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Spatially Explicit Modeling of Community Occupancy using Markov Random Field Models with Imperfect Observation: Mesocarnivores in Apostle Islands National Lakeshore

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We developed a spatially explicit community occupancy model based on Markov random fields that accounts for spatial auto-correlation and interspecific interactions in occupancy while also accounting for interspecific interaction in detection. Simulation showed the model can distinguish different mechanisms of environmental sorting competition and spatial-autocorrelation. We applied our model to camera trap data from a Fisher(*Pekania pennanti*)-Marten(*Martes americana*) and Coyote(*Canis latrans*)-Fox(*Vulpes vulpes*) system in Apostle Island National Lakeshore. Results showed the observed partitioning pattern between marten and fisher distributions could be better explained by a flipped mainland-island source-sink pattern rather than competition, while we detected some evidence that on top of the mainland-island source-sink pattern, there was a positive association between fox and coyote that deserved further study.

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Introduction

Drivers of distributions of species and community structures are among the most important questions in ecology. There exists various classical theories e.g. niche theory (Hutchinson (1957)), and Lotka-Voterra models Lotka (1910); Volterra (1928). These theories concentrated on species-specific characteristics interacting with the environment and considered presence as a function of niche optimizing and inter-species interactions. Conceptually, in these approaches, species were ecologically unique and modeling geographic patterns conditioned on site characteristics in a high-dimensional niche space and all interactions happened in such space (e.g. niche partitioning). This paradigm emphasizes drivers associated with differences in species life histories. In contrast, (MacArthur and Wilson (2001)) emphasized the importance of random patch-level colonization and extinction probabilities in forming species richness patterns which further was adopted by Stephen Hubbell's neutral theory on community assemblage (Hubbell (2001), see Volkov et al. (2003) for a review). Meta-population modelling was another example of spatial explicit theory emphasized the importance of dispersal (Hanski (1983)). This paradigm emphasized differences in patch characteristics, especially their geographic arrangements.

Recent research suggested that communities reflect both species- and patch-level drivers, i.e . neither species nor sites were exchangeable. Leibold et al. (2004) extended meta-population models to community assembly, and considered the spatial process and natural history processes at the same time. The relative influence of species characteristics and site characteristics remained unclear in most communities. Research on plant communities (e.g. Lasky et al. (2017)), marine systems (e.g. Shurin et al. (2009); Göthe et al. (2013); Meyer (2017)), and microbial systems to separate species characteristics and spatial characteristics in both experimental and natural communities (see Logue et al. (2011) for a review) suggested that a gradient from almost fully spatial-driving to almost fully natural history-driving in community assemblage. Island systems provide useful natural experiments for exploring community assembly dynamics Kadmon and Allouche (2007) although most studies have occurred in tropical systems which tend to be biologically rich Sklenář et al. (2014); Hubbell (1997), however, even in typical island settings neither large mammal communities nor temperate systems have generated much attention. Reasons may include cryptic life histories of large mammals and the relative rarity of temperate island archipelagos.

It is important to model different processes explicitly to understand their relative importance(Cottenie (2005); Dray et al. (2006)). Probabilistic Graph Modeling (PGMs, Koller and Friedman (2009)) is a general framework for modeling systems with unspecified dependence structures (e.g. competition between species, spatial auto-correlation between sites). Markov Random Field modeling (MRF) is a kind of PGM that defines joint distributions of sets of random variables linked by non-directed graphics which allow cycles (Vanmarcke (2010); Cressie (1992)). MRF has long been used to model spatial correlations in ecology and agriculture, e.g. in spatial ecology (Hughes et al. (2011); Hepler et al. (2018)), as well as temporal analysis (Zhu et al. (2005)) and interspecific interactions (Harris (2016)). It was also widely used for modeling networks in social systems (West et al. (2014)), genetic associations (Wei and Li (2007)), as well as competing species (Harris (2016)).

Due to a recent flourish of camera-trapping research, ecologists now can get vast amounts of detection and non-detection data which can be used to infer presence-absence (P/A) of moderate to large-sized animals. However, imperfect detection (e.g. false absence due to animal detection constrain) remains a challenge (Kéry and Schmidt (2008)). Occupancy modeling (MacKenzie et al. (2003)) addresses imperfect detection and infers true P/A and detection rates from repeat sampling. This idea was also explored by computer vision and image modeling communities earlier (e.g. after development of the EM (Expectation-Maximization) algorithm which allows maximum likelihood estimation when models depend on unobserved latent variables (e.g. true occupancy Dempster et al. (1977))). MRF with imperfect observations were also explored in the image reconstruction context (Chalmond (1989), Ibáñez and Simó (2003)). Following the basic framework of hierarchical modeling, we can build various occupancy-like models based on the idea that observations are samples taken from detection distributions conditioned on unobserved latent

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true patterns that follow other characteristic distributions. Multispecies occupancy models developed by Rota et al. (2016) used a multinomial-logistic regression which estimated different predictors for different coexistence patterns. Kéry and Royle (2008) used a hierarchical structure to model species interactions that can be viewed as a Bayes network (Koller and Friedman (2009)). These techniques facilitate research on assembly of animal communities on both island and other landscapes. However neither Kéry and Royle (2008) nor Koller and Friedman (2009) can model interactions of species and spatial correlations simultaneously. Since for Rota et al. (2016), the number of possible patterns were too large and for Kéry and Royle (2008) the spatial correlation had a non-direct nature. In contrast, MRF models allowed cycles in the interaction network, i.e. there was no need for a root species that all other species were conditioned on, meanwhile, MRF was the classical model for modeling spatial autocorrelations. Thus MRF-based occupancy-like models could be an alternative choice for joint modeling of site and species-specific drivers. The objective of this study was to develop a model that can capture spatial auto-correlation and interspecific interactions while controlling for environmental predictors and, consequently, understanding the drivers of distributions of competing species pairs in the Apostle Islands National Lakeshore (APIS, Wisconsin, USA).

We focus on two pairs of plausibly competing species: fisher(*Pekania pennanti*)-marten(*Martes americana*) (FM system) and coyote(*Canis latrans*)-red fox(*Vulpes vulpes*) (CF system). In APIS, 30% of sites with fisher detections also had marten detections and 15% of sites that had marten detections also had fisher detections (2014-2017), in contrast, 64% of sites that had red fox detections also had coyote detections and while 28% of sites that had coyote detections also had red fox detections (Fig.1). Our goal was to understand reasons why competing species pairs show different coexistence patterns on landscape. In niche-based theories, a partition pattern like fisher and marten could be understood as spatial niche partitioning due to competition, while coexistence could be achieved by partitioning other niche dimensions such as time. In these theories, competition was a factor promoting partition pattern. In dispersal related theories, species were more likely to exist close to the source of dispersing individuals which is usually a stable mainland population, if species were independent, they would coexist on islands closer to mainland with higher probability subject to dispersal capability. Since we observe a spatially partitioned pattern for fisher-marten, it may be explained by competition (niche-based)or different source-sink dynamics(dispersal-based). Significanlty we observe that marten tend to occur on more distant islands. For coyote and fox, coexistance at closer islands, could be explained by dispersal from mainland but we also would like to evaluate whether there exists any association between them other than mainland distance dependency.

