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Estimating partial regulation in spatio-temporal models of community dynamics

Running title: Spatio-temporal species interactions

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Abstract

Niche-based approaches to community analysis often involve estimating a matrix of pairwise interactions among species (the "community matrix"), but this task becomes infeasible using observational data as the number of modeled species increases. As an alternative, neutral theories achieve parsimony by assuming that species within a trophic level are exchangeable, but generally cannot incorporate stabilizing interactions even when they are evident in field data. Finally, both regulated (niche) and unregulated (neutral) approaches have rarely been

fitted directly to survey data using spatio-temporal statistical methods. We therefore propose a spatio-temporal and model-based approach to estimate community dynamics that are partially regulated. Specifically, we start with a neutral spatio-temporal model where all species follow ecological drift, which precludes estimating pairwise interactions. We then add regulatory relations until model selection favors stopping, where the "rank" of the interaction matrix may range from zero to the number of species. A simulation experiment shows that model selection can accurately identify the rank of the interaction matrix, and that the identified spatio-temporal model can estimate the magnitude of species interactions. A forty-year case study for the Gulf of St. Lawrence marine community shows that recovering grey seals have an unregulated and negative relation with demersal fishes. We therefore conclude that partial regulation is a plausible approximation to community dynamics using field data, and hypothesize that estimating partial regulation will be expedient in future analyses of spatio-temporal community dynamics given limited field data. We conclude by recommending ongoing research to add explicit models for movement, so that meta-community theory can be confronted with data in a spatio-temporal statistical framework.
Keywords: neutral theory; community regulation; spatio-temporal model; Gulf of St. Lawrence; community matrix

Introduction

For at least 50 years, ecologists have conducted research on niche theory, which postulates that each species within a community occupies a unique ecological niche and that pairwise interactions arise from overlap in niche (Hutchinson 1957). Niche theory has encouraged ongoing research to measure the per-capita impact of one species on another for all pairs of species in a community or guild. In sharp contrast, several authors have introduced 'neutral theories' of ecology (Hubbell 2001, Harte 2011) in which species are viewed as exchangeable within a given trophic level or guild. Despite their clear differences, there is considerable empirical support for both niche and neutral theory. As with most binary distinctions in ecology (top-down v. bottom up, ratio-dependent v. prey-dependent, etc.), each theory may generate accurate and useful predictions of community dynamics for a particular temporal, spatial, taxonomic, and trophic scale. However, ecologists currently have few quantitative tools for combining insights from niche and neutral theories.

Inferring pairwise interactions remains one of the primary research goals in theoretical and applied ecology. However, species interactions are difficult to measure because the strength and sign of pairwise interactions depend on many circumstances, including (but not

limited to): the presence of additional species (Hixon and Carr 1997); environmental conditions (Morris 2003); and recent evolutionary history (Stegen et al. 2012). Manipulative experiments in micro- and mesocosms remain the gold-standard for inferring species interactions, but an increase in the number of species results in a factorial increase in the number of experimental treatments that must be conducted (Wootton and Emmerson 2005). Given these logistical difficulties, researchers have proposed two largely-independent approaches for predicting community dynamics: linear approximations using time series statistics, and neutral theories involving ecological drift.

Linear time-series approximations to community dynamics typically involve estimating the community matrix, defined as the matrix of impacts from increasing the abundance of one species on the per-capita productivity of every other species. The community matrix can be efficiently estimated using a multispecies extension of the Gompertz model for density dependence (Ives et al. 2003). Conveniently, this model also permits estimating the covariance of unexplained variation (termed "process errors" in the following). The estimated community matrix in this case represents a first-order Taylor series approximation to regulatory interactions, and Pfister (1995) gives support that this approach will estimate interactions with a sign and strength that matches manipulative experiments. Once the community matrix and process error covariance are estimated, results can be processed to yield a plethora of potential indicators of community stability, e.g., resilience or reactivity (Ives 1995, Neubert and Caswell 1997). Deyle et al. (2016) extend this framework to permit estimates of context-dependent species interactions but do not explicitly address the neutral-to-niche continuum.

By contrast, neutral theories typically postulate that all species (MacArthur and Wilson 1967) or individuals (Hubbell 2001) have identical characteristics. Given this assumption, changes in broad-scale community patterns can then be explained via ecological drift, i.e., the random replacement of individuals or species within a local pool. This approach avoids estimating interactions for different species (because all species/individuals have identical interactions), and remaining parameters (fundamental biodiversity and immigration numbers) can be estimated from the species-abundance distribution (Etienne and Alonso 2005). Once parameters are estimated, species turn-over rates and species-abundance curves can be projected forward and backwards in time.

Both time-series and neutral theories for community structure and dynamics would benefit from including spatial variation explicitly. For example, Thorson et al. (2014) demonstrate that estimates of density dependence in time-series population models will be

biased whenever density varies spatially and density dependence acts locally, and that including spatial variation also improves precision by using spatial replication to increase statistical efficiency. A spatial analogue of time-series models for community dynamics may therefore result in improved accuracy and precision for predicting pairwise interactions and community stability. Spatial variation also underlies many important mechanisms for community stability (Chesson 2000), such that the estimate of spatio-temporal variation in productivity is useful in its own right. Similarly, neutral theories have generally included space explicitly, e.g., by including the density of individuals (Hubbell 2001) or energy (Harte 2011) as model elements. However, research has underlined the importance of spatial variation in environmental conditions (Gilbert and Lechowicz 2004, Gilbert et al. 2006) or spatio-temporal variation in habitat suitability (Dornelas et al. 2006) to predictions arising from neutral theory. We therefore hypothesize that estimating spatial and spatio-temporal variation in productivity within neutral theory will in some cases improve estimates of community dynamics.

We therefore develop a spatio-temporal approach to estimating community dynamics, where data can be used to discriminate between neutral or highly regulated dynamics. In particular, we focus on determining the number of regulatory relations that are identifiable from a given community data set. To do so, we propose a new approach, which proceeds from the null hypothesis that all species follow identical, unregulated ecological drift (neutral dynamics) and successively adds axes of regulation until adding an additional regulatory relation is not parsimonious. This approach provides a continuum between estimating 0 and P^2 parameters for density dependence (approximating neutral and fully-regulated dynamics, respectively, where P is the number of species), and estimating fewer than P^2 parameters is accomplished without zeroing out any single pairwise interaction. We then demonstrate the approach using a simulation experiment and a case study involving growth of grey seals impacting the fish community in the Gulf of St. Lawrence. Using these examples, we show that we can identify "partial regulation" (a combination of neutral and regulated components) in artificial and real-world data sets while accounting for spatio-temporal variation in productivity and density. By potentially estimating few than P^2 parameters for the species interactions, we also hypothesize that our spatio-temporal approach will be computationally feasible for large communities.

