsic growth rate of the opposite species had little effect (Fig. 4c, d). However, the intrinsic growth rate of the opposite species exerted a slightly stronger effect than in the case of intraspecific density dependence (Fig. 4c, d). For α_{GC} , the isoline interval decreased as r_C increased (Fig. 4d).

DISCUSSION

We propose a new framework for analyzing the context dependence of population dynamics in a two-species system, in which we use the intrinsic growth rates of each species as a proxy for environmental suitability, and then assess how the strength of intra- and interspecific density dependence varies with environmental suitability. Our results showed that the strength of both intra- and interspecific density dependence decreased as the environmental suitability of the focal species increased, but the environmental suitability of the

opposite species had little effect. Thus, in a two-species system the strengths of intra- and interspecific density dependence are primarily dependent upon the environmental suitability of the focal species.

Here, the strength of intraspecific density dependence decreased as the intrinsic growth rate of the focal species increased, which is contrary to the results of many previous studies in which the strength of intraspecific density dependence increased as the intrinsic growth rate increased (Lillegård et al. 2008; Zehnder & Hunter 2008; Pasinelli et al. 2011; Roy et al. 2016; Gamelon et al. 2019; Koetke et al. 2020). On the other hand, a few studies have shown a negative relationship between environmental suitability and the strength of density dependence (Agrawal et al. 2004; Lines et al. 2020). Thus, the strength of intraspecific density dependence has various responses to environmental changes among different species and habitats.

Previous studies that examined how interspecific density dependence varies along an environmental gradient revealed that increasing productivity (Fowler 1982; Gurevitch 1986; Wilson & Shay 1990; DiTommaso & Aarssen 1991; Wilson & Tilman 1991; Turkington et al. 1993; Belcher et al. 1995; Kadmon 1995; Twolan-Strutt & Keddy 1996; Sammul et al. 2000, 2006; Carlyle et al. 2010; LaManna et al. 2017) and abiotic environmental stress (Bertness & Ewanchuk 2002; Wood et al. 2010; Bennett et al. 2015; LaManna et al. 2016; Calizza et al. 2017; Clark et al. 2018; Wainwright et al. 2019) can produce an increase, decrease, or no change in the sign and strength of interspecific density dependence. The inconsistent results obtained from gradient-based approaches suggest that there is no obvious general pattern in interspecific density dependence along a certain environmental gradient. There are several possible explanations for the failure to find a general pattern in interspecific density dependence along environmental gradients. First, the sign and strengths of interspecific density dependence have different responses to productivity and environmental stress among species and habitats (Kawai & Tokeshi 2007; Rees 2013; Chamberlain et al. 2014). Furthermore, the strength of interspecific density dependence may vary nonlinearly across a single environmental gradient (Bimler et al. 2018). The framework proposed here could not be affected by these limitations of the gradient-based approach, because the different environmental gradients can be integrated into environmental suitability. Indeed, here we showed that for both *C. dalli* and *G. furcata*, the strength of interspecific density dependence of each species decreases when its own environmental suitability, expressed as intrinsic growth rate, increases. Thus, by combining an environmental gradient-based approach with our framework, our knowledge of the context-dependence of species interactions will be greatly improved, especially in terms of the pattern and underlying mechanisms of spatial variation in interspecific competition and facilitation.

The negative relationship between the strengths of both intra- and interspecific density dependence and intrinsic growth rate detected for both *C. dalli* and *G. furcata* can be explained by a unique role of substrate microtopography on intraspecific competition in rocky intertidal sessile organisms (Raimondi 1990; Noda et al. 1998). Both desiccation stress and predation intensity for these organisms vary at a small spatial scale depending on the surface microtopography of their substrate. Therefore, in an unsuitable locality, where intrinsic growth rates are low, recruitment of sessile organisms is restricted to a small number of suitable sites with a specific microtopographic condition (Raimondi 1990; Noda et al. 1998).

