



Co-occurrence of invasive and native carnivorans affects occupancy patterns across environmental gradients

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Abstract Understanding species interactions and their effects on distributions is crucial for assessing the impacts of global change, particularly for invasive species. Co-occurrence models can help investigate these effects when interactions are likely given shared traits. For such an assemblage of invasive and native carnivorans, we examined how patterns of co-occurrence change across space and environmental gradients using a static multispecies occupancy model that

accounts for imperfect detectability and models co-occurrence as a function of environmental variables, and also extended it to be temporally dynamic. We focused on invasive raccoons, which pose threats to humans and wildlife globally. In Japan, raccoons prey on many native taxa, but little is known about interactions with sympatric carnivorans. We searched for signals of competitive exclusion of native raccoon dogs (tanuki) and invasive masked palm civets by applying the model to detection data from a broad-scale trapping effort over 6 years. Forest cover was the strongest predictor of occupancy for individual species and raccoon co-occurrences, and raccoon occupancy

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probability increased with forest cover conditionally depending on the co-occurring carnivoran: only tanuki absence or civet presence had positive responses. However, tanuki occupancy probability increased with forest cover despite any co-occurrence. Thus, we found no evidence of competitive exclusion by raccoons, contrary to our expectations. As parts of the world with invasive raccoons can also have invasive tanuki, our findings may have broad management implications. The model we present should be useful for inferring signals of biotic interactions between species with low detectability over multi-year time frames.

Keywords Competitive exclusion · Invasive species · Occupancy model · Multispecies · Carnivoran · Biotic interaction

Introduction

As global change shifts species' distributions and thus rearranges ecological communities (Blois et al. 2013), it is increasingly vital that we better understand how novel interactions between species will affect their distributions (Wiszniewski et al. 2013). Interaction networks between species, whether positive (i.e., mutualism, commensalism) or negative (i.e., competition, predation, parasitism), can help maintain community stability and resilience during episodes of environmental perturbation (Oliver et al. 2015). Failing to account for species interactions can hamper our ability to make accurate forecasts of species responses to future change (Gilman et al. 2010; Blois et al. 2013). For example, the introduction of invasive species into a community can alter existing interactions through the displacement of weaker competitors and predation on native species (Tylianakis et al. 2008), and the magnitude of these effects can increase with a changing climate (Walther et al. 2009). Currently, invasive species are recognized as the largest global cause of species extinctions second only to habitat destruction (Bellard et al. 2016), which makes studies on the spatial nature of interactions involving invasive species all the more urgent.

As direct observations of species interactions in nature are difficult, many studies indirectly infer interactions from macroscale species co-occurrence

patterns, which necessarily comes with caveats (Morales-Castilla et al. 2015). For example, although negative co-occurrence patterns between species may be a signal of competition, they may also be the result of differing environmental preferences. Further, co-occurrence could be the result of either a lack of shared resources or differences in diel activity. Nonetheless, when there is *a priori* knowledge of shared species traits that make interactions likely, examining co-occurrence patterns can be informative about how species interact at the macroscale.

Species distribution models, broadly defined as models that estimate the relationship between environmental variables and species' occurrence localities (Franklin 2010; Peterson et al. 2011), are often employed to predict occurrence patterns across space for individual species. Co-occurrence between species has been predicted by overlaying (or "stacking") multiple species' model predictions (Guisan and Rahbek 2011), or by modeling with "biotic" predictor variables that hold information about interacting species (Araújo and Luoto 2007). In contrast, multi-species distribution models estimate how the presence of individual species is affected by co-occurrence with other species in a community, usually by examining correlations between co-occurring species that have environmental relationships drawn from a common distribution (Ovaskainen et al. 2010; Pollock et al. 2014; Warton et al. 2015). An additional consideration when modeling co-occurrences is accounting for imperfect detection, which can result in prediction errors that lead to misinterpretations of co-occurrence patterns (Beissinger et al. 2016). Occupancy models solve this problem by modeling detection as dependent on the species occupancy state (presence or absence) (MacKenzie et al. 2017), and multispecies occupancy models (MSOMs) have been developed for community predictions (Iknayan et al. 2014). However, there are several key shortcomings that apply to most MSOMs. Those that explicitly include interactions have primarily been limited to species pairs (MacKenzie et al. 2004), some require assumptions about the directionality of species interactions (Richmond et al. 2010; Scully et al. 2018), and they generally model co-occurrence as a correlation and thus cannot examine how interactions affect environmental responses. To date, MSOMs have not been applied to communities with invasive species, which have mostly been the focus of studies on individual

species (Gormley et al. 2011; Preston et al. 2012) or restricted to species pairs (Waddle et al. 2010; Farris et al. 2016).