Methods

Time series models for the dynamics of natural communities typically involve a nonlinear function for growth of each population:

$$\mathbf{n}_{t+1} = f(\mathbf{n}_t) \circ \exp(\boldsymbol{\varepsilon}_{t+1}) \quad (1)$$

where $\mathbf{n}_t$ is a vector of abundances for each of P species in time t (i.e. $\mathbf{n}_t = \{n_{1,t}, n_{2,t}, \ldots, n_{P,t}\}^{\mathrm{T}}$), $f(\mathbf{n}_t)$ is a potentially nonlinear, vector-valued function representing inter- and intra-specific interactions for all species in the community, and we use $\circ$ to indicate the Hadamard (elementwise) product of two vectors. $\boldsymbol{\varepsilon}_t$ is a vector of random effects that approximates unmodeled variation in community dynamics, including time-dependence in f (which is assumed to be fixed in Eq. 1). Process errors are generally assumed to follow some exchangeable process, e.g.:

$$\boldsymbol{\varepsilon}_t \sim \mathrm{MVN}(\mathbf{0}, \boldsymbol{\Sigma}_{\mathrm{process}}) \quad (2)$$

where $\boldsymbol{\Sigma}_{\mathrm{process}}$ is the covariance of process errors. We take the first-order Taylor's series expansion of $\mathbf{x}_t \equiv \ln(\mathbf{n}_t)$ around $\bar{\mathbf{x}}_t$, defined as the average observed value for $\ln(\mathbf{n}_t)$ during an interval $T_{min} \leq t \leq T_{max}$. This results in a linear approximation to dynamics:

$$\mathbf{x}_{t+1} = \boldsymbol{\alpha} + \mathbf{C}\mathbf{x}_t + \boldsymbol{\varepsilon}_{t+1} \quad (3)$$

where $\mathbf{C}$ is a simple transformation of the community matrix such that a 1% increase in species j results in a $c_{i,j}$% increase in productivity for species i (in other words: $c_{i,j} = \frac{\partial}{\partial \ln[n_j]} \ln[f(n_i)]$), average productivity is:

$$\boldsymbol{\alpha} = \ln[f(e^{\bar{\mathbf{x}}})] - \mathbf{C}\bar{\mathbf{x}} \quad (4)$$

and process errors $\boldsymbol{\varepsilon}_t$ now accounts for both time-dependence in $\mathbf{C}$ and $\boldsymbol{\alpha}$, as well as second- and higher-order components of the Taylor-series approximation.

Using this approximation, community dynamics are stable as long as the modulus of all eigenvalues of $\mathbf{C}$ are between -1 and 1. In this case, community equilibrium is:

$$\mathbf{x}^* = (\mathbf{I} - \mathbf{C})^{-1}\boldsymbol{\alpha} \quad (5)$$

and it is relatively easy to calculate metrics of community stability including (1) the variance around this equilibrium or (2) the reactivity of the stationary distribution (i.e., the ratio of the expected distance from community state $\mathbf{x}$ to equilibrium $\mathbf{x}^*$, given that $\mathbf{x}$ is drawn from its stationary distribution).

There are three potential problems with this formulation for community dynamics:

1. *Partial regulation*: Equilibrium properties of this model (Eq. 5) have previously been derived only for the case of stable dynamics, i.e., when the eigenvalues of $\mathbf{C}$ are inside the unit circle. However, many reasonable ecological models contain non-hyperbolic equilibria (for which the modulus of the dominant eigenvalue is equal to 1). In this case,

there is one or more axis that cannot be distinguished from following a random-walk process in log-densities.

2. *Veil of uncertainty*: Following the argument in Strong (1986), we suspect that many communities have regulation that is only distinguishable sporadically and for long time series (i.e., due to densities reaching extreme values, or due to density-dependent responses to infrequent environmental conditions). In these cases, many real-world data sets will not have any appearance of (or information about) the form of regulation that has permitted the community to persist long enough to generate the observed diversity of species. In these cases, we believe that it is pragmatic to begin with the assumption of no regulation (i.e., $\mathbf{C} = \mathbf{I}$), and then identify axes of regulation until there is no further information to identify regulation. This process may result in a stable community matrix (i.e., $\mathbf{C} - \mathbf{I}$ having rank P), but may also result in an estimate of the community matrix with neutral stability.
3. *Curse of dimensionality*: The number of parameters in the community matrix $\mathbf{C}$ increases as P^2. However, adding subsequent species to a community dynamics analysis often results in adding species with fewer and fewer observations. We therefore seek an approximation to $\mathbf{C}$ that might have fewer parameters than P^2, but where model-selection tools can be used to identify the degree of dimension-reduction, and where model selection can potentially result in the unrestricted $\mathbf{C}$ (with P^2 degrees of freedom) being identified as parsimonious.

For these three different but interrelated reasons, we propose a procedure for estimating partial regulation in natural communities.

Partial regulation, and its connection to neutral dynamics

In the following, we develop a new parameterization for the community matrix. We begin with a re-parameterization of our linear approximation (Eq. 3):

$$\Delta\mathbf{x}_{t+1} = \boldsymbol{\alpha} + \mathbf{B}\mathbf{x}_t + \boldsymbol{\varepsilon}_{t+1} \quad (6)$$

such that $\mathbf{B} = \mathbf{C} - \mathbf{I}$, where abundance $\mathbf{x}_{t=1}$ in the first year is estimated for each species. In particular, we seek a form of $\mathbf{B}$ where one or more linear combinations of log-density for each species follows ecological drift (i.e., $\mathbf{B}$ has one or more eigenvalues equal to zero), and where the rank R of $\mathbf{B}$ ($0 \leq R \leq P$) contains information regarding the mix of neutral and regulated components to community dynamics. Specifically, a rank R for the interactions matrix $\mathbf{B}$ implies that $P - R$ linear combinations of log-density follow ecological drift. Given that $\mathbf{B}$ has rank R, then $\mathbf{B}$ has at most $P^2 - (P - R)^2$ degrees of freedom. In particular, we

use a parameterization such that parameters $\boldsymbol{\theta}$ can be uniquely mapped onto $\mathbf{B}$ (i.e., $g(\boldsymbol{\theta}) \mapsto \mathbf{B}$, where g is a differentiable function), and where we can place bounds on the non-zero eigenvalues. Appendix S1 proposes two functions for this task, where method #1 restricts $\mathbf{B}$ to have real-valued eigenvalues while method #2 allows both real and complex eigenvalues. However, exploratory analysis shows that restricting $\mathbf{B}$ to have real-valued eigenvalues is more numerically stable for parameter estimation, so we use this version for subsequent case-study and simulation examples. Importantly, both methods allow the model to bridge between 0 and P^2 parameters for density dependence, and both methods allow estimation of non-zero interactions for all pairs of species even when $R < P$ (i.e., $b_{p,p^*} \neq 0$ for all species p and p^* even when estimating fewer than P^2 density-dependence parameters)

Having defined this model, we note that the case of $R = 0$ results in $\mathbf{B} = \mathbf{0}$, such that $\Delta\mathbf{x}_{t+1} = \boldsymbol{\alpha} + \boldsymbol{\varepsilon}_{t+1}$. In this case, log-density for each species follows a random-walk process with drift $\boldsymbol{\alpha}$, i.e., geometric growth rate for each species is normally distributed with mean $\boldsymbol{\alpha}$ and covariance $\boldsymbol{\Sigma}_{\text{process}}$. Random-walk dynamics represent a process where each population follows an exponential increases or decay on average but has stochastic variation around this level (termed "ecological drift"). Although this definition allows species-specific growth rates, we recover the standard definition of neutrality (e.g., as defined by Hubbell (2001)) if α_p is identical for all species. When $\boldsymbol{\alpha} = \mathbf{0}$ for each species, then the community follows ecological drift starting from initial abundance $\mathbf{x}_{t=1}$.

We hypothesize that ecological drift (i.e., $R = 0$) is a reasonable approximation to community dynamics over short time periods, where $\boldsymbol{\alpha}$ governs whether abundance for each individual species is expected to increase or decrease over short periods. However, long-term dynamics of this model are not biologically realistic when $\mathbf{B} = \mathbf{0}$ and $\boldsymbol{\alpha} = \mathbf{0}$ because, in the limit as time goes to infinity, the expected population size for each species will go to infinity. This occurs because each species follows a random-walk process in log-space, such that extinction is impossible and the variance in log-space goes to infinity. When specifying neutral dynamics, the model can be estimated with as few as one freely-estimated parameter ($\boldsymbol{\Sigma}_{\text{process}} = \sigma^2\mathbf{I}$). Longer term dynamics can also be stabilized by deriving a value of $\boldsymbol{\alpha} < \mathbf{0}$ that results in finite asymptotic population sizes given the magnitude of process error. Presumably such a model could be parameterized to generate lognormal species-abundance curves, following a calculation similar to Engen and Lande (1996), although we do not pursue the idea here.