Based on the modern coexistence theory (Chesson 2000, 2003, 2018; Chesson & Kuang 2008; Barabás et al. 2018), a necessity condition for population persistence of species *i* in a two-species system (invasion criterion)—that is, species *i* has a positive population growth rate when its own density is low and the density of the competitor species *j* is at equilibrium (Broekman et al. 2019; Grainger et al. 2019)—can be written for a Gompertz model as:

$$R_{inv,i} = r_i [1 - (r_j / r_i) \times (\alpha_{ij} / \alpha_{jj})] > 0, (4)$$

where $R_{inv,i}$, r_i , r_j , α_{jj} , and α_{ij} are invasion growth rate of species *i*, intrinsic growth rate of species *i*, intrinsic growth rate of species *j*, the strength of interspecific density dependence for species *j*, and the strength of interspecific density dependence of species *j* on species *i*, respectively (see Supporting Information for a detailed derivation). Thus, the invasion growth rate of species *i* ($R_{inv,i}$), for example, increases as increasing r_i and decreasing $(r_j / r_i) \times (\alpha_{ij} / \alpha_{jj})$. Consequently, a small difference in intrinsic growth rates between two species (i.e., a small fitness difference: r_i [?] r_j) and a low ratio of the strength

of interspecific density dependence to that of intraspecific density dependence (i.e., a large niche difference: small α_{ij}/α_{jj} and small α_{ji}/α_{ii}) favor mutual invasion (Broekman et al. 2019; Grainer et al. 2019). In the case of neutral coexistence, the intrinsic growth rates of the two species must be the same ($r_i = r_j$), and the strengths of intra- and interspecific density dependence of the two species must be the same ($\alpha_{ii} = \alpha_j = \alpha_{jj} = \alpha_{ji}$).

These theoretical rules dictating the conditions necessary for stable coexistence derived from the modern coexistence theory illuminate several features of the coexistence mechanism operating in the *C. dalli* – *G. furcata* system. First, within a wide range of environmental suitability, *C. dalli* and *G. furcata* coexisted owing to niche differences between them. This is because the strength of intraspecific density dependence for opposite species is 6- to 10-fold larger than the strength of interspecific density dependence from opposite species, regardless of variation in the intrinsic growth rates of either species (Fig. 3). Second, neutral coexistence (Hubbell 2005), often said to be important to maintaining species diversity in various assemblages (Wootton 2005), did not occur in any situation. Even if both species exhibited similar intrinsic growth rates, the strength of intraspecific density dependence for opposite species is on average 10-fold larger than the strength of interspecific density dependence from opposite species (Fig. 3). Finally, if environmental suitability decreases for the focal species *i* but increases for the opposite species *j* the chance of successful invasion of the focal species will decrease, because decreasing r_i and increasing α_{ij}/α_{jj} decreased the invasion growth rate of the focal species for both *C. dalli* and *G. furcata* (Fig. 4).

Our proposed framework has several limitations. First, this framework cannot be applied to situations in which invasion has failed in order to evaluate the causes, because it requires that both target species can be continuously observed. Second, the relationship between the strengths of intra- and interspecific density dependence and the intrinsic growth rates indicates pattern but not processes, because differences in intrinsic growth rates among localities will be multicausal phenomena, as suggested by the inconsistent relationship between strength of intraspecific density dependence and intrinsic growth rate in various studies (e.g., Agrawal et al. 2004; Lillegård et al. 2008; Zehnder & Hunter 2008; Pasinelli et al. 2011; Roy et al. 2016; Gamelon et al. 2019; Koetke et al. 2020; Lines et al. 2020). Compared with the framework proposed here, future work should focus on the integration of this framework with the environmental gradient approach, which could be helpful for interpreting the mechanism underlying the pattern between strength of intraspecific density dependence and intrinsic growth rate through decomposing the effect of each environmental component.