A novel addition recently proposed by Rota et al. (2016) results in a more flexible MSOM that can be fit for two or more species, does not require any *a priori* assumptions about interactions, and can model co-occurrence as a function of environmental variables in a single time period. As interactions (with co-occurrence as proxy) are explicitly accounted for by this model, if we expect the occupancy state of one species to affect that of another, we can examine the model results for these signatures. In addition to marginal occupancy probabilities (i.e., generalized estimates pertaining to individual species), conditional occupancy probabilities (i.e., estimates dependent on the presence/absence of another species) can also be derived from this model. Importantly, the conditional occupancy probability can inform how co-occurrence with a potential interactor alters the focal species' response to the environment regardless of shared environmental preferences, as well as provide evidence for potential competitive exclusion.

The present study expands upon the static Rota et al. (2016) MSOM to define a dynamic multi-year model and uses it to examine how patterns of co-occurrence change across environmental gradients for an assemblage of invasive and native carnivorans. This temporally dependent model considers species' occupancy of previous years when estimating occupancy probability at the present time step. Further, as this model assumes imperfect detection, it is especially suitable for species with low detectability such as crepuscular or nocturnal carnivorans. Such a model should allow generalizable and rare insight into how multiple elusive species interact along different gradients (e.g., from urban to rural areas) while also considering the known occupancy history for each species across sites. In addition, it should help elucidate relationships between co-occurrence and the environment that lead to testable hypotheses regarding how species interactions may change over the examined environmental gradients. This is especially relevant for invasive species management, as particular environments with high predicted impact on native species caused by interactions with invasive species can be targeted for increased monitoring or action. It should also be emphasized that this methodology has great potential to allow for monitoring and

assessments of the impact of invasive species on native populations within relatively quick time frames.

The North American raccoon (*Procyon lotor*, hereafter "raccoon") is a mid-sized carnivoran that is invasive in areas across the globe, including Europe (Beltrán-Beck et al. 2012; Bartoszewicz et al. 2008), the Middle East (Farashi et al. 2013), Central Asia (Heptner and Sludskii 2002), and Japan (Ikeda et al. 2004). Ubiquitous in its native range of North and Central America, the raccoon can be found in habitats ranging from lowland to mountainous areas, and from forest to scrubland and desert (Zeweloff 2017). Throughout their invaded range, raccoons are responsible for health threats to humans and domestic animals by carrying zoonotic diseases such as roundworm and rabies (Duscher et al. 2017). In particular, the raccoon is a serious management concern in Japan because of its multiple roles as disease vector, agricultural pest, and threat to native wildlife (Ikeda et al. 2004). Introduced primarily via the pet trade in the 1970's, raccoons have since become naturalized throughout most of the country (Ikeda et al. 2004). They are the largest wild predator in most Japanese urban and suburban areas (Koike 2006), and are known to prey on endangered salamanders, freshwater clams, land crabs, and bird eggs (Ikeda et al. 2004; Hayama et al. 2006). Although eradication plans have been recommended based on results from field studies (Ikeda 2006) and modeled expansion rates (Koike 2006), only several studies have investigated competitive interactions between raccoons and other Japanese carnivorans. The native raccoon dog (*Nyctereutes procyonoides*, hereafter the Japanese name "tanuki" to avoid confusion) and the invasive masked palm civet (*Paguma larvata*, hereafter "civet") share a number of traits with raccoons, including a strong association with forest cover, varying degrees of arboreal behavior, omnivorous diet with high overlap, and attraction to areas of human activity (Matsuo and Ochiai 2009). These similarities make interactions between them likely at sites where they co-occur. Although tanuki are also invasive in Europe and similarly targeted for removal, in Japan, where they are native, there is increasing concern they are competitively excluded from suitable areas by invasive raccoons (Ikeda et al. 2004; Abe et al. 2006). However, a lack of consensus persists about the nature of interactions between these species, as current knowledge is based on a few local-scale studies with