Spatio-temporal community dynamics

Previous research suggests that spatio-temporal models can provide more accurate and precise estimates of single-species density dependence (Thorson et al. 2014). We therefore estimate parameters using a spatio-temporal version of the community-dynamics model. This involves replacing all scalar-valued variables with vectors representing density at each of *S* sites within a 2-dimensional spatial domain (Cressie and Wikle 2011). We specifically replace the vector of log-abundance $\mathbf{x}_t$ for each species in year *t* with a matrix $\mathbf{X}_t$ with dimension *P* by *S* representing log-density $x_{t,p,s}$ in time *t* for species *p* at site *s*, replace productivity $\boldsymbol{\alpha}$ with $\mathbf{A}$ representing productivity $a_{p,s}$ for species *p* at site *s*, and replace process errors $\boldsymbol{\varepsilon}_t$ with $\mathbf{E}_t$ representing unexplained variation $\varepsilon_{t,p,s}$. The model therefore becomes:

$$\mathbf{X}_{t+1} = \mathbf{A} + (\mathbf{I} + \mathbf{B})\mathbf{X}_t + \mathbf{E}_{t+1} \quad (7)$$

where the expectation of initial log-abundance for each species and site ($x_{t=1,p,s}$) is estimated as a fixed offset β_p from the productivity at that site. Specifically, we specify $x_{t=1,p,s} = a_{p,s} + \beta_p + \varepsilon_{t=1,p,s}$, where the variance of initial log-abundance away from its expectation is identical to the variance of process errors (future studies could explore more-complicated specifications for initial conditions). We also specify a distribution for spatial variation in productivity:

$$\mathrm{vec}(\mathbf{A}) \sim \mathrm{MVN}(\boldsymbol{\mu}_A, \mathbf{R}_{\mathrm{spatial}} \otimes \boldsymbol{\Sigma}_\mathbf{A}) \quad (8)$$

where $\boldsymbol{\mu}_A$ is the median productivity across space, $\boldsymbol{\Sigma}_\mathbf{A}$ is a *p* by *p* diagonal matrix where each diagonal element is the pointwise spatial variance σ_p^2 for each species p, and $\mathbf{R}_{\mathrm{spatial}}$ is a spatial correlation matrix. Spatial correlations are defined such that the pairwise correlation between location s and $s + h$ follows a Matérn function with smoothness of one:

$$\mathbf{R}_{spatial}(s, s+h) = \frac{1}{2^{\nu-1}\Gamma(n)} \times (\kappa|h|)^n \times K_\nu(\kappa|h|) \quad (9)$$

where κ is a parameter governing the distance h at which two locations are effective uncorrelated, n is a smoothness parameter [fixed at 1.0; Simpson *et al*. (2012)] and K_ν is the Bessel function. Process errors $\mathbf{E}_t$ are also defined spatially:

$$\mathrm{vec}(\mathbf{E}_t) \sim \mathrm{MVN}(\mathbf{0}, \mathbf{R}_{\mathrm{spatial}} \otimes \boldsymbol{\Sigma}_\mathbf{E}) \quad (10)$$

We use a reduced-rank approximation for covariance among species, $\boldsymbol{\Sigma}_\mathbf{E} = \mathbf{L}\mathbf{L}^{\mathrm{T}}$, such that $\boldsymbol{\Sigma}_\mathbf{E}$ has rank *k* and is calculated from a *p* by *k* matrix $\mathbf{L}$ (Warton et al. 2015, Thorson et al. 2016). In the following, however, we specify full rank for $\boldsymbol{\Sigma}_\mathbf{E}$ (i.e., $K = P$). This model makes three important simplifying assumptions: (1) that interactions are constant over space and time (i.e., $\mathbf{B}$ is not indexed by location or year), (2) that spatial variation in productivity is

statistically independent among species, and (3) that the decorrelation distance for each species is identical (i.e., κ does not vary among species). Each of these assumptions could be relaxed in future research, but we do not explore them further here.

Parameters are estimated using sampling data, and we assume that sampling data are proportional to local density for each species. We use the following observation model for continuous-valued data (i.e., samples in units of biomass):

$$\mathrm{P}\left(C = c_p(i) | x_{t(i),p(i),s(i)}\right) \quad (11a)$$

$$= \begin{cases} \exp\left(-z_{p,2}\lambda_p(i)\right) & \text{if } C = 0 \\ \left(1 - \exp\left(-z_{p,2}\lambda_p(i)\right)\right) \times \mathrm{Lognormal}\left(C; , \ln\left(\frac{\lambda_p(i)}{1 - \exp\left(-z_{p,2}\lambda_p(i)\right)}\right), z_{p,1}^2\right) & \text{if } C > 0 \end{cases}$$

where $z_{p,1}$ is the standard deviation (in log-space) for non-zero samples, and $z_{p,2}$ governs the relationship between the probability of not encountering the species in a sample and the predicted density for species *p*, such that probability of a zero sample (*C=0*) is identical to a Poisson distribution with intensity $z_{p,2}\lambda_p(i)$ (i.e., Pr $(C > 0)$ is described using a generalized linear mixed model using a complementary log-log link). We use a lognormal distribution so that future studies could interpret the magnitude of residual variation $z_{p,1}^2$ relative to spatio-temporal process errors ($\mathbf{\Sigma_E}$). Alternatively, if samples are count valued (i.e., have units numbers) we use the Poisson distribution:

$$\mathrm{P}\left(C = c_p(i) | x_{t(i),p(i),s(i)}\right) = \mathrm{Poisson}(\lambda_p(i)) \quad (11b)$$

where in either case, $\lambda_p(i) = \exp\left(x_{t(i),p(i),s(i)}\right)$, where $x_{t(i),p(i),s(i)}$ is the estimated log-density for the species, year, and site of the i^{th} observation. If sampling is proportional to local density with detectability q_p for each species, and detectability is constant over time and space but not perfect ($q_p \neq 1$), then this will bias estimates of productivity ($a_{p,s}$) and absolute density ($\mathbf{X}_t$) but will not otherwise affect estimates of interactions ($\mathbf{B}$) or relative differences in density across time and space for a single species ($x_{t,p,s} / \sum_{t=1}^{T}\sum_{s=1}^{S} x_{t,p,s}$).

Parameter estimation for spatio-temporal community dynamics

While estimating parameters, we treat the parameters governing interactions ($\boldsymbol{\theta}$), process error covariance ($\mathbf{L}$), the geostatistical range for correlations (κ), average productivity for each species ($\boldsymbol{\mu}_\mathrm{A}$), the magnitude of spatial variation in productivity for each species (σ_p^2), the average offset of initial log-abundance from productivity for each species (β_p), and potentially the parameters governing the observation model if using catch-in-biomass data ($\mathbf{z}$) as fixed effects. This set of parameters is arguably the minimum number required to account

for spatial variation (i.e., a Grinnelian niche) for each species, correlated responses to spatio-temporal variation, and the potential for species interactions. We treat as random the spatial variation in productivity ($\mathbf{A}$), and the spatial variation in density for each species and year ($\mathbf{X}_t$). We treat density as random, rather than process errors ($\mathbf{E}_t$) because this results in a more separable specification for random effects without affecting the overall likelihood of fixed effects. This increased separability for random effects then leads to faster parameter estimation. Modeling random effects is a procedure for eliciting the expected covariation in data arising from a proposed set of fixed effects. Although fixed effects can generally be estimated for neutral models without recourse to numerical integration techniques (e.g., Etienne and Alonso 2005), the increased complexity of our model required using numerical integration within a mixed-model statistical framework for estimating the small number of fixed effects. Despite our use of numerical integration for random effects representing density and spatial variation, the model involves a small number of free parameters relative to the amount of available data. Our model using full process-error rank and the observation model for counts (Eq. 11b) bridges between $1 + 3.5P + 0.5P^2$ parameters (when dynamics are unregulated) and $1 + 3.5P + 1.5P^2$ parameters (when dynamics are fully regulated). For biomass sampling data (Eq. 11a), our chosen configuration also involves an additional $2P$ parameters for the observation model.