There is a longstanding debate among ecologists concerning how population parameters, such as intrinsic growth rate and the strength of density dependence, regulate population dynamics across a species distribution range. Many previous studies have explored the mechanisms leading to changes in population parameters and their effects on population dynamics or stable coexistence, whereas few studies have predicted the variation in population parameters. Our study demonstrates a new framework that allows the strengths of intra- and interspecific density dependence of pairs of co-occurring species to be predicted, using intrinsic growth rates of each species as a proxy for environmental suitability, in a two-species system. In the *C. dalli* – *G. furcata* system, the strength of intra- and interspecific density dependence decreased as the focal species' intrinsic growth rate increased, which is not consistent with previous results. This suggests that the strengths of density dependence have various responses to environmental changes among different species and habitats. Furthermore, combining this framework with modern coexistence theory can provide a deeper understanding of the coexistence mechanisms in a two-species system. However, our framework cannot be used to detect causes of failure of invasion or to reveal the mechanism by which the strengths of intra- and interspecific density dependence are related to intrinsic growth rates. Thus, future work could try to combine the environmental gradient-based approach with our framework to deepen our understanding of the context dependence of species interactions.

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SUPPORTING INFORMATION

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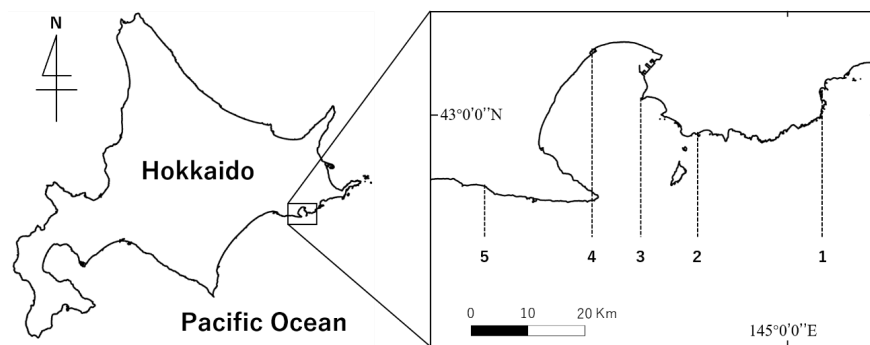


Figure 1 Study site locations. The census area was located along the Pacific coast of eastern Hokkaido, Japan. The five sites from east to west are Site 1, Site 2, Site 3, Site 4, and Site 5.

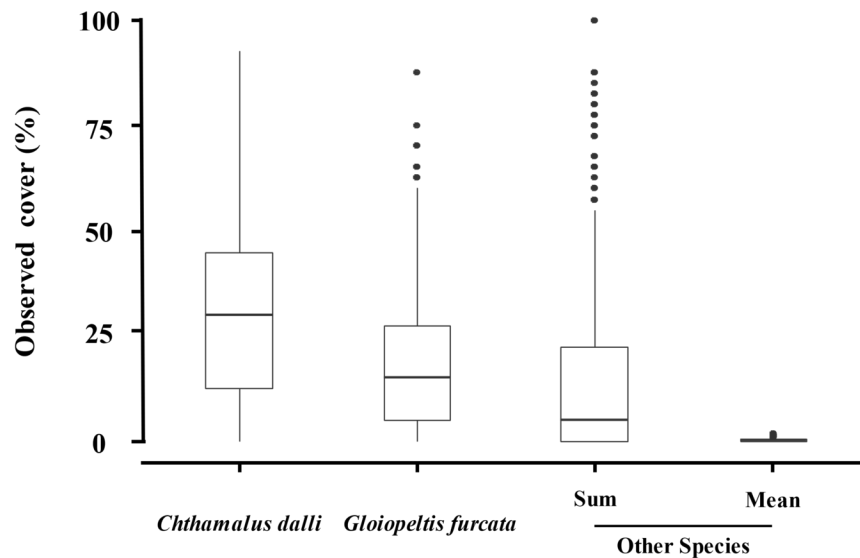


Figure 2. The observed coverage of *C. dalli* and *G. furcata*, average coverage of other species, and total coverage of other species for all quadrats in each year during the census period. Box-and-whisker plots show the median (horizontal bold line inside the box), interquartile range (box), range (whiskers), and outliers (circles). The average of other species in each plot was calculated by the total area of other species in each plot divided by the number of species observed.