differing results (Abe et al. 2006; Okabe and Agetsuma 2007; Kuriyama et al. 2018). Competitive exclusion of tanuki by raccoons was suggested to explain differential habitat use, namely greater use of forest core areas and lesser use of forest edge and farmland by tanuki (Abe et al. 2006). However, existing differences in spatial and temporal habitat use may limit direct contact and thus actual competition (Okabe and Agetsuma 2007). Further, tanuki population density was impacted negatively by raccoon count, yet positively by civet count, perhaps due to habitat partitioning or competition with raccoons and shared resources with civets (Kuriyama et al. 2018). Importantly, no study on this system has used a multispecies modeling approach to explore raccoon co-occurrence patterns, and it remains unknown how these patterns may change across environmental gradients for a large spatial extent.

Here, we use a three-species MSOM with temporal dependency to find signals of competition within this assemblage of invasive and native carnivorans based on trapping data from 2010–2015. We focus on Kanagawa prefecture just south of Tokyo, where raccoons became naturalized around Kamakura city in 1988, one of three main naturalization points in Japan (Ikeda et al. 2004), and raccoon density is known to be especially high. Raccoon expansion was reported to have increased from 13% of the total prefectural area in 2001 to 27% in 2004 (Hayama et al. 2006), but by 2010 raccoons are thought to have colonized most suitable sites—hence, there should be no strong effect of distributional disequilibrium, which is an issue of concern for studies on invasive species. We address three overarching questions: (1) How does occupancy for these species respond to environmental conditions, and how does co-occurrence affect the response?; (2) Is there evidence that raccoons are competitively excluding either tanuki or civets?; and (3) What are the geographic patterns of occupancy for these species across Kanagawa?

Materials and methods

Occupancy data

We acquired data for a multi-year raccoon trapping program from the Kanagawa Prefecture Department of Environment and Agricultural Policy (URL: [http://](http://www.pref.kanagawa.jp/div/0505/)

www.pref.kanagawa.jp/div/0505/; in Japanese). Community volunteers, including local farmers, each set a single trap (Havahart #1079 large one-door, or similar models) on their property targeting raccoons for varying amounts of time (day and night) from 2010 to 2015 and sent forms detailing the results back to the Department on an annual basis. In the few areas where raccoon removal programs were being implemented (e.g., Yokosuka and Yokohama), there were cases where some traps were also set in public parks. In addition to raccoons, this dataset includes information on detection for all animals caught, number of trapping days spent, and date of capture. A majority of the baits implemented were dog/cat food or sweet snack foods, as suggested during training sessions conducted by the Department; some exceptions existed, but no regional biases were observed. As trapping design was not standardized across sites, trap coordinates were matched to 1 km grid cells that cover the prefecture (Japanese Standard Mesh System; Biodiversity Center of Japan 2016), and we recorded summarized detection/non-detection (1,0) per grid cell. Thus, the detection summary per grid cell is similar in nature to gamebag data, which has been used for documenting distributional changes in raccoons (Fischer et al. 2015). For time periods that lacked detection data for grid cells that had detection data for other time periods, these entries were designated as NA. Volunteers did not report whether trapped animals were released or exterminated, though no major differences between regions are expected to exist. All three species were detected across the study extent, and thus no clear distributional limits exist that could bias co-occurrence patterns (Fig. S1).

We divided each year in the dataset into four 3-month seasons and summarized all grid-cell detections per season. Each season was treated as a discrete “survey” for the year (or “sampling occasion” *sensu* MacKenzie et al. 2002) and total detections were simplified to detection/non-detection per visit for each species per grid cell. The dataset used for analysis (without specific trap coordinates to protect individual privacy) is available from the Dryad Digital Repository is available for download online (<https://doi.org/10.5063/F1X34VS1>).

Environmental data

Habitat selection for raccoons in both native and introduced ranges has been shown to be associated with proximity to urban areas, forests, and water bodies (Prange et al. 2004; Beasley et al. 2007; Ordeñana et al. 2010; Duscher et al. 2018). Further, both tanuki and civet are highly associated with forest, and use shelter and food resources in urban areas (Saito and Koike 2013). We used this information to select environmental predictor variables for Kanagawa from Japan's National Land Numerical Information (NLNT) and the Biodiversity Center of Japan (BCJ). These included vector data for streams (year 2008; NLNT 2008) and wetlands (year 1995; Biodiversity Center of Japan 2005) and raster data at 1 km resolution for land use (year 2009; NLNT 2009) and human population density (year 2010; NLNT 2010). Metadata sources for these datasets can be found in Table S1.