To identify maximum likelihood estimates for fixed effects, we identify their values that maximize the marginal likelihood function when integrating across random effects. To do so, we use Template Model Builder, TMB (Kristensen 2014, Kristensen et al. 2016) called from within the R statistical environment (R Core Team 2015), and use the Microsoft R Open build for low-level parallelization of all computations (https://mran.revolutionanalytics.com/). For computational efficiency, we also use a stochastic partial differential equation approximation to all multivariate-normal distributions (i.e., $\mathbf{A}$ and $\mathbf{E}_t$), and also approximate these function-valued variables as being piecewise-constant in the neighborhood of a small number of "knots", where the number of knots is chosen as a balance of computational speed and precision (Lindgren et al. 2011, Thorson et al. 2014, 2015). Estimating parameters using Template Model Builder involves the following steps: (1) specify the joint log-likelihood of data and random effects; (2) given specified values of fixed effects, use TMB to identify values of random effects that maximize the joint log-likelihood; (3) given these values for fixed and random effects, use TMB to calculate the Laplace approximation to the marginal likelihood for fixed effects, and its gradient with respect to fixed effects (see e.g., Skaug and

Fournier 2006); and (4) use the marginal likelihood and its gradients within a nonlinear minimizer in R to identify maximum likelihood estimates for fixed effects.

We identify model convergence by confirming that the absolute-value of the final gradient of the marginal likelihood with respect to fixed effects is <0.01 for all parameters, and that the Hessian matrix is positive definite. After identifying maximum likelihood estimates for fixed effects and confirming convergence, TMB then identifies empirical Bayes estimates of random effects, and uses a generalized delta method to calculate standard error estimates for all fixed and random effects. An R package MIST to apply this Multispecies Interactions Spatio-Temporal model to new data sets is available on the first author's GitHub page (https://github.com/James-Thorson/MIST), and we used v1.1.0 (DOI 10.5281/zenodo.260143). By using maximum likelihood methods for parameter estimation, we allow hypothesis testing and probabilistic comparisons of neutral and niche approaches, as advocated by McGill et al. (2006).

Simulation experiment

We conducted a simulation experiment to explore the statistical properties of our proposed model. Specifically we seek to determine:

1. whether we can accurately estimate the interaction matrix (**B**); and
2. whether model selection tools can accurately identify the number of regulatory relationships (*R*), where this number can range from zero (i.e., **B**=**0**) to *P* (i.e., **B** is estimated with the restriction that its eigenvalues have range between -1 and 1).

To conduct this experiment, we simulated 50 replicated data sets, where each data set involves dynamics for four species over 40 years. Dynamics occur at 25 sites that are randomly distributed following a 2-dimensional uniform distribution within a square domain, where each site is sampled in numbers twice per year (2,000 samples total per species). We simulated data using Eq. 7-10 and 11b, where $\boldsymbol{\mu}_A = 2.0$, $\sigma_{\text{spatial}} = 0.01$, $\boldsymbol{\Sigma}_E = 0.05\mathbf{I}$, where $\mathbf{R}_{\text{spatial}}$ is specified such that correlations drop to 10% at 20% of the length of an edge of the square spatial domain. We specified the interaction matrix:

$$\mathbf{B} = \begin{pmatrix} -0.4 & -0.4 & -0.1 & -0.05 \\ -0.4 & -0.4 & -0.1 & -0.05 \\ -0.1 & -0.05 & -0.3 & -0.3 \\ -0.1 & -0.05 & -0.3 & -0.3 \end{pmatrix} \quad (12)$$

i.e., where **B** is composed of two species modules (Holt 1997), where species 1 and 2 are the first competitive module, and species 3 and 4 are the second competitive module. We also included weak competition among modules (such that all species have non-zero interactions), but where species 1 and 3 have stronger among-module competition than species 2 and 4

(such that all species have a unique set of interactions). Given this structure, community dynamics has two regulated and two unregulated components, i.e., **B** is within the family of matrices generated by $R = 2$ (which has 12 degrees of freedom). We also compare results against a null model wherein **B** is estimated as a diagonal matrix with independent parameters along the diagonal and process errors are also independent ($\boldsymbol{\Sigma}_E$ is diagonal). This null model includes single-species density dependence in place of community-level regulation, and illustrates the magnitude of error arising from ignoring community interactions. Finally, we conduct a sensitivity analysis illustrating the effect of less-informative data. To do so, we conduct another simulation experiment that is identical except that initial log-abundance is decreased to $\boldsymbol{\mu}_A = 1.0$. In both simulation experiments, we record the proportion of simulation replicates that result in non-convergence, and restrict results to converged models.

Case study application

To demonstrate this method, we use data for four species (Atlantic cod, thorny skate, white hake, and grey seal) in the Gulf of St. Lawrence from 1971 to 2012, which we previously published by Swain et al. (2015). This time series spans two (thorny skate) to four (white hake) generations at historical levels of natural mortality and age at maturation. Data for Atlantic cod, thorny skate, and white hake are obtained from a bottom trawl survey of fishes, and represent samples of biomass divided by area-swept by the bottom trawl (termed "catch-per-unit-effort", CPUE, analyzed using Eq. 11a). Sampling follows a simple random design involving 63-231 samples per year (5,588 samples total), and for computational efficiency we assign each sampling location to the nearest of 100 uniformly distributed "knots" such that we estimate density at each of 100 knots ($S = 100$) and spatial variation occurring at fine scales is attributed to residual variation ($z_{p,1}^2$ in Eq. 11a). Data for grey seal are estimates of seal density obtained from analysis of seal tag sightings during this period. The data set therefore contains a mix of survey observations and model output. The data set has previously been analyzed by Swain et al. (2015), and it is not feasible to simultaneously estimate spatio-temporal community dynamics and reconstruct seal densities from raw tag-resighting data. However, the joint analysis of survey data as a Poisson process and tag-resighting data as a Markovian movement process would be an interesting topic for future research.

Results

Simulation experiment

We first explore results from our simulation experiment, where we simulate dynamics for four species with two regulated and two unregulated components (i.e., true $R = 2$). In this case, model selection identifies a model with 2 regulated relationships in almost all simulation replicates, with 3 and 4 relations identified in a small proportion, and independent dynamics are never identified (Fig. 1 top panel). The model with 2 regulated relations converges in almost all simulation replicates (2%), although the model with independent dynamics is slightly more stable numerically (0% nonconvergence). Models with 2 or more regulated relations are able to improve predictions of density relative to either independent dynamics, or a model with only one regulatory relation (Fig. 1 bottom panel). Visualizing estimates of the interaction matrix ($\mathbf{C} = \mathbf{B} + \mathbf{I}$) shows that the model generates essentially unbiased estimates of both within-module competition (e.g., species 1 and 2) and among-module competition (e.g., species 1 and 3, Fig. 2). Sensitivity analyses show that decreased sample sizes for sampling result in increased rates of non-convergence and degraded ability to identify the rank of the interaction matrix, but maintains approximately unbiased estimates of species interactions (Appendix S2, Fig. S1-S2). We therefore conclude that the model is able to accurately identify instances of partial regulation, e.g., to evaluate the strength of evidence in favor of neutral or niche-based approaches to community regulation, but that estimating full regulation ($R = 4$) does not substantially degrade performance when estimating local density.