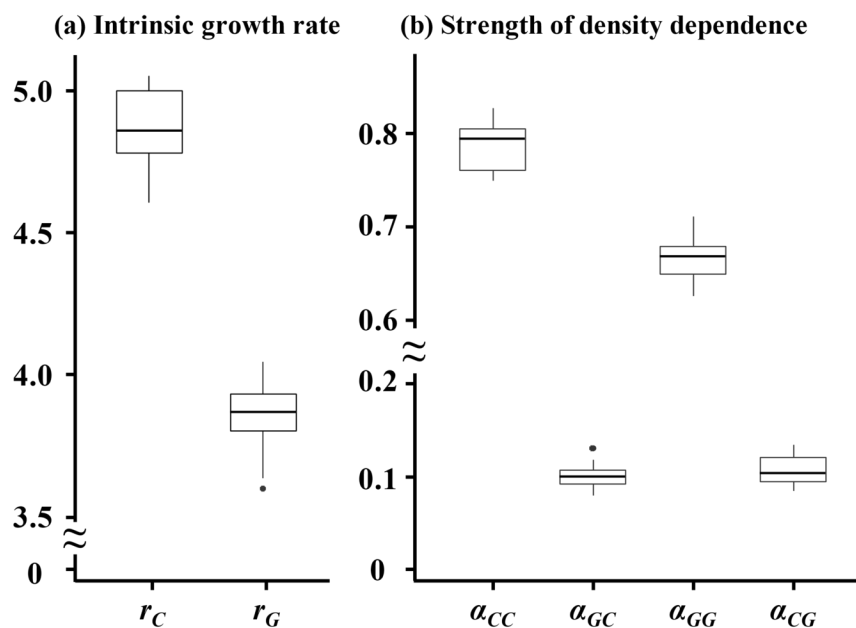


Figure 3 The posterior median of six population parameters in 33 quadrats. Box-and-whisker plots show the median (horizontal bold line inside the box), interquartile range (box), range (whiskers), and outliers (black dots). (a) Intrinsic growth rate of *Chthamalus dalli* and *Gloiopeltis furcata*. (b) The strengths of intra- and interspecific density dependence of *C. dalli* and *G. furcata*. r_C and r_G are the intrinsic growth rates of *C.*

dalli and *G. furcata*, respectively, α_{CC} and α_{GG} are the strength of intraspecific density dependence for *C. dalli* and *G. furcata*, respectively, and α_{CG} is the strength of interspecific density dependence of *G. furcata* on *C. dalli*, and vice versa for α_{GC} .