We used this data to generate four environmental predictor variables to predict occupancy for the three carnivorans: forest cover, agricultural extent, wetland perimeter length, and human population density. All data analysis was performed using the R statistical programming language v3.4.4 (R Core Team 2018). From the land use dataset, we summed the "rice paddies" and "other agricultural" classes to derive a general "agriculture" class, and extracted this and the "forest" classification. To characterize the area of shallow wetland accessible to terrestrial carnivorans, we developed a "wetland perimeter length" variable representing the summed length of stream lines and wetland perimeter. To accomplish this, we converted the wetland polygons to polyline, merged them with the stream layer, and calculated total line length in meters per grid cell using the R package *sp* (Pebesma and Bivand 2005). The highest pairwise correlation between our four environmental predictor variables was 0.53 (forest and human population density), and thus we determined there were no problems of collinearity. As a measure of survey effort, we also used the number of trapping days per site per sampling occasion as a predictor variable for detection. All variables were centered and scaled using the `scale()` function with defaults in R.

Model specification

We modified a multispecies hierarchical occupancy model originally specified by Rota et al. (2016) to explore the effect of co-occurrence on occupancy across environmental gradients for the focal carnivoran assemblage. This model, which we implemented using JAGS v4.3.0 (Plummer 2017) with the R package **R2jags** (Su and Yajima 2015), extends the single-species framework of MacKenzie et al. (2002) to two or more species and models co-occurrence as a function of environmental variables. The observed occupancy state, y_{sijt} , for species s at site i during survey j at time t , is an imperfect observation of the latent (unobserved) true occupancy state z_{sit} (1 or 0). For this study, years are represented by t , each of which has $j = 4$ surveys that correspond to the specified seasons. These repeat samples j per year t are used to model p_{sijt} , the probability of detection (MacKenzie et al. 2017). The observed occupancy state y_{sijt} is derived as the product of the true occupancy state z_{sit} and the detection probability p_{sijt} , which ensures that species absence cannot result in detection, but also that non-detections can be observed even when the species is truly present (MacKenzie et al. 2017). The observed occupancy state y_{sijt} is thus conditional on the true occupancy state z_{sit} , and both are modeled as Bernoulli random variables (Eqs. 1, 2).

$$z_{sit} \sim \text{Bernoulli}(\psi_{sit}) \quad (1)$$

$$y_{sijt} | z_{sit} \sim \text{Bernoulli}(z_{sit} p_{sijt}) \quad (2)$$

Rota et al. (2016) modeled the true occupancy states z_{sit} as functions of the set of occupancy probabilities for all species with the multivariate Bernoulli distribution using the Bayesian programming language STAN. However, as JAGS v4.3.0 does not support this distribution, we instead modeled z_{sit} using categorical random variables (Eq. 3; *pers. comm.* Christopher Rota; also see Fidino et al. 2019), where modeled categories corresponded to the different possible occupancy states of the system stored in a matrix M (Eq. 4). For three species, the occupancy state [111], for example, would denote all species present, whereas [110] would denote species 1 and 2 present and species 3 absent (Table 1). We derived occupancy probabilities for each state ($\psi_{111}, \psi_{110}, \dots$) using the formulations for natural parameters described in detail

Table 1 Different occupancy states of the carnivoran assemblage considered in this study

R	T	C	ψ	Description
0	0	0	ψ_{000}	None detected
1	0	0	ψ_{100}	Raccoon
0	1	0	ψ_{010}	Tanuki
0	0	1	ψ_{001}	Civet
1	1	0	ψ_{110}	Raccoon + tanuki
1	0	1	ψ_{101}	Raccoon + civet
0	1	1	ψ_{011}	Tanuki + civet
1	1	1	ψ_{111}	All detected