Case study: Gulf of St. Lawrence community dynamics

Model selection from our case study identifies the model with three regulatory relationships as being parsimonious, thus identifying strongest evidence for partially regulated dynamics in this community. The estimated interaction matrix (Table 1) shows a strong, negative impact of grey seals on thorny skate, and a weak negative relation of grey seals on Atlantic cod (where the former is statistically significant using a 2-sided Wald test; -0.213, SE=0.078, $p < 0.01$). By contrast, Atlantic cod and white hake both have significant, positive impacts with thorny skate. The eigen-decomposition of this interaction matrix (Fig. 3) shows that the unregulated component of community dynamics is associated with the negative relation between grey seals and all fish species (top-left panel). Other relations have weak regulation (i.e., eigenvalues different from 1.0).

Inspecting density maps for each species (Fig. 4) shows that thorny skate has gone from being ubiquitous to having low density everywhere except in deeper water along the north-eastern seaward boundary. In contrast, grey seal has shown a marked increase in density in

shallower waters, particularly near the western coast of Prince Edward Island. By contrast, Atlantic cod showed an initial increase and subsequent decrease in density. Cod distribution shifted toward the central Magdalen Shallows during the increase and out of it during the decrease. In recent years, cod densities have decreased the most off the west of Prince Edward Island, the region where the increase in grey seal density has been most marked. White hake were initially distributed in warm deeper water along the north-eastern seaward boundary and in warm shallow inshore waters. Their density initially increased slightly in these areas and then declined. This decline was most severe in inshore areas, where white hake are now very rare. The estimated magnitude of process errors ($\mathbf{\Sigma}_{\text{process}} = \mathbf{LL}^{\mathbf{T}}$; Fig. 5) shows that Atlantic cod has the highest residual variation in density (a log-standard deviation of 0.22), while other species have lower residual variation (log-standard deviation of <0.20). Residual correlations are generally positive, and are stronger among the three fish species than between fishes and grey seals. This implies that processes in addition to pairwise interactions (e.g., environmental conditions) may cause synchronous variation in productivity for these fishes.

Discussion

In this paper, we have hypothesized that short-term dynamics for ecological communities will involve a mixture of regulated and unregulated components, and that the associated community matrix will be parsimonious in some cases. We then demonstrated a model for spatio-temporal community dynamics that uses model selection to identify regulation along a continuum ranging from neutral dynamics (where every species follows unregulated ecological drift) to stable dynamics (where the full community matrix of pairwise interactions is estimated). A simulation experiment confirms (1) that model selection is able to accurately identify the number of regulatory relationships given sufficient data, (2) that lack of convergence is associated with insufficient data to identify the number of regulatory relations, and (3) that models are generally able to estimate pairwise interactions. A case study illustrates our proposed approach for a trophically-linked community involving a recovering top predator (grey seals). Previous spatio-temporal models for ecological communities have generally involved a factor-analysis approach (Warton et al. 2015, Thorson et al. 2016), where dynamics for P species is approximated using R spatio-temporal factors ($0 \leq R \leq P$). We have replaced this phenomenological description of spatio-temporal dynamics with a model that explicitly estimates significant pairwise interactions, but have retained both (1) the ability to estimate correlations in spatio-temporal dynamics

among species, and (2) the likely improvement in statistical efficiency from using spatial replication to estimate interactions.

We propose this approach to remedy issues in previous neutral and time-series approaches to community dynamics. In particular, time-series approaches require estimating pairwise interactions that increase as the square of the number of species, and this will likely not be parsimonious (or even identifiable) for large communities. Similarly, neutral models have important limitations, *inter alia*, previous criticism for failing to capture spatial variation (Gilbert and Lechowicz 2004, Gilbert et al. 2006) or spatio-temporal variation in habitat suitability for individual species (Dornelas et al. 2006). By contrast, our approach can be interpreted as a short-term approximation to neutral spatio-temporal dynamics when there are no regulatory relations ($R = 0$, such that $\mathbf{B} = \mathbf{0}$) and no drift ($\mathbf{A} = \mathbf{0}$). In this limiting case, our approach can be reduced to two parameters: the characteristic spatial scale, and the magnitude of spatio-temporal variation. The approach can then be expanded to include correlated responses to spatio-temporal variation, thereby accounting for similar responses to environmental conditions. Although we use numerical integration (rather than analytical integration as has been used previously to describe neutral dynamics, e.g., Etienne and Alonso (2005)), we argue that our approach bridges low- and high-dimensional applications.

Previous authors have noted that neutral theory is likely not a suitable approximation to community dynamics for species at different trophic levels (Hubbell 2001), for which the assumptions of identical per-capita impacts is particularly unlikely. By contrast, our study has shown that partially regulated community dynamics is occurring across two trophic levels in the Gulf of St. Lawrence. Specifically, the increase in predators (grey seals) is offset by a decrease in three prey species (fishes), while other axes of community dynamics are generally regulated. We acknowledge that this unregulated component of community dynamics will probably experience regulation in the future (i.e., the log-density of seals cannot follow a random-walk process forever). However, our model identifies that interactions between grey seals and fishes cannot be distinguished from unregulated dynamics during the past forty years.

Estimates of species interactions from this model agree well with the results of more detailed process-oriented studies for the Gulf of St. Lawrence marine community. The model estimates that grey seal abundance has followed a density-independent exponential increase. This is consistent with grey seal population studies which estimate a roughly exponential increase in grey seal abundance in Atlantic Canada over the past 55 years (Hammill et al. 2014a). Despite a 50-fold increase in abundance, there is little evidence for a decline in

productivity over this period. Increasing seal population size was negatively associated with densities of all three fish species. These three species are (or have been) important prey of grey seals in the Gulf of St. Lawrence (Benoit and Bowen 1990, Hammill et al. 2014b). Their on-going declines, despite currently negligible fishing mortality, are the consequence of large increases in natural mortality, which appear to reflect increased predation by grey seals (Swain and Benoît 2015). The negative impact of seals is estimated to be strongest for thorny skate. Because of their slow life history (e.g., late maturation), thorny skate are expected *a priori* to be most vulnerable to increasing predation rates.

Importantly, our approach is low-dimensional relative to whole-of-ecosystem models that are frequently used for marine communities (Christensen and Walters 2004, Fulton et al. 2011). An alternative low-dimensional approach to community modelling involves pre-specifying community modules (e.g., trophic or competitive structures), where species from different modules have weak or nonexistent interactions. However, small changes in the specification of food webs can results in large differences in community properties (Abrams 1993). We therefore argue that the linear approximation to nonlinear dynamics (projecting Eq. 1 onto the space spanned by Eq. 3) remains a suitable approximation to short-term community dynamics (Ives et al. 2003), without requiring *a priori* specification of community interactions. Researchers have previously used model selection to exclude interactions that were not significantly different from zero (e.g., Hampton et al. 2006). However, we show that we can reduce the number of estimated parameters even without "zeroing-out" any pairwise interactions. In our case, we eliminate parameters by specifying that some axes of the community are unregulated, so that dynamics of these axes correspond to a random-walk process. This random-walk approximation for some axes of community dynamics appears to be a useful approximation over short time scales (e.g., when analyzing a small number of generations for some components of the community).