For the FM system, we pose two working hypothesis for the observed pattern:

1) Distribution of both species on the islands reflect similar mainland-distance dependency (spatial effects). while separation at the site level was due to competition (interaction effects)

2) Distribution of both species on the islands reflect differing mainland-distance dependencies but show minor competition at the site level.

For the CF system, we pose two working hypothesis for the observed pattern:

1) Distribution of both species in the islands reflect spatial factors. Coexistence facilitated by separation in time.

2) Trophic position and life-history drives distribution (foxes avoid coyotes at the site level[interaction effects]), spatial effects at the island level are minor.

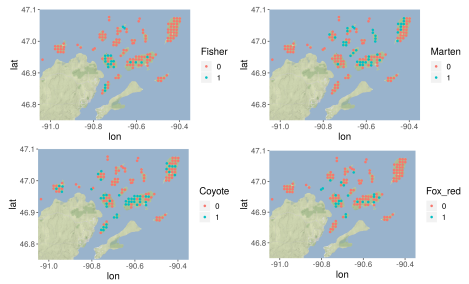

Figure 1. Detection of 4 target species on the islands, 0 (red): not detected, 1 (green): detected, dots represent camera locations on the APIS

Methods

Study Area.

APIS is located on the southwest shore of Lake Superior (USA) and lies in the transition zone between temperate and boreal forest regions. APIS is distinct from tropical islands (where much research on community assembly has occurred) because of severe winters and relative low primary productivity. Ten species of native carnivores were detected during 2014-2017 Allen et al. (2017) (Fig.1). How these species coexist and how richness differs between islands is a fundamental question for understanding community dynamics in temperate island systems.

Camera Trapping Surveys.

During 2014-2017, APIS staff and collaborators conducted camera-trapping surveys to determine distributions and relative abundances of mammal carnivores in the National Lakeshore Allen et al. (2017). Twenty-one of 22 islands which make up the archipelago were surveyed using a $1km^2$ lattice (grid) sampling frame. Within each grid cell there was one camera trap. Baits were placed on 1/2 cameras at deployment and at the remaining 1/2 during mid-deployment camera checks. Since there was no full snapshot of the whole island system at any time, we assume the underlying distribution did not change during the survey period. We divided surveys into 60-day blocks to create repeat observations.

Spatial Explicit Community Occupancy Analysis using Binary Markov Random Field Model.

We used a binary Markov Random Field (MRF) model (a.k.a. Ising model Ising (1925)) to model the distribution of competing species in a spatial explicit manner. Coding of true occupancy status followed the convention in network science, i.e. $+1$ for presence and -1 for absence. This symmetric coding was more conventional in physics but less so in ecology. Models with a centering term that modeled the "large scale" response due to environmental predictors (centered autologistic model Hughes et al. (2011)) which tried to detect auto-correlation in the residuals of large scale response due to environment were used in

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ecology. However theoretical studies on this model by Wolters (2017) suggested better performance of a symmetrical coding rather than centering the model when associations (e.g. competition, spatial autocorrelations) were expected strong and because centered models will predicted non-linear relationships between strength of association and log odds of two species being coexist/co-absent while symmetrical coding did not have this problem. Further, symmetrical coding avoided the cross product between different terms (i.e. environment and interactions) in the negative potential function (log probability mass function (pmf) up to a constant difference) of this model (Koller and Friedman (2009)) which helped us to evaluate relative contributions of different mechanisms. Further parameters of a symmetrical-coding model had better conditional interpretation, e.g. regression coefficient β was the conditional log odds of presence given all other sites and species. This property was important in understanding strength of different mechanisms (Blanchet et al. (2020), argument 2).

To make comparisons between spatial and interspecific drivers in shaping species' spatial distributions in the islands, two components were considered simultaneously in the graph associated with the joint distribution: 1) a nearest neighborhood spatial autocorrelation at camera-site level (site level hereafter,Hepler et al. (2018)) within and among islands and 2) local species associations at site level (We assume that partial associations reflect interactions, similar to Harris (2016)). We denote the design matrix for environmental covariates as $\mathbf{X}$ and response of certain species k ($k = 1, 2.., w$) to environment $\mathbf{X}$ as β_k. Further in this case study, due to the different nature of site linkages within and across islands, inter-island and intra-island correlations were modeled separately. We denote the strength parameters of these two correlations as η^{ex} and η^{in}, and known adjacency matrix $\mathbf{D}^{ex}$, $\mathbf{D}^{in}$ (eqn.1). Mainland-island with linkage matrix D^{ml} shares the same strength of inter-island spatial autocorrelation in this study. We denote the presence and absence vector of species i on the landscape as $\mathbf{Z}_i$ Then the joint distribution of all species at all sites has form:

$$
\begin{aligned}
P(\mathbf{Z}_1, ..., \mathbf{Z}_w|\theta) \propto exp[\sum_{k=1}^{w}(&\mathbf{X}\beta_k\mathbf{Z}_k \\
&+\eta_k^{ex}\mathbf{Z}_k^T\mathbf{D}^{ml} \\
&+\frac{1}{2}\eta_k^{in}\mathbf{Z}_k^T\mathbf{D}^{in}\mathbf{Z}_k \\
&+\frac{1}{2}\eta_k^{ex}\mathbf{Z}_k^T\mathbf{D}^{ex}\mathbf{Z}_k \\
&+\sum_{l>k}\gamma_{lk}\mathbf{Z}_k^T\mathbf{Z}_l)]
\end{aligned}
\tag{1}
$$

Note that the first term accounts for an environment response (mainland-island effect), the second accounts for mainland-island process (as a special environment predictor, mainland-island spatial effect), the third term accounts for intra-island spatial auto-correlations (spatial effect), the fourth term accounts for inter-island spatial auto-correlations (and can be other types of auto-correlations) and the last term accounts for all inter-specific interactions. In the mainland-island setting, we assumed that there were no inter-island spatial auto correlation so $\mathbf{D}^{ex}$ has all 0 as its entriess.

Accounting for Imperfect Detection and Short-term Interactions.