The first three columns refer to raccoon, tanuki, and civet, respectively, while ψ refers to the occupancy probability estimated for each state. Refer to Online Appendix A for how these are calculated using different combinations of the natural parameters (f_1, f_2 , etc.), and Online Appendix B for how the conditional occupancy probabilities are calculated using different combinations of ψ

in Rota et al. (2016), and stored them for each year t in matrix Ψ_{it} (Eq. 3). In this model formulation, the natural parameters $f_1, f_2, f_3, f_{12}, \dots$ correspond to the log odds a species (or multiple species) occupies a site, and can be used to obtain occupancy probabilities (Rota et al. 2016, see Online Appendix A for derivations). The categories modeled based on the occupancy probabilities in Ψ_{it} are stored in x_{it} , which are then used to index the corresponding occupancy states for each species s at site i during year t and assigned to z_{sit} (Eq. 4).

$$x_{it} \sim \text{Categorical}(\Psi_{it}) \tag{3}$$

$$z_{sit} = M[x_{it}[i, t], s] \tag{4}$$

Both the detection probability p_{sijt} and each natural parameter (from which occupancy probabilities $\psi_{111}, \psi_{110}, \dots$ are derived) can be modeled as linear functions of predictor variables. We modeled p_{sijt} as a function of the number of trapping days, effort_{sit} (Eq. 5).

$$\text{logit}(p_{sijt}) = a_0 + a_1 \text{effort}_{sit} \tag{5}$$

We modeled each natural parameter ($f_1, f_2, f_{12}, f_{13}, f_{23}$; where numbers correspond to species) in the first year as a function of the 4 environmental predictor variables. For site i (i.e., grid cell i), $frst_i$ represents the forest cover in hectares, $agri_i$ the agricultural extent in hectares, $wetl_i$ the wetland perimeter in

meters, and $pden_i$ the human population density in number of recorded individuals. Eq. 6 shows the equation for the natural parameter f_1 (representing species 1) for year 1. We modeled all two-way interactions, but as we did not expect any clear relationships with the environment for a three-way interaction in this system and were focused on two-way interactions in this study, we set f_{123} to 0. Finally, using the derivation methods outlined in Rota et al. (2016), we calculated the marginal and conditional occupancy probabilities for each species and interaction (ψ_M and ψ_C , respectively; see Online Appendix B).

$$f_1 = b_0 + b_1 frst_i + b_2 agri_i + b_3 wetl_i + b_4 pden_i \tag{6}$$

We additionally made our model temporally dependent by adding a temporal autologistic term (Royle and Kéry 2007; Zipkin et al. 2012). For years $t > 1$, we modeled the natural parameter for each species s (each of f_1, f_2, f_3) with an additional autologistic parameter ϕ_s , which was dependent on the occupancy state of species s at site i during the previous year $t - 1$ (z_{sit-1}). Eq. 7 shows the equation for f_1 (representing species 1) for year t , where $t > 1$.

$$f_{1t} = b_0 + b_1 frst_i + b_2 agri_i + b_3 wetl_i + b_4 pden_i + \phi_1 z_{1it-1} \tag{7}$$

We did not use a fully dynamic model here (i.e., site colonization/extinction; MacKenzie et al. 2003), as inference was focused on occupancy estimates derived from ψ . Further, we did not expect occupancy patterns to change substantially during this time period, as all species were already well established in the region.

We used vague priors for all parameters (normal with $\mu = 0$ and $\tau = 0.25$) as we lacked prior information on the relationship of occupancy to the chosen predictor variables for these carnivorans. We ran 3 chains for 20,000 iterations after a burn-in of 10,000 and thinned our chains by 20, resulting in 500 samples per chain. The model was initialized using naïve (observed) estimates of occupancy states for each species and a random draw of occupancy for sites with no detections over all seasons in a given year. We verified convergence for model coefficients by calculating the Brooks–Gelman–Rubin convergence diagnostic ($\hat{R} < 1.1$) and confirming stability of the posterior predictions via trace plots. We calculated ψ_M for each species and ψ_C for each species pair

following Rota et al. (2016) using the full posterior distribution to generate response curves for all predictor variables. We also calculated occupancy predictions for all grid cells in the Kanagawa study extent with data, and generated maps of ψ_M for all species. We evaluated the model by examining the results of posterior predictive checks (i.e., Bayesian p values) similar to those based on model deviance recommended for multispecies occupancy models by Broms et al. (2016), but that instead compare summary statistics of the posterior predictions to those of the observed data. Specifically, they calculate the proportion of posterior predicted values that were higher (or lower) than the observed value (the minimum of the two was chosen), where values represented mean frequencies of each occupancy state either predicted or observed over all years. Bayesian p values greater than 0.05 indicate no lack of fit for each particular occupancy state. We also ran the same posterior predictive checks after iteratively excluding one year's data to judge the sensitivity of each state to the variance of the data across years. Additionally, to determine whether removal of individuals would change our results, we fit a removal model (MacKenzie et al. 2017) using this same parameterization with modified data: for each set of j observations y_{sijt} , we assigned all observations in a year following a positive detection (1) to NA. The JAGS code that specifies the model can be found in Online Appendix D.