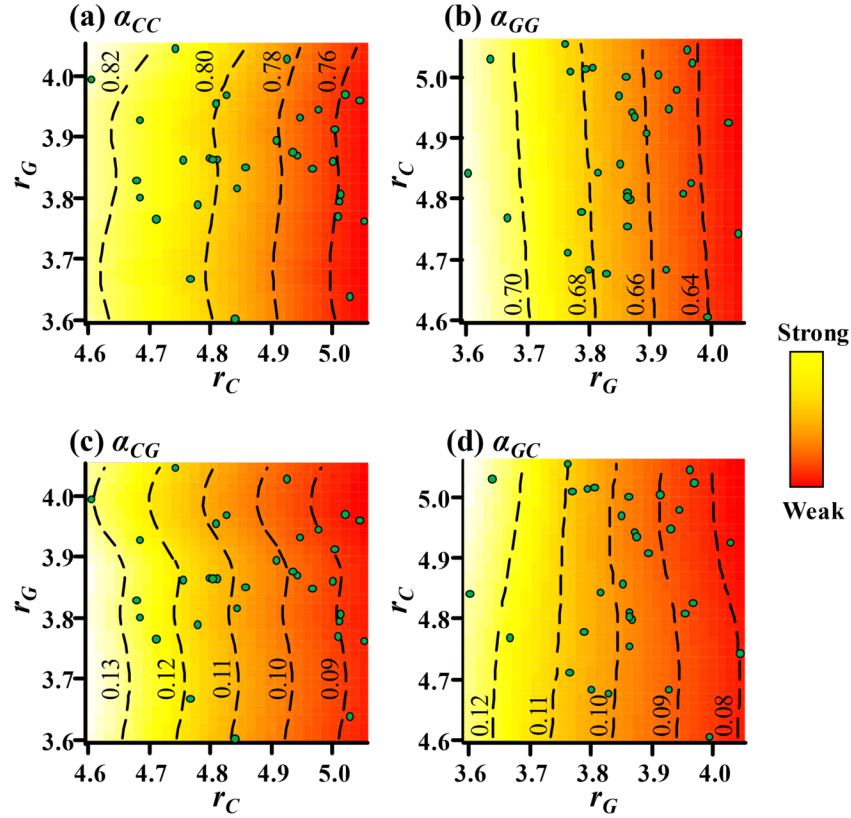


Figure 4 Predicted changes in the strengths of intra- and interspecific density dependence of *Chthamalus dalli* and *Gloiopeltis furcata* depending on intrinsic growth rates. (a) Strength of intraspecific density dependence of *C. dalli* (α_{CC}). (b) Strength of intraspecific density dependence of *G. furcata* (α_{GG}). (c) Strength of interspecific density dependence of *C. dalli* on *G. furcata* (α_{CG}). (d) Strength of interspecific density dependence of *G. furcata* on *C. dalli* (α_{GC}). In (a) and (c), the x-axis is the intrinsic growth rate of *C. dalli* and the y-axis is the intrinsic growth rate of *G. furcata*; the axes in (b) and (d) are opposite. Yellow represents strong and red represents weak intra- or interspecific density dependence. The dashed lines in the figure show contours of the strength of density dependence. Green dots indicate the environmental suitability of each locality.

Table 1 Candidate models for each strength of intra- and interspecific density dependence. r_C and r_G are the intrinsic growth rates of *Chthamalus dalli* and *Gloiopeltis furcata*, respectively. Variables given as a function $f(X)$ are spline functions; others are linear variables. Interactions marked with \times include all main effects. Each model specification was used to model all parameters of the strength of intra- and interspecific density dependence.

Type	Model specification	Model specification
	GLM	GAM
Interaction	$r_C \times r_G$	$f(r_C) \times f(r_G)$

Type	Model specification	Model specification
Combination	$r_C + r_G$	$f(r_C) + f(r_G)$
Single variable (C, d)	r_C	$f(r_C)$
Single variable (G, f)	r_G	$f(r_G)$
Parametric term (C, d)		$f(r_C) + r_G$
Parametric term (G, f)		$f(r_G) + r_C$

Table 2 AIC scores of candidate models. The model with the lowest score was chosen as the optimal model (bold). Models with $\Delta\text{AIC} < 2$ are shown in italics.

Model specification	AIC	AIC	AIC	AIC
	α_{nn}	α_{r}	α_{rr}	α_{r^*}
$r_C \times r_G$	-247.7315	<i>-255.7227</i>	-253.8088	<i>-324.3108</i>
$r_C + r_G$	-249.7105	<i>-256.8372</i>	-255.6200	-304.9885
r_C	-250.0084	<i>-255.7227</i>	-155.6726	-193.0939
r_G	-149.7584	-178.4914	-255.4406	-305.4089
$f(r_C) \times f(r_G)$	-263.5615	<i>-256.8372</i>	-257.5495	-325.2908
$f(r_C) + f(r_G)$	-269.1716	<i>-257.1918</i>	-259.8575	-305.3658
$f(r_C)$	-263.9614	-255.1532	-155.8247	-193.0466
$f(r_G)$	-149.7584	-178.4914	<i>-258.8420</i>	-305.8951
$f(r_C) + r_G$	-266.2992	<i>-256.8372</i>	-255.6200	-304.9885
$f(r_G) + r_C$	-251.8580	-257.2078	<i>-259.8519</i>	-305.3564