Following the logic of occupancy-like modeling (MacKenzie et al. (2003)), we model observed detection-nondetection as repeated samples from a detection process. Associations in short-term detection can also be informative about species interaction. We further assume that the interspecific interactions are local (i.e. no spatial auto correlations considered in the detection process). We used another binary MRF (Ising model) conditioned on occupancy status of species to model the detection process. In total there were two binary MRF models 1) latent occupancy 2) detection condition on occupancy. Only species occupying a certain site will be included in the detection MRF and species not occupying will have probability of non-detection of 1. Formally, denote y_{kij} as species k's detection status at site i during period j. The likelihood function at site i and detection period j is given by eqn.2.

$$
\begin{aligned}
P(y_{1ij}, y_{2ij}, ...|Z_{1i}, Z_{2i}, ..., \theta) \propto \\
exp(\sum_{k=1}^{w}[\mathbf{X}_{ij}^{det}\beta_k^{det}y_{kij}I_{Z_{ki}=1} \\
+\sum_{l>k}\gamma_{lk}^{det}y_{kij}y_{lij}I_{Z_{ki}=1}I_{Z_{li}=1}])
\end{aligned}
\tag{2}
$$

which $I_{\{\}}$ is the indicator function and $I_{Z_{li}=1} = 1$ only if $Z_{li} = 1$ and $I_{Z_{li}=1} = 0$ otherwise. The indicator function will "knock out" the species from detection interaction if it was not occupying that site. The reasoning behind this knocking out was that we assume that non-detection was caused by absence of species thus should be understand as a do-calculus (Pearl (1995)) rather than conditioning. Unlike the occupancy part, this conditional likelihood function is tractable for reasonable numbers of species (e.g. < 10) because of the relatively small size of the underlying graph. The joint likelihood function of the whole detection history, conditioned on occupancy was the product of each site and period. The joint (unnormalized) likelihood function of observed detection data then can be calculated by multiplying eqn.1 and eqn.2. The missing $\mathbf{Z}$s can be estimated similarly with unknown parameters.

Priors were set to be vague normal distributions. Due to the relative small number of repeats and lack of environmental variation in our APIS case study. We put a normal prior with variance 0.1 on intercept of detection (0.95 HDR for detection rate: [0.22,0.78]) as part of our assumptions. Again this was not necessary for the model per se (as seen in simulation), but part of the case study. Sensitivity analysis on this part was also conducted. Posterior distributions were simulated through a Markov chain Monte Carlo (MCMC) algorithm (Hastings (1970)). To overcome the double-intractable nature of the posterior (Murray et al. (2012); Møller et al. (2006)), we followed the single parameter change method proposed by Murray et al. (2012). The full description of the algorithm used can be found in Appendix S1. Diagnostic evaluation of MCMC results were done using R package `coda` (Plummer et al. (2006)).

Selection Between Stepping-Stone and Mainland-Island Model.

We compared two general models for spatial auto-correlation between islands in this study.

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Table 1. Model Parameters

Parameter	Dimension	Ecological Meaning	Remarks
Y_{kij}, y_{kij}	{-1,1}	detection of species k at site i and detection period j	data
n	integer	number of sites considered	known
w	integer	number of species considered	known
p, p'	integer	number of predictors in occupancy/detection	known
$\mathbf{X}_{ij}^{det}$	$n \times p$	environmental predictors for detection site i period j	known
$\mathbf{X}$	$n \times p$	environmental predictors for all sites	known
$\mathbf{D}^{ml}$	$n \times 1$	distance from mainland, special in case study	known
$\mathbf{D}^{in}, \mathbf{D}^{ex}$	$n \times n$	adjacency matrix for intra/inter island auto-correlation	known
$\mathbf{Z}_k$	$\{-1, 1\}^n$	Latent occupancy of species k	latent
β_k	$p \times 1$	response of species k to environment in occupancy	estimate
β_k^{det}	$p' \times 1$	response of species k to environment in detection	estimate
η_k^{ex}	1×1	strength of (intra-island) spatial auto-correlation for species k	estimate
η_k^{in}	1×1	strength of inter-island spatial/temporal auto-correlation for species k	estimate
γ_{lk}	1×1	interspecific association between spp.k and spp.l in occupancy	estimate
γ_{lk}^{det}	1×1	interspecific association between spp.k and spp.l in detection	estimate

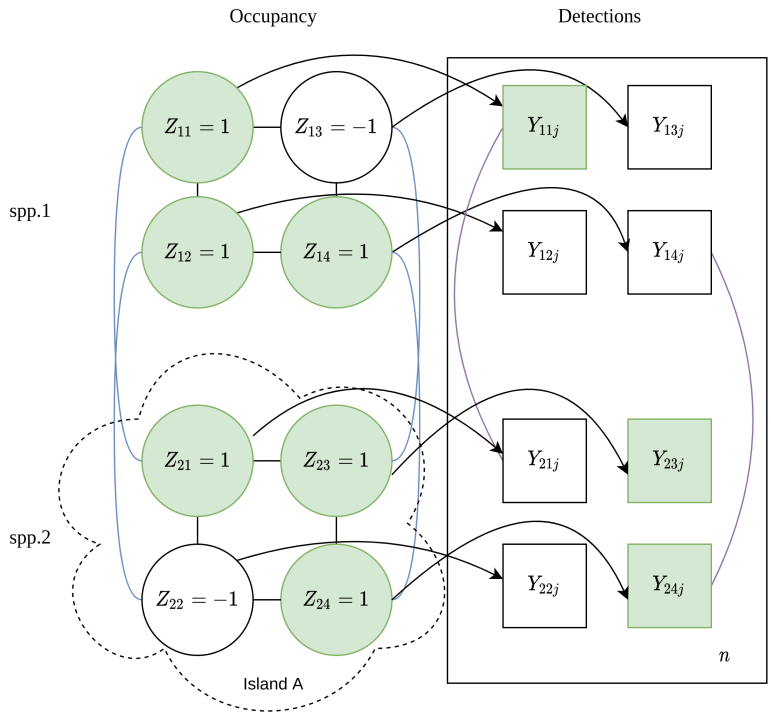

Figure 2. Dependence structure on single island, with two species Square indicates observed detections while circle indicates latent occupancy, green shows 1 or detection/occupancy, edges indicates conditional dependence. Upper parts showed species 1 while lower was for species 2, note that only if two species coexist can there be an edge between the detection

1) A *stepping-stone model* assumed that sites at edge of an island can be a neighbor to sites on another island in a MRF sense. We assign this linkage using Delaunay triangulation (Okabe et al. (2009), Fig.S1). Strength of correlation was assumed to decay exponentially through the normalized distance (Shurin et al. (2009)). Sites on the closest islands have linkage to mainland and the log odds of having species occupying such site decay exponentially through the normalized distance to mainland (Shurin et al. (2009)).

2) A *mainland-island model* assumed that sites on different islands were conditionally independent given their distance to mainland, the log odds of having species occupying a site decayed exponentially through the normalized distance to mainland(Shurin et al. (2009)).