As an example of how we may expect the results to align with our ecological expectations, consider that the occupancy probability of species 1 is affected by co-occurrence with species 2 along the range of environmental variable x , but not vice versa. We should observe that the conditional probability ψ_C for species 1 along the range of x differs depending on the presence/absence (i.e., occupancy state) of species 2. However, ψ_C for species 2 along the range of x should not differ regardless of the occupancy state of species 1. Whether or not co-occurrence between these species affects their conditional occupancy probabilities, their marginal occupancy probabilities ψ_M , which incorporate the sum of all possible occupancy combinations, should not be affected. Derivation of ψ_M for each individual species and ψ_C for each species pair will help us assess our first and second objectives, and predicting the values of ψ_M for each species across Kanagawa will help us assess our third objective.

Results

Model evaluation, intercepts, and coefficients

The model converged after 20,000 MCMC iterations and the posterior predictive checks resulted in Bayesian p values above 0.05 for most occupancy states when averages were taken across all years (Fig. S2). The posterior predictions for the tanuki and raccoon-civet occupancy states were on average higher than observed, resulting in p values of 0.02 which indicates lack of fit. However, when we iteratively removed data for each year and recalculated the p values, we found that the removal of years 2012 or 2015 resulted in p values higher than 0.05 for all occupancy states (Table S4). As the highest p values (i.e., those with the closest fit between posterior predictions and observed values) for each state were different across the different year-removal iterations, we decided to report our results for the full dataset. We must therefore interpret the results for model coefficients for both tanuki and raccoon-civet, as well as the raccoon-civet conditional model response (ψ_C), with some uncertainty. The marginal model responses (ψ_M) are summed over all occupancy state combinations associated with a species, and thus these responses are unlikely to be affected much by any single occupancy state.

The model resulted in predictor variable responses that varied in strength and direction for each occupancy state (Fig. 1). We refer to the response strength of the model intercepts and coefficients using two gradations: “strong” responses do not overlap zero at the 95% credible interval, while “weak” responses do not overlap zero at the 50% credible interval (see Table S3 for exact values). Only strong responses are discussed in this section, shown with the notation (mean \pm standard deviation) of the posterior distribution, and these varied both by species and variable (Table S3). Forest cover coefficients had strong positive responses for raccoon (1.13 \pm 0.35), tanuki (2.44 \pm 0.48), and raccoon/civet (1.49 \pm 0.37), but a strong negative response for raccoon/tanuki (− 1.43 \pm 0.47). Wetland perimeter coefficients had strong negative responses for civet (− 0.28 \pm 0.11) and raccoon/civet (− 0.27 \pm 0.14). Human population density coefficients had strong negative responses for raccoon (− 0.61 \pm 0.10) and civet (− 0.30 \pm 0.14), yet a strong positive response for raccoon/tanuki

(0.66 ± 0.32). The occupancy intercept for raccoon/tanuki had a strong negative response (-0.76 ± 0.34), while the intercept for raccoon/civet had a strong positive response (1.17 ± 0.24 ; indicating the effects of co-occurrence between these species on occupancy). Detection intercepts had a strong positive response for raccoon (0.47 ± 0.04) and strong negative responses for tanuki (-1.24 ± 0.10) and civet (-0.31 ± 0.05), while survey effort (number of trapping days) had no significant effect on detection for any species at either the 95% or 50% credible

interval (Table S3). Thus, raccoons were most likely to be detected and tanuki least likely, with survey effort having a minimal effect (Fig. S8). The temporal autologistic coefficients indicated that past occupancy was a good indicator of present occupancy for all species, though to varying degrees, with raccoons being the lowest (1.73 ± 0.15), tanuki being mid-range (2.25 ± 0.31), and civets being highest (2.94 ± 0.21). Lastly, the removal model had variable coefficients that were very similar to the original