Finally, we note that our model does not explicitly account for individual movement. Modelling movement is important to ongoing research regarding spatially explicit neutral models (Etienne and Rosindell 2011), and is also central to "mass effects" and "patch dynamics" models for meta-communities (Shoemaker and Melbourne 2016). Furthermore, movement in search of preferred habitats often modifies predicted outcomes from pairwise competitive interactions (Morris 2003). Future research can explore incorporating advective-diffusive movement within multispecies spatio-temporal models (Thorson et al. In press, Hooten and Wikle 2010), but previous approaches are computation-intensive and would likely inhibit simulation testing. We therefore encourage further development of approximate

or exact solutions to advective-diffusive movement within spatio-temporal models of community dynamics. In particular, mixed-effects models show great promise in providing a general approximation to the statistical mechanics that also underlies theory for neutral models.

Acknowledgments

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636 ## Data Availability

637 Data used in the case study were previously analyzed by Swain et al. (2015) and are publicly
638 available at http://dx.doi.org/10.5061/dryad.n43qf. Statistical analysis used R package MIST
639 v1.1.0 (https://doi.org/10.5281/zenodo.260143), and updated versions can be obtained via
640 GitHub (https://github.com/James-Thorson/MIST).

Table 1 – Estimates and standard errors (in parentheses) for the interaction matrix ($\mathbf{C} = \mathbf{B} + \mathbf{I}$), where e.g. the 1st row and 2nd column represents the per-log-capita impact of white hake and on per-capita productivity of Atlantic cod. This interaction matrix includes three regulatory relations ($R = 3$) amongst all four species (see Fig. 3).

	Atlantic cod	**white hake**	**thorny skate**	**grey seal**
Atlantic cod	0.860 (0.024)	0.095 (0.024)	-0.031 (0.010)	-0.060 (0.033)
white hake	-0.013 (0.007)	0.999 (0.008)	0.004 (0.003)	-0.021 (0.015)
thorny skate	0.165 (0.048)	0.124 (0.045)	0.631 (0.060)	-0.213 (0.078)
grey seal	-0.000 (0.002)	-0.004 (0.003)	0.000 (0.001)	0.985 (0.005)

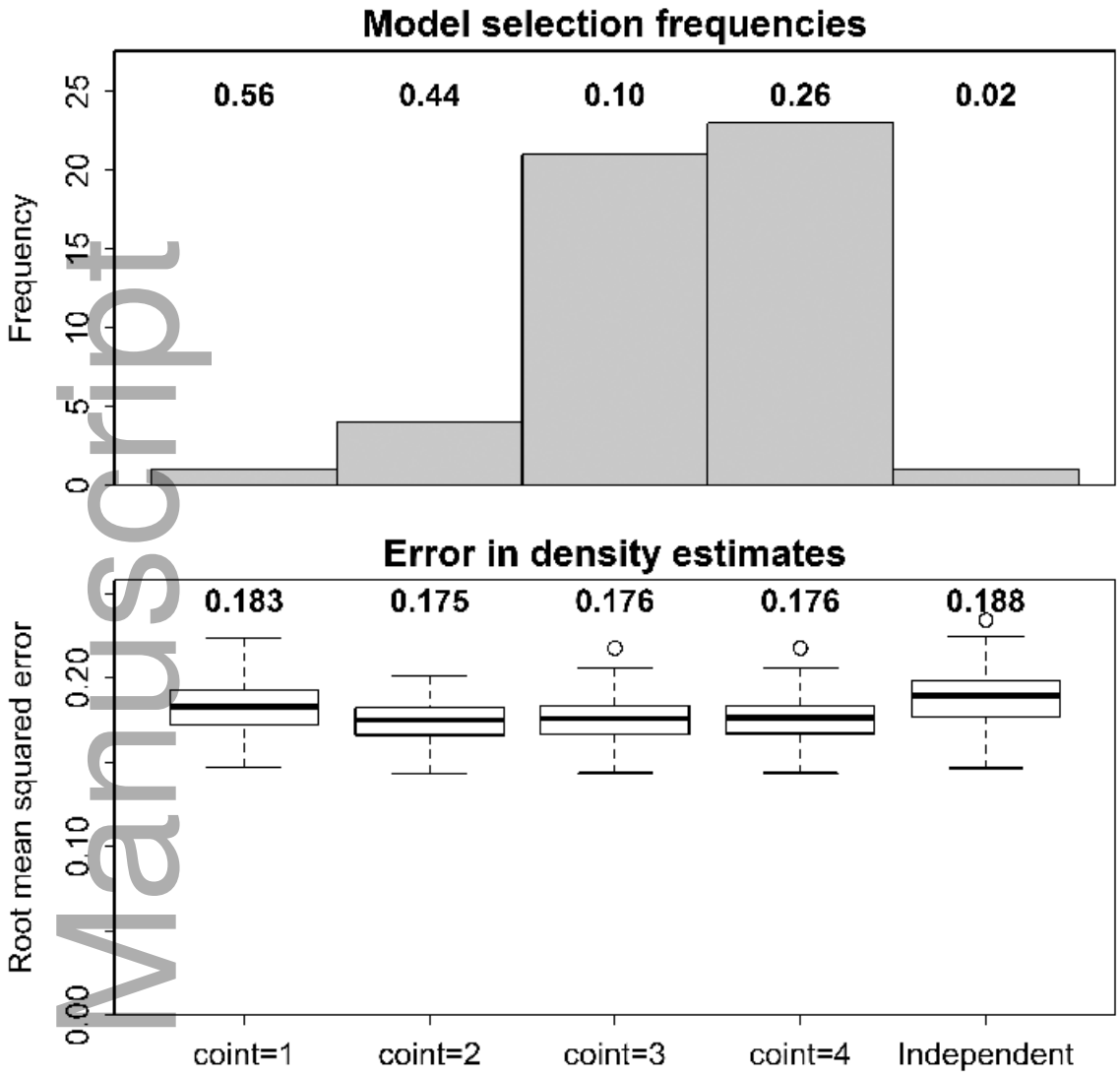
Fig. 1 Illustration of model selection results (top panel) using the Akaike Information Criterion to select the number of regulatory relations R in the interaction matrix **B** (the bold number above each bar represents the proportion of simulation replicates where the model did not converge), and boxplots illustrating root-mean-squared-error (RMSE) in estimates of log-abundance for each species (bottom panel), $\sqrt{(ST)^{-1}\sum_{t=1}^{T}\sum_{s=1}^{S}\left(x_{s,t,p}-\hat{x}_{s,t,p}\right)^2}$, where $x_{s,t,p}$ is simulated and $\hat{x}_{s,t,p}$ is predicted log-abundance for each model (the bold number above each boxplot shows the average RMSE for all species and simulation replicates).

Fig. 2 – Illustration of estimated interaction matrix (C=B+I), where e.g., the top-left panel shows the element c_1,1 (note the different x-axis ranges for diagonal and off-diagonal panels), and where the grey histogram represents the estimates from the estimated interaction matrix C from the model where R is selected using the Akaike Information Criterion, the red histogram represents estimates from the model where B is an estimated diagonal matrix (i.e., assuming single-species dynamics), and where the blue line is the true value (note the different range in the x-axis for each panel).

Fig. 3 – Illustration of the eigen-decomposition of the interaction matrix (C=B+I) for our case study. Each panel displays an eigenvalue (listed in the top), and displays values for the column-eigenvector associated with that eigenvalue. An eigenvalue of 1.000 indicates a dimension for community dynamics that follows a random-walk process.

Fig. 4 – Illustration of estimated density $\mathbf{X}_t$ for each of four species (columns) in the Gulf of St. Lawrence for five evenly-spaced years (rows: $t \in \{1971, 1981, 1992, 2002, 2012\}$) spanning the 42 year period with available data. Colors for each species represent density relative to maximum (red) and minimum (blue) density observed for that species.