Bayes Factor (BF), a Bayesian generalization of Likelihood ratio test, can be used for model selection (Gelman et al. (2013)). We can calculate the posterior predictive distribution of data following Raftery et al. (2006). One obstacle to using BF in this model is the intractable likelihood function. However we could follow Descombes et al. (1999) to use an augmentation method to cancel out the intractable normalizing constant in likelihood (Appendix.). Since the ratio is also estimated, robustness diagnostics following Descombes et al. (1999) could be conducted.

. Different processes can drive coexistence to different directions, e.g. environmental sorting promotes coexistance while competition promotes partitioning. A different question, compared with the strength and direction of each process was: in the *observed* pattern, what was the contributes of

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each process? For instance, it is possible that species A and B compete, however we observe that they still coexist because of environmental sorting? In this case, we may argue that competition destabilized the observed (coexisting) pattern because it prefers partitioning while environmental sorting stabilized the observed pattern because it favors a coexisting pattern. We propose to use negative potential functions (a.k.a. Hamiltonian) as a statistic to evaluate the contribution of each term on the observed pattern. This proposal was inspired by the original statistical physics convention in which each term in the negative potential function was an energy of different form(Koller and Friedman (2009)). These statistics also were used in various fields in analysis of stability of systems (Ezaki et al. (2017); Becker and Karplus (1997)). Statistically, a negative potential function can be viewed as a log probability mass function (pmf) up to a constant difference. Large positive terms stablize the observed pattern (by making probability of this term large). Note that this was the contribution on the probability mass of the observed pattern, i.e. a high positive contribution to the negative potential function means the corresponding term made the probability mass on the observed pattern high. Hence we avoid using the term log likelihood since the contribution was to understand as *which mechanism (term) made the observed pattern more likely to occur* here, i.e. a parameter was fixed and we were evaluating probability mass of the observed patterns. Posterior distributions for different terms of negative potential functions were calculated using posterior samples of occupancy status and model parameters. All implementations were in R (R Core Team (2019)) and C++ (Eddelbuettel and Sanderson (2014); Eddelbuettel and François (2011)). Implementations can be found on author's github here.

Simulations.
Simulations were conducted using the same spatial arrangement of APIS' camera trapping grids, as well as regular grids sized 10×10, 15×15, 20×20 and 25×25. On APIS' camera grids, we tested three mechanisms: 1) Competition, 2) No-interaction and 3) Sorting. In competition simulations, two species had same reaction to environment (or distance to mainland for APIS) and a negative association. In no-interaction simulations, two species had opposite reaction to environment or distance to mainland (represent niche difference/flipped source sink) and no association. In sorting simulation, two species had same but relative weak reaction to environment or mainland distance and a positive association. There were spatial auto-correlations on all mechanisms. On regular girds, we tested two species on a random draw landscape with one environmental predictor (note that we did not randomize this environment) while on APIS, we used distance to mainland as the predictor since there was a lack of environmental variations. Detailed simulation settings see Table.S1 and Table. S2. In simulations, all parameters had vague priors.

Posterior Predictive Checking.
We performed posterior predictive distribution checks using 6 statistics in the APIS case study. They were; 1) the frequency of detection for fisher and marten and 2) frequency of detection for coyote and fox, this represented how often we see the species; 3) mean overall sites that had at least one detection for fisher and marten or 4) for coyote and fox, this represented the naive occupancy; 5) correlations between naive occupancy in each system (FM or CF), in which naive occupancy was 1 if species was ever seen at that site and -1 otherwise; 6) number of sites had confirmed coexist for two species. In total 2,000 posterior predictive detection histories with the same time frame as the original APIS data were sampled and posterior predictive p-values for each statistic were calculated. Small p-values indicated variations the model failed to capture.

Results

Simulations.
Summary statistics of posterior medians of key parameters (Interaction in occupancy, interaction in detection, reaction to environment and strength of spatial auto-correlation). Fig.3 showed that we generally could recover correct inference using regression models but were conservative on spatial auto-correlation due to relative small number of grids, as also shown in Hughes et al. (2011).

FM System.
In total 3×10^6 samples were drawn after 5×10^4 burning in and thinned by 300. Diagnostics showed sufficient mixing of the chain (Fig.S2). Log Bayes factors (log posterior odds of two models) for mainland-island models and stepping stone models were estimated to be 9.82, hence data decisively supports mainland-island rather than the stepping stone model following the recommended cutoff of Kass and Raftery (1995)). Further analysis will be based on the Mainland-Island model.

Table.2 shows the posterior estimations of model parameters of interest for the mainland – island model of the FM system. We detected a significant positive distance dependency in fisher ($\eta^{ex} = 2.479, CI = [0.976, 4.744]$) and a negative distance dependency in marten's occupancy ($\eta^{ex} = -0.789, CI = [-1.907, -0.0558]$).

Table 2. Posterior estimation of model parameters in Fisher-Marten mainland-island system η^{ex} represented the distance dependency, $\eta^{ex} > 0$ meant decay through distance, η^{in} represented the intra-island spatial auto-correlation, γ^{oc} represented the association between species in occupancy and γ^{det} represented the association between species in detection, $P(\theta > 0|data)$ was the posterior probability that certain parameter was greater than 0

Parameter	Median	95% CI	$P(\theta > 0\|data)$
Fisher η^{ex}	2.48	[0.976,4.74]	1.00
Marten η^{ex}	-0.789	[-1.91,-0.0558]	0.016
Fisher η^{in}	0.0378	[-0.232,0.328]	0.60
Marten η^{in}	0.260	[0.0551,0.444]	0.99
γ_{oc}	0.0870	[-0.215,0.393]	0.71
γ_{det}	-0.0122	[-0.326, 0.322]	0.47

However, we did not detect significant association between these species in either occupancy or detection ($CI = [-0.215, 0.393]$, $[-0.326, 0.322]$). Marten showed a intra-island spatial auto-correlation 0.260 $CI = [0.0551, 0.444]$). These findings support hypothesis 2 for the partitioning pattern of fisher and marten on APIS.

Posterior distributions of negative potential functions in the FM system for different terms Fig.4 showed again that association has no significant contribution to the distribution pattern of the FM system. The FM system seemed to be dispersal/environment driven for fisher, while dispersal/environment had similar level of contribution with intra-island spatial auto-correlation for marten.