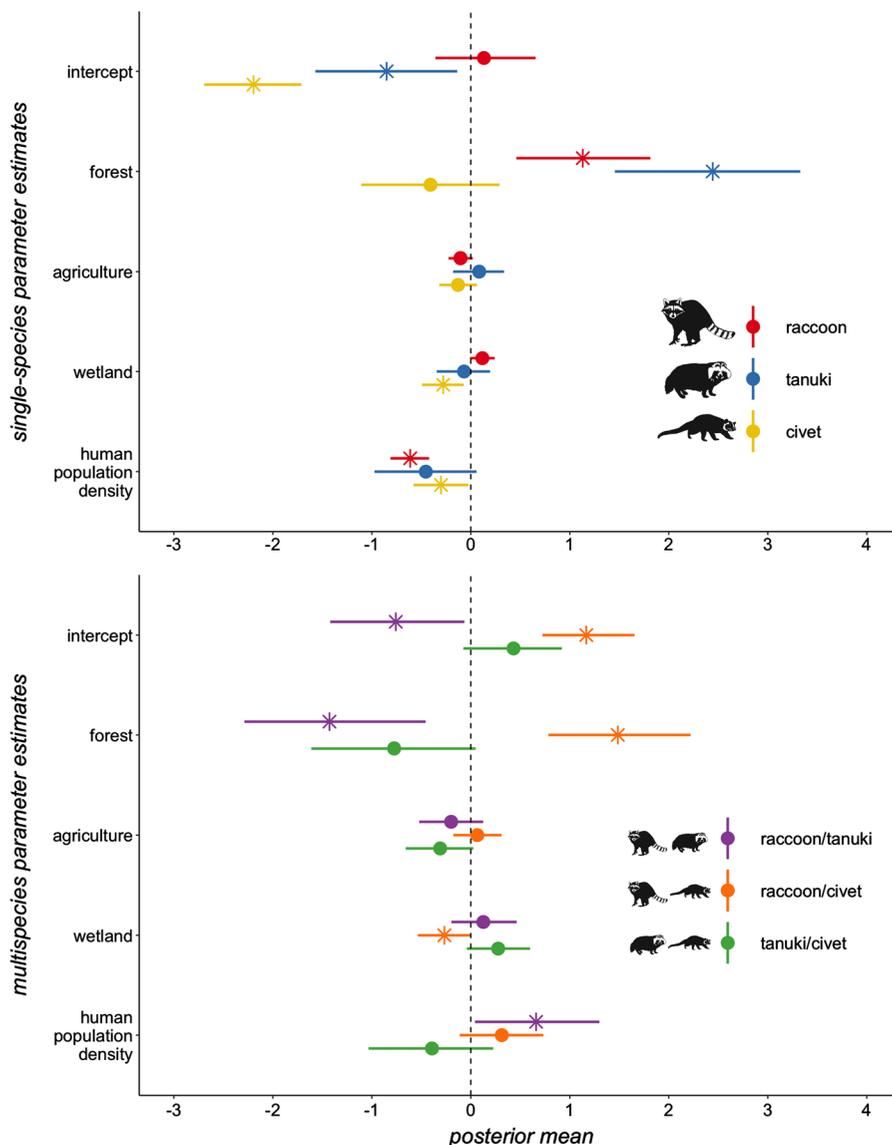


Fig. 1 Single-species and multispecies parameter estimates for occupancy probability with 95% credible intervals. Asterisks represent coefficients with strong relationships to occupancy (i.e., credible intervals do not include 0)

model, and thus did not change the results in any appreciable way (Fig. S10).

Environmental responses to individual species occupancy

The model response of the marginal occupancy probability (ψ_M), or the sum of occupancy probability over all the possible occupancy combinations where the focal species is present, differed by species over predictor variable ranges (Fig. 2). In this section, “strong” and “weak” responses are discussed, and these are noted in parentheses (see Table S3 for exact values). Forest cover had a positive relationship with ψ_M for raccoon (strong), tanuki (strong), and civet (weak). The response was most dramatic for raccoon and tanuki, though raccoon ψ_M peaked at intermediate forest-cover values (Fig. 2). Agricultural cover had a slight positive relationship with tanuki ψ_M (weak) and negative relationship with ψ_M for raccoon (weak) and civet (weak). Wetland perimeter had a positive relationship with raccoon ψ_M (weak), yet a negative relationship with civet ψ_M (strong). Human population

density had negative relationships with ψ_M for raccoon (strong), civet (strong), and tanuki (weak).