668 Fig. 5 – Estimated covariance of process errors ($\mathbf{\Sigma_E}$) for the Gulf of St. Lawrence community
669 dynamics case study (where we have assumed full-rank covariance, i.e., $K = P$)



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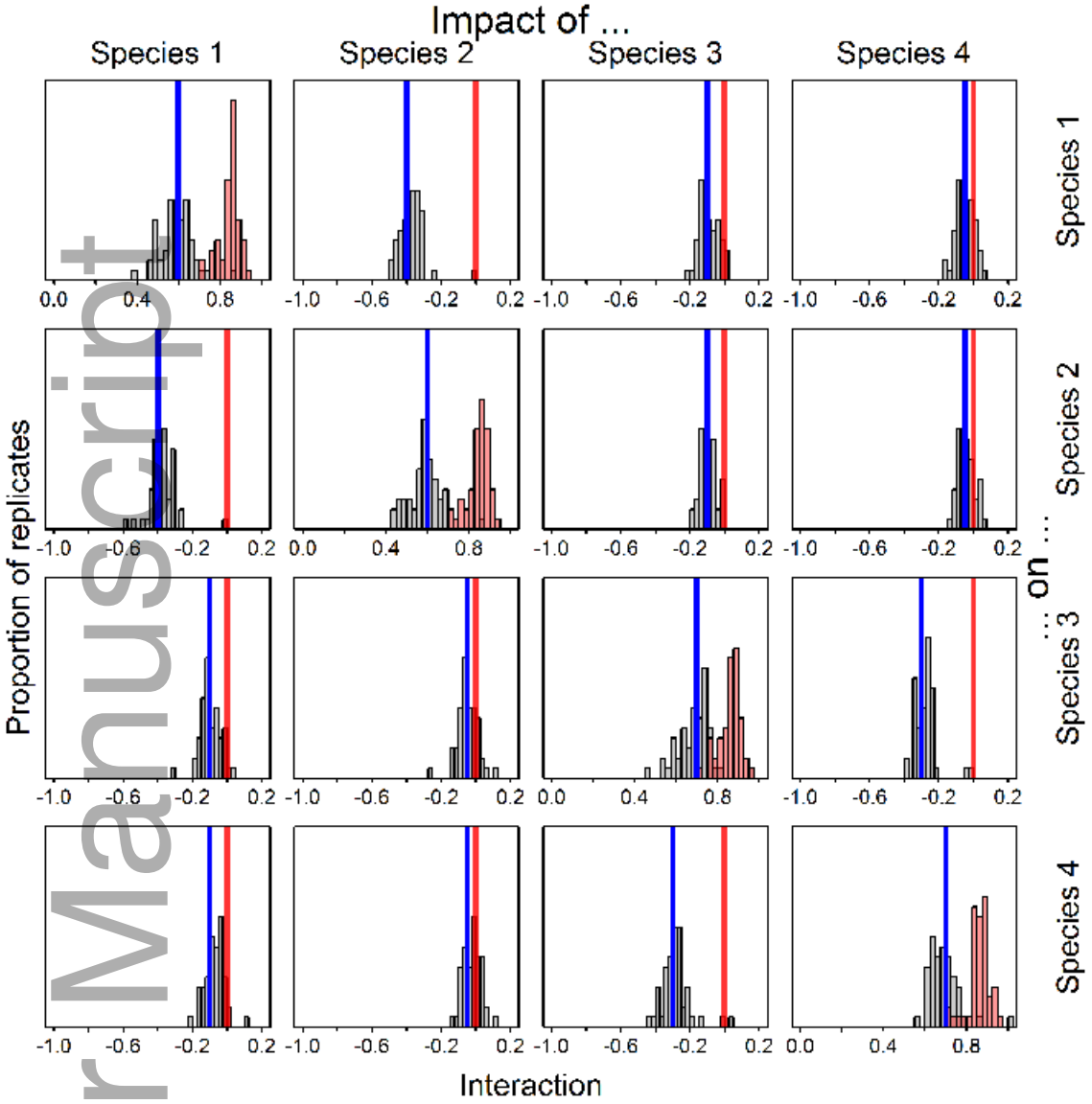

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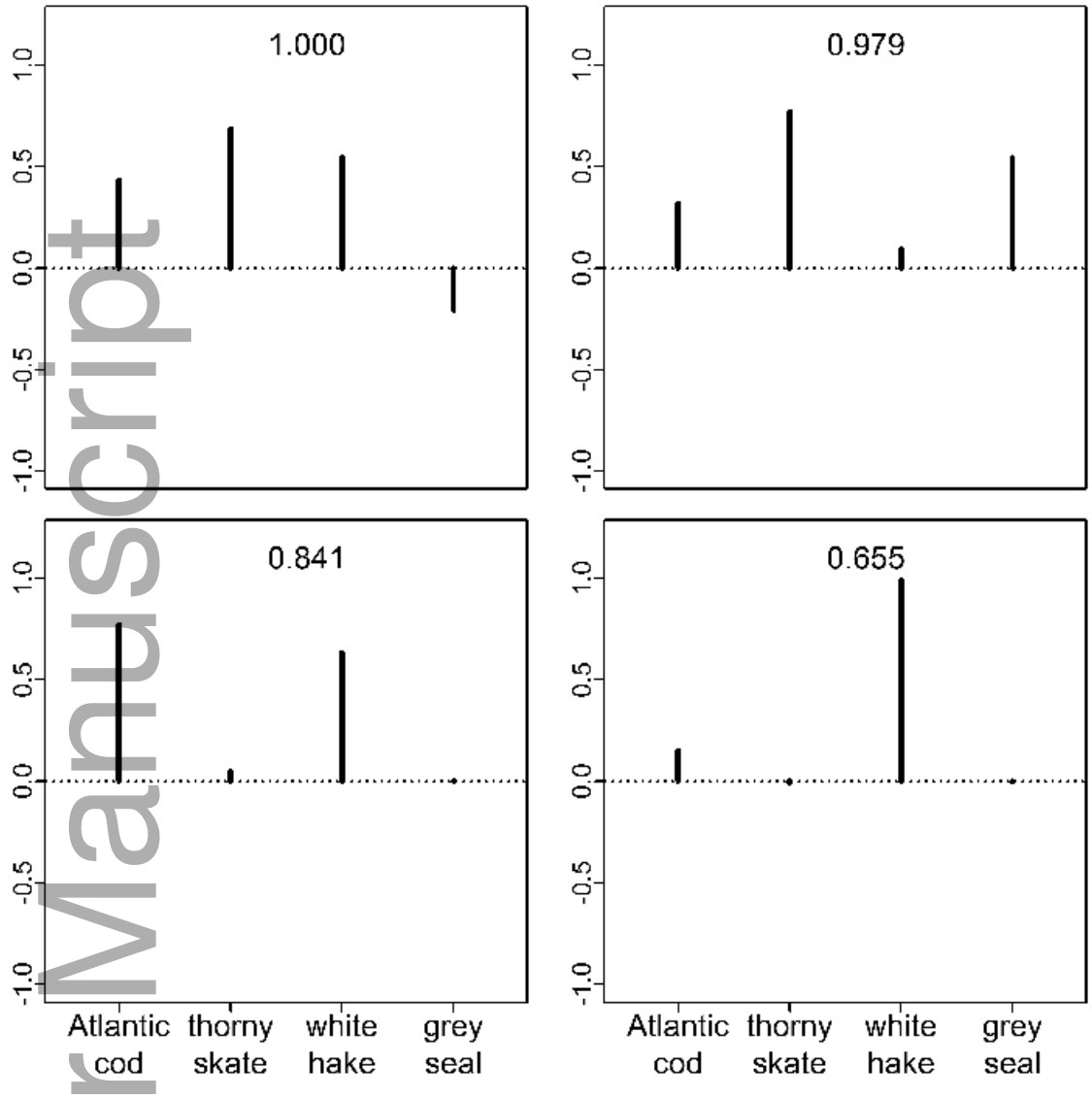