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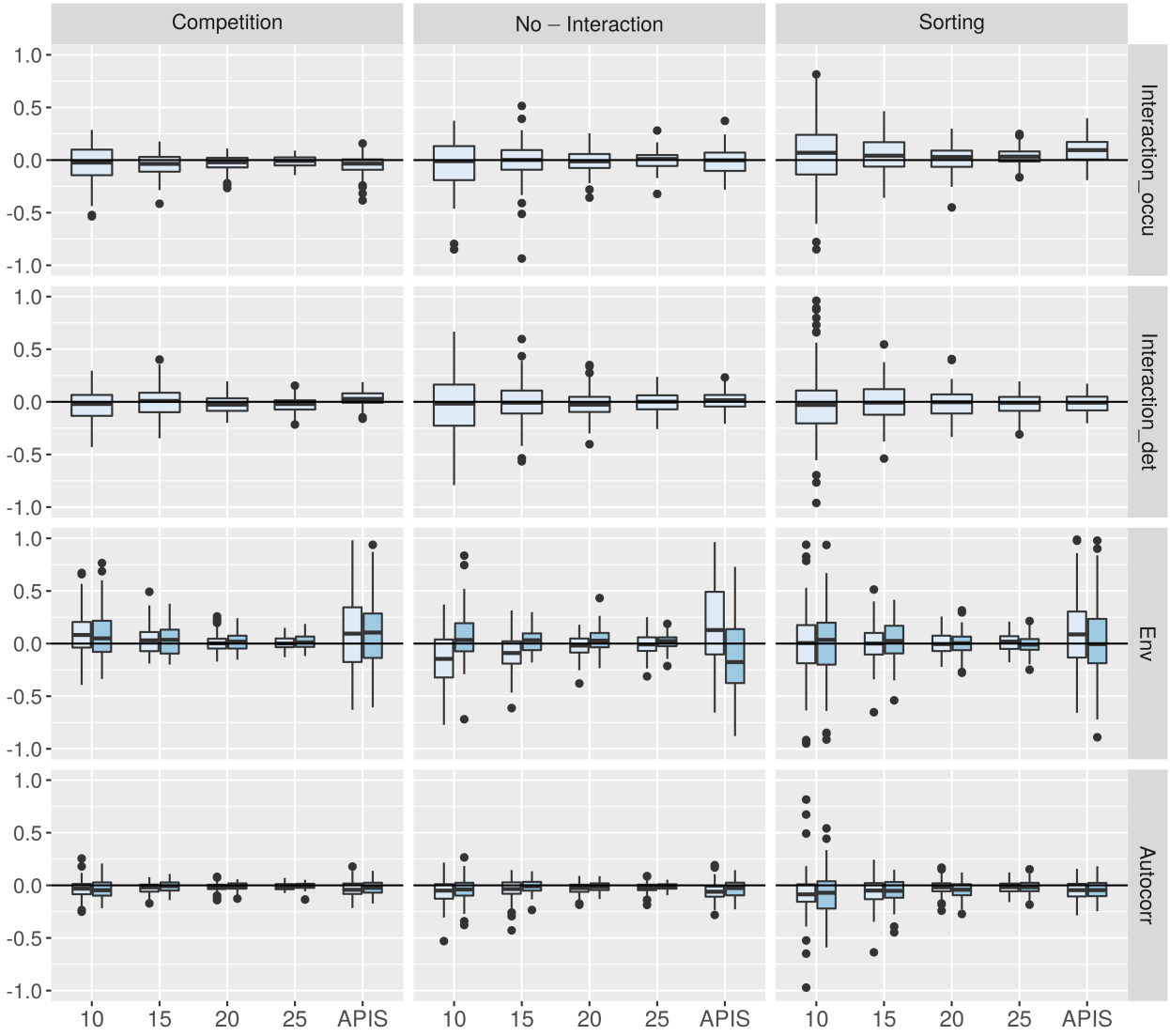

Figure 3. Difference between posterior medians and true parameter values of 100 simulated data sets First column: *Competition*, species had same environment dependency and negative interspecific interaction, Second column: *No interaction*, species had different environment dependency and no interaction, Third column: *Sorting*, species had same environment dependency and positive interspecific interaction. Rows corresponding to parameters estimated in the model. First row: Interaction in occupancy, Second row: Interaction in detection, Third row: Reaction on environment, Fourth row: Spatial autocorrelation. X axis was the size of lattice or APIS (155 grids). Shading of boxes indicates each of the two "species" simulated

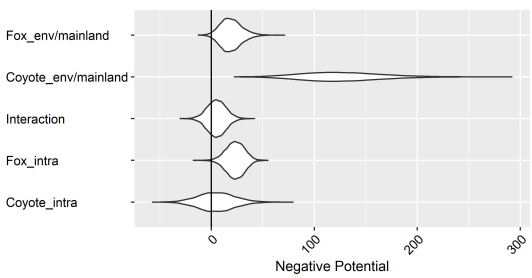

Figure 4. Posterior distribution of different terms in negative potential function Value represent the contribution of certain term in the negative potential function (log likelihood plus constant), note that we combined mainland-island and intercept which represent the overall environment.

Posterior predictive checking showed no conflict between data and our model, all 6 p-values were greater than 0.05 Fig.5.

CF System.

Log Bayes factors (log posterior odds of two models) for mainland-island and stepping stone models were estimated to be 42.2, hence data decisively supported the mainland-island rather than the stepping stone model following the recommended cutoff of Kass and Raftery (1995)). Further analysis will be based on the Mainland-Island model. Table.1 shows posterior estimation of model parameters. We detected a significant positive distance dependency in fox but not coyote (Coyote:$\eta^{ex} = 0.552, CI = [-0.378, 1.69]$ Fox: $\eta^{ex} = 2.41, CI = [0.428, 6.30]$). Meanwhile, posterior association in occupancy was estimated positive ($\gamma_{oc} = 0.234, CI = [-0.041, 0.53]$, $p(\gamma_{oc} > 0|data) = 0.95$). These findings suggest that on top of dispersal/environment drivers, we have some evidence of a positive association

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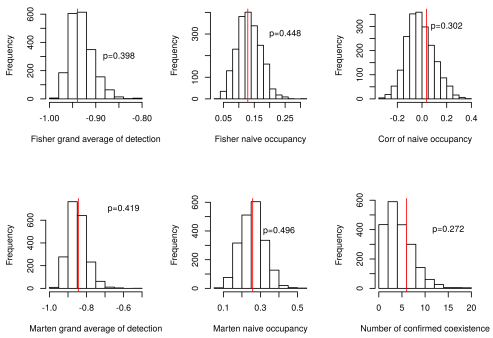

Figure 5. Posterior predictive check for the FM system There were no conflicts between data (red line) and predictive distributions of our model according to the 6 statistics used

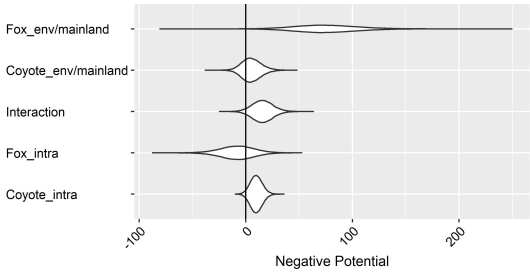

Figure 6. Posterior distribution of different terms in negative potential function Value represent the contribution of certain term in the negative potential function (log likelihood), note that we combined mainland-island and intercept which represent the overall environment.

between two species at grid level that need further evaluation.