Effect of co-occurrence on species occupancy across environment gradients

The response of the conditional occupancy probability (ψ_C), or the probability that the focal species is present dependent upon the occupancy state of another species, varied considerably across species pairs (Figs. 3, 4). Raccoon ψ_C had clear positive responses to forest cover when tanuki was absent and civet present, but slight negative responses when tanuki was present and civet absent (Fig. 3). On the other hand, tanuki ψ_C had positive responses to forest cover regardless of the occupancy states of raccoon or civet (Fig. 4). Civet ψ_C had responses similar to raccoon ψ_C (Fig. S3), although the tanuki/civet coefficient for forest cover had only a weak relationship (Table S3). Raccoon ψ_C had a somewhat more positive response to human population density when tanuki were absent (Fig. S4), though the response varied little across the range of observed values, while tanuki ψ_C was higher

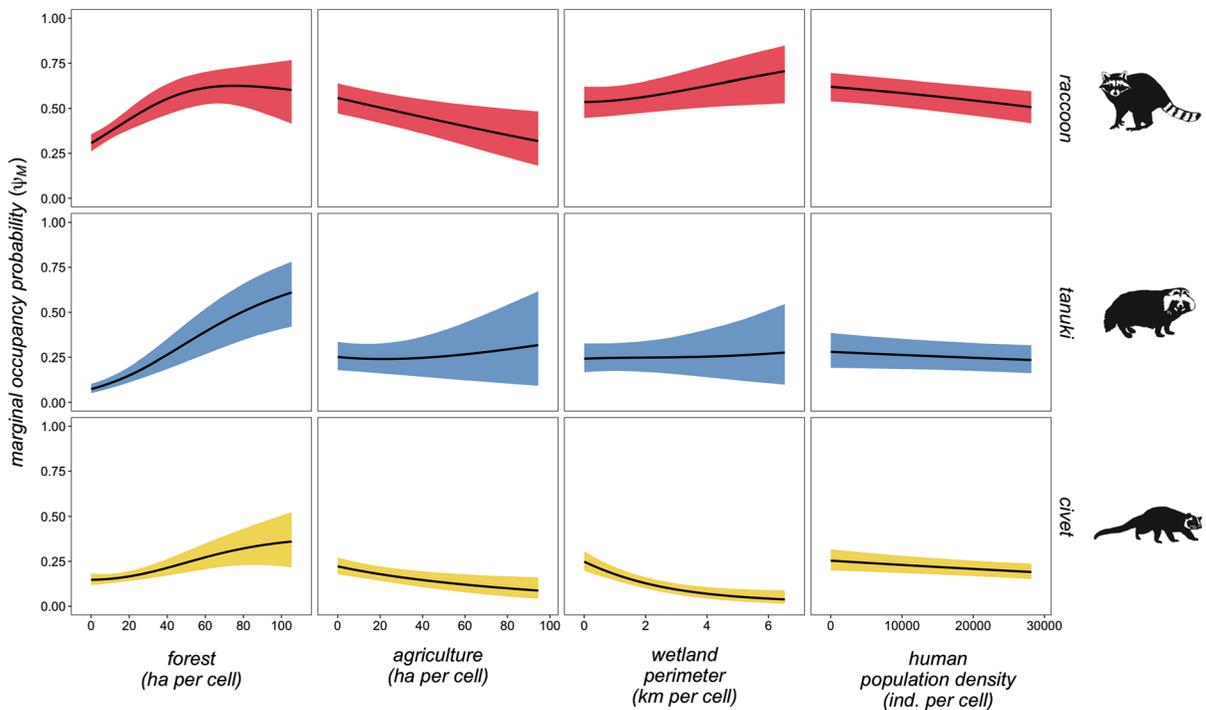


Fig. 2 Predictor variable response curves for occupancy probability of each individual species (i.e., marginal occupancy probability, summed over all occupancy states species was

detected), in black with colored 95% credible intervals: raccoon (red), tanuki (blue), and civet (yellow)