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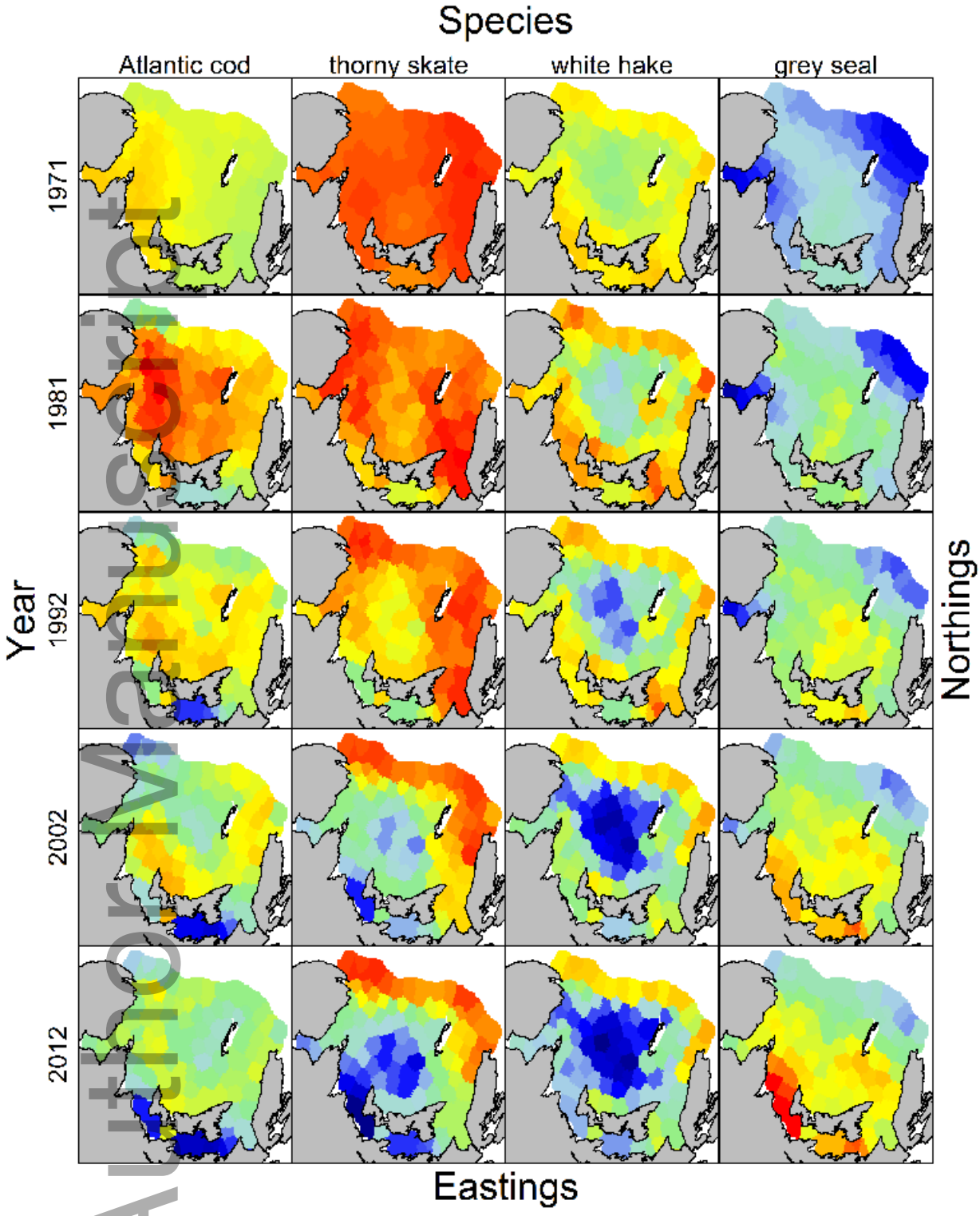

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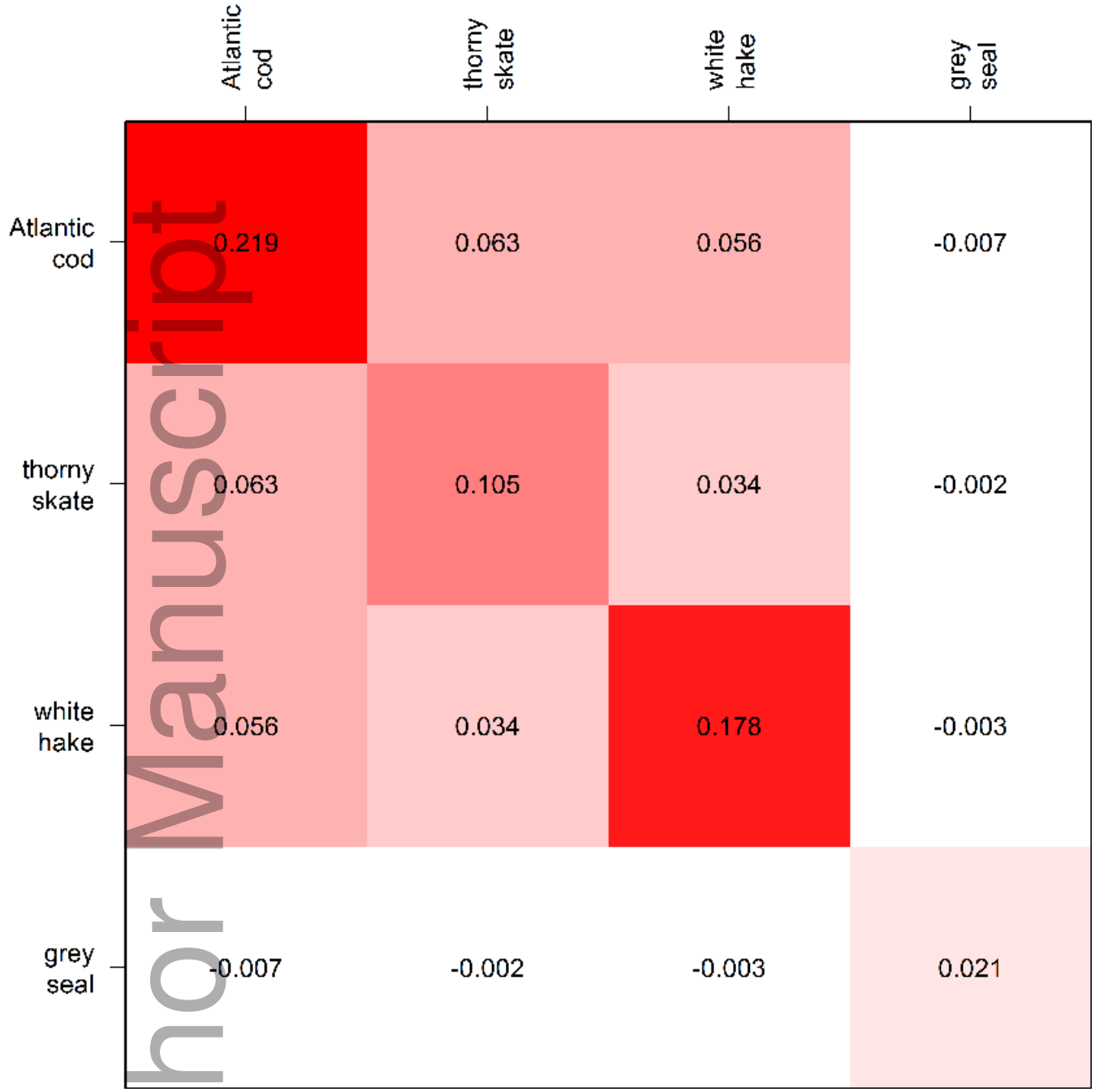

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