Table 3. Posterior estimation of model parameters in Coyote-Fox mainland-island system η^{ex} represented the distance dependency, $\eta^{ex} > 0$ meant decay through distance, η^{in} represented the intra-island spatial auto-correlation, γ^{oc} represented the association between species in occupancy and γ^{det} represented the association between species in detection, $P(\theta > 0|data)$ was the posterior probability that certain parameter was greater than 0

Parameter	Median	95% CI	$P(\theta > 0\|data)$
Coyote η^{ex}	0.552	[-0.378 1.69]	0.88
Fox η^{ex}	2.41	[0.428 6.30]	0.99
Coyote η^{in}	0.196	[-0.0186 0.426]	0.96
Fox η^{in}	-0.0696	[-0.345 0.207]	0.30
γ_{oc}	0.234	[-0.0411 0.528]	0.95
γ_{det}	0.427	[0.211 0.646]	1.00

Posterior distribution of negative potential function in CF system of different terms was shown in Fig.6. Similar to the FM system, dispersal/environment was also driving the CF system. In contrast, spatial auto-correlation and interspecific interaction seemed to be important also. Note that we detected a significant positive association in 60 days scale in detection may due to some behavioral interaction between them.

Posterior predictive checking showed no conflict between data and our model, all 6 p-values were greater than 0.05 Fig.7.

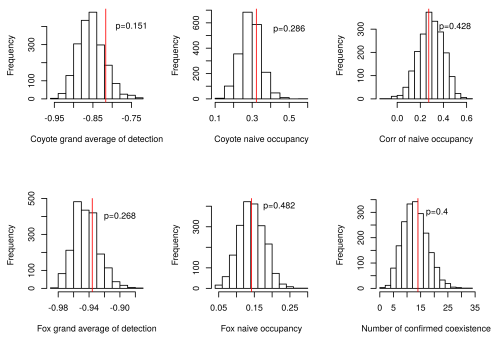

Figure 7. Posterior predictive checking for CF system There were no conflict between data (red line) and predictive distribution of our model according to the 6 statistics used

Discussion

We developed and tested a MRF-based, multispecies, spatially explicit, occupancy model which allowed evaluation of the relative contributions of spatial and life history drivers. This model enables ecologists who conduct research on community structure to consider spatial and life history drivers jointly and explicitly. Though the model assumed patterns constant though time (single season), it is straightforward to extended it into a multiseason model. Compared with Bayesian network-based multispecies frameworks proposed by Kéry and Royle (2008), our method did not ask for a species to be the root of the network and allows cycles in the network. Moreover, analysts can condition occupancy on another species to accommodate a single dominant competitor. Compared with Rota et al. (2016), our method had a better interpretation especially when a species network was large since in our method, interaction between species were modeled explicitly by auto-regression terms. Neither Kéry and Royle (2008) nor Rota et al. (2016) were spatially explicit. Partly because the graph represented the spatial correlation, it had no natural direction and could be represent by a directed graph like Kéry and Royle (2008) did for species while the number of possible patterns was too large to assign unique linear predictors for each pattern as in Rota et al. (2016). Markov random field modeling was used in quantifying interspecific interactions by Harris (2016) and can help identify interactions between species when controlling for environment and other confounding interactions (e.g. apparent competition where A, B both interact with C while no interaction between A and B)(Blanchet et al. (2020)).

Our results on two pairs of plausibly competing species as components of the meso-carnivore community also showed that community structure reflected drivers associated with two broad theoretical paradigms. First we detected positive intra-island spatial-autocorrelation for 2 species out of 4. This spatial autocorrelation term will make sites no longer exchangable even when distance to mainland was controlled. Spatial autocorrelation also had different strengths for the four species considered which means species also were not exchangeable even when considering spatial processes. Coyotes and foxes had different strengths of dependence on mainland distance, likely due to different dispersal ability, i.e. coyotes(which are larger) likely can disperse farther than foxes and, thus have weaker distance dependency.

Note that we detected an opposite direction of mainland distance dependency on occupancy of fisher and marten.

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The FM system provides a possible example where the mainland serves as sink rather than source for a species in a meta population point of view. This spatial pattern was recently verified independently using genetic techniques (Smith et al., in review) A more general meta-community framework should be used in considering island or island-like systems. If two species follow similar dispersal patterns but need to partition spatially we should expect closer islands to be more likely occupied by one of the species than the further islands and partitioning should happen on islands with similar close distances to mainland (i.e. perpendicular to the mainland-island dispersion direction). However, we observed similar level of *co-absence* on island regardless of their distance to mainland, i.e. martens were not occupying close island regardless whether there was fisher or not. Meanwhile the partitioning of fisher and marten happened in parallel (distance dependency) rather than independently of distance (ie competition) to the mainland-island dispersal direction which was different from what we would expect based on hypothesis 1 (i.e. distance dependency with competition). We did not observed fisher and marten occupying sites closer to mainland or partitioning at site level. The FM system appeared to better conform to hypothesis 2 because fishers dispersal direction appeared to be from mainland to islands while martens dispersal appeared to be from islands to mainland. However these results were solely from distribution data and additional evidence from genetics, movement measurements, or behavior etc. would be needed to further support this argument.

For the CF system, we observed that spatial auto-correlation had a strong influence on coyote distribution. This may due to relative small size of the islands compare to coyote home ranges. Typical coyote home ranges were in $10km^2$ scale (Mills and Knowlton (1991); Hibler (1977)) which is around the full size of islands in APIS. Home range size reported for red fox was smaller and in $1 \sim 10km^2$ scale(Ables (1969); Dekker et al. (2001); Trewhella et al. (1988)) and was smaller in size than individual islands in APIS. Together with mainland distance dependency, spatial correlation patterns of coyote and fox were consistent with our knowledge of their movement ability, i.e. coyotes have stronger dispersal ability and larger home ranges and thus weaker distance dependency and stronger intra-island spatial autocorrelation compared with foxes. Patterns of coyotes and foxes demonstrate that species are not interchangeable (Island Biogeography Theory) and that distance dependency is modified by life history characteristics.

The FM system also had a spatial auto-correlation effect. Furnas et al. (2017) reported a meta-analysis on home range sizes in California, USA. Their results showed that female fishers had approximately 6 km^2 at 20 km to the coast to approximately 13 km^2 at 120 km while males had home range sizes that varied from 12 km^2 at 20 km to approximately 27 km^2 at 120 km to coast. We did not detect strong intra-island spatial auto correlation in fisher, which may indicate a relatively small home range for these animals on islands compared to other studies, which was consistent with our prior knowledge that fisher's home range declines when close to coasts (Powell (1982); Yaeger (2005)). Studies of marten home ranges in Canada indicate their home ranges can vary from $10 \sim 100km^2$ scale (Smith and Schaefer (2002)), we also detected spatial auto-correlation for marten. Further home range and movement study may be needed to confirm our findings based on distributions on these islands. Studies in Canada on interaction between coyote and foxes showed that they typically partition through habitat use. But this pattern depends heavily on prey abundance (Theberge and Wedeles (1989)). Evidence also showed coyote may aggressively kill red foxes (Gese et al. (1996)). The positive correlation between foxes and coyotes may suggest that foxes trade off predation risk for prey availablity in a prey-limited system. Prey biomass should be measured to further explain the positive correlation pattern. Further study should be conducted to further evaluate these spatial distribution based findings.

Conclusion

We implemented a MRF based multi-specific occupancy that can account for both spatial auto-correlations and inter-specific interactions simultaneously. We used this technique in a case study on two pairs of presumably competing species in the Apostle Island National Larkeshores. The analysis showed the observed partitioning pattern of fisher and marten can be explained by a flipped source-sink pattern on the island. However more evidence from movement and genetics might be needed to further confirm this observation from distribution study. Meanwhile we detected a positive association among coyote and fox different from studies on mainland systems which deserves further study.

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Supplementary Materials

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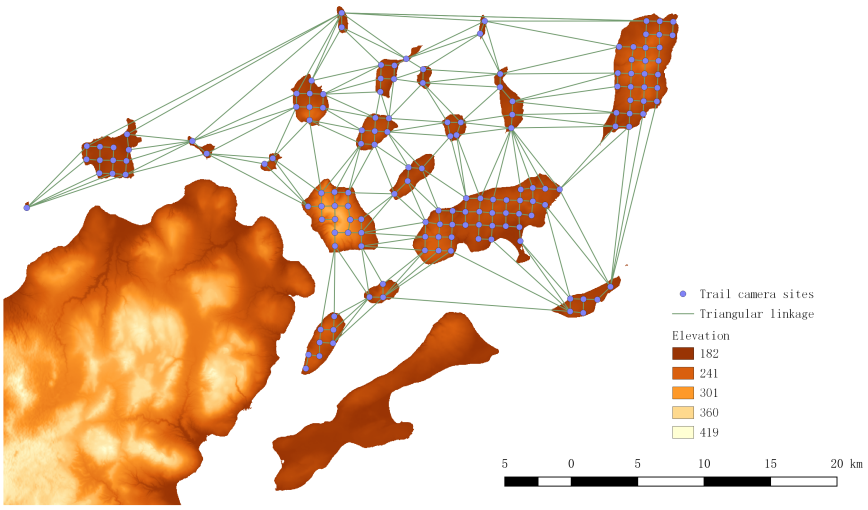

Figure S1. Graph used in Stepping stone model

Stepping Stone Graph

MH Algorithm and Bayes factor

Before Moller's work in 2006, Bayesian inference on MRF models was precluded because the intractable normalizing constant is a function of parameters of interest. Moller proposed an auxiliary variable based on the Metropolis–Hastings ratio (Møller et al. (2006)). A further development due to Murray et al. (2012) is called the single parameter change method. In our case, we follow Murray et al. (2012) by sampling an auxiliary variable X to follow the MRF distribution whose parameters are proposed θ'. Together with imperfect detection, the Metropolis–Hastings ratio is given by eqn.S1.

$$MH(\theta'|\theta) = \frac{\pi(\theta')p(y|Z)q_{\theta'}(Z)q_{\theta}(X)}{\pi(\theta)p(y|Z)q_{\theta}(Z)q_{\theta'}(X)} \tag{S1}$$

The sample can be drawn using the Coupling From the Past algorithm (CFTP Propp and Wilson (1996)) or long enough Gibbs chain for approximation. We tested the difference between using perfect sample taken by CFTP algorithm and Gibbs sample in the single parameter exchange algorithm. Results showed if iteration for Gibbs is large enough (e.g. >150) the posterior distribution sampled by these two method were essentially the same (see example of Fig.S4). CFTP and Gibbs were implemented in `R` and `C++` modified from `R` package `IsingSampler` Epskamp (2015) with help of `RcppArmadillo` Eddelbuettel and Sanderson (2014) and sparse matrix `C++` class provided by `R` package `Matrix` Bates and Maechler (2019) and `Armadillo` to optimized for the sparse graph as we have (open sourcesed as `R` package `SparseIsingSampler` available on `GitHub`).

Posterior sample of $\mathbf{Z}$ will also be taken using a Gibbs algorithm, with fully conditional odds of being $+1$ as

$$\frac{P(Z_{ki}=+1|Z_{-ki},y)}{P(Z_{ki}=-1|Z_{-ki},y)} = \frac{p(y_{1i.},y_{2i}....y_{wi.}|Z_{ki}=1,z_{.i})exp(X_i\beta_k+\sum_{j\in n(i)}\gamma_{ij}^{oc}Z_j)}{p(y_{1i.},y2i....y_{wi.}|Z_{ki}=-1,z_{.i})exp(-X_i\beta_k-\sum_{j\in n(i)}\gamma_{ij}^{oc}Z_j)} \tag{S2}$$

To calculate the Bayes factor, we need to calculate the likelihood of each sample then using the harmonic rule (Raftery et al. (2006)). To calculate the likelihood, we take a sample $\mathbf{Y}$ from a pre-specified parameter setting ϕ, the ratio of normalizing constant $C(\theta)$ and $C(\phi)$ can be calculated as the expectation: $Eq_{\theta-\phi}(\mathbf{Y})$. We can calculate log likelihood added by $-log(C(\phi))$ which is intractable. However, by choosing the same ϕ for two competing models, we can calculate BF of two models by canceling out the intractable constant induced by ϕ.

Simulation

MCMC Diagnostic

We showed the trace plot and auto-correlation function of the interspecific interaction strength in occupancy γ_{oc} as an example of diagnostic

Release of Prior on Detection Rate

Again it is not necessary to set this prior in a more general setting. But on APIS case study, if we release this prior on intercept of detection rate, the posterior had multiple modes for fisher and marten model, due to the fact that fisher's low naive detection

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Table S1. Simulation setting for regular lattice

Parameter	Competition	No interaction	Sorting
β_1	0.5	0.5	0.3
β_2	0.5	-0.5	0.3
η^{in}	0.25	0.25	0.25
γ_{oc}	-0.3	0	0.3
γ_{det}	-0.2	0	0.2

Table S2. Simulation setting for APIS

Parameter	Competition	No interaction	Sorting
η_1^{ex}	1	1	0.3
η_2^{ex}	1	-1	0.3
η^{in}	0.2	0.2	0.2
γ_{oc}	-0.3	0	0.25
γ_{det}	-0.2	0	0.2

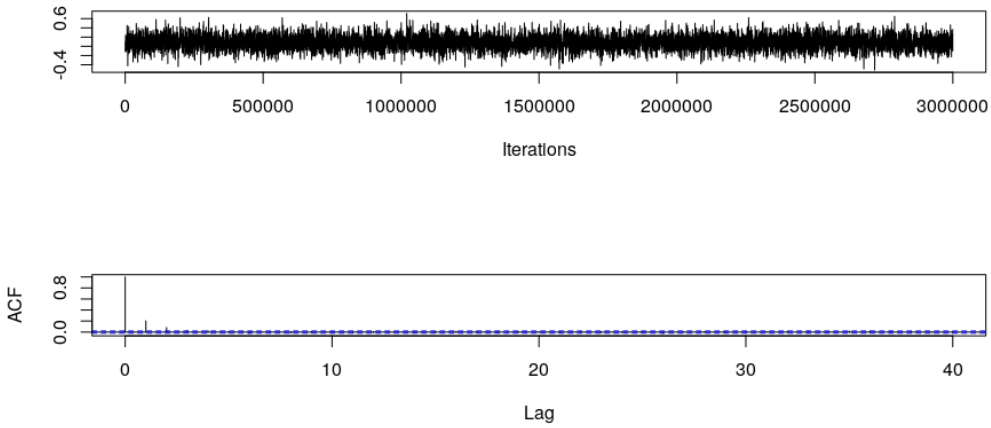

Figure S2. MCMC for γ_{oc} in FM

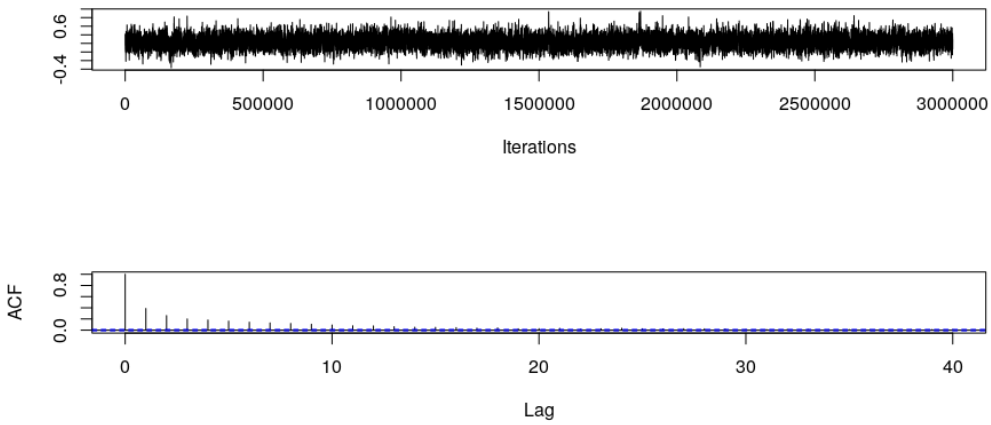

Figure S3. MCMC for γ_{oc} in CF

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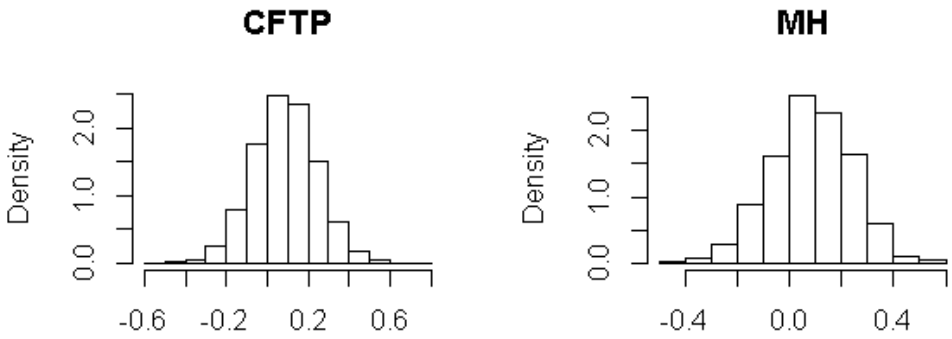

Figure S4. One example of same task using CFTP and MH

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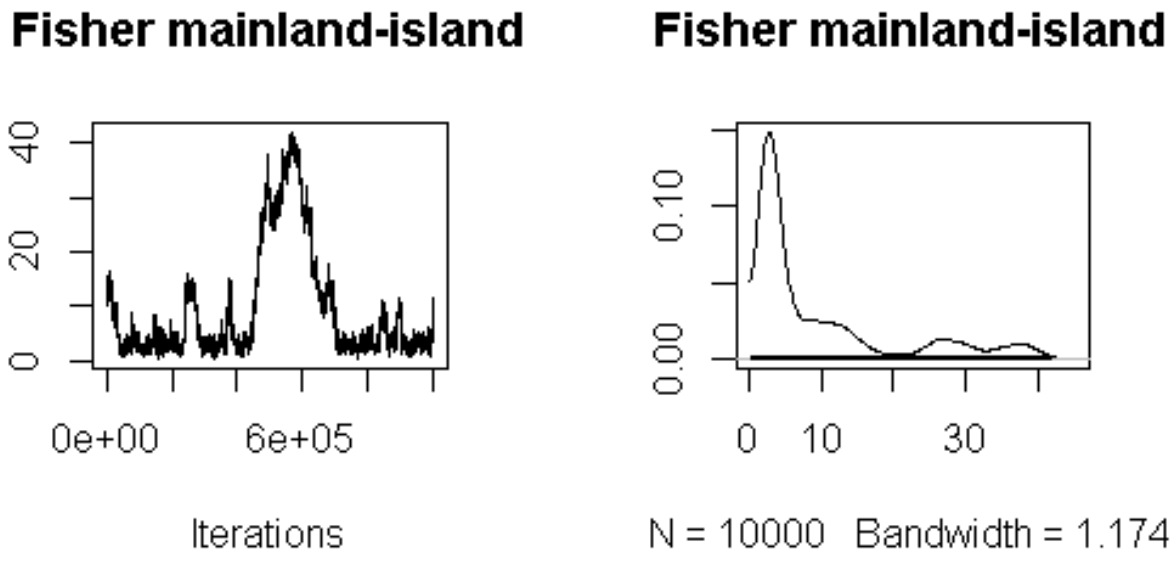

Figure S5. Multiple modes in fisher's mainland-island strength if release the prior

can due to both low occupancy or low detection, these result won't influence our result about fisher and marten system but rather influence the numerical result of spatial auto correlation strength. This will cause a very large and unrealistic mainland-island strength in fisher S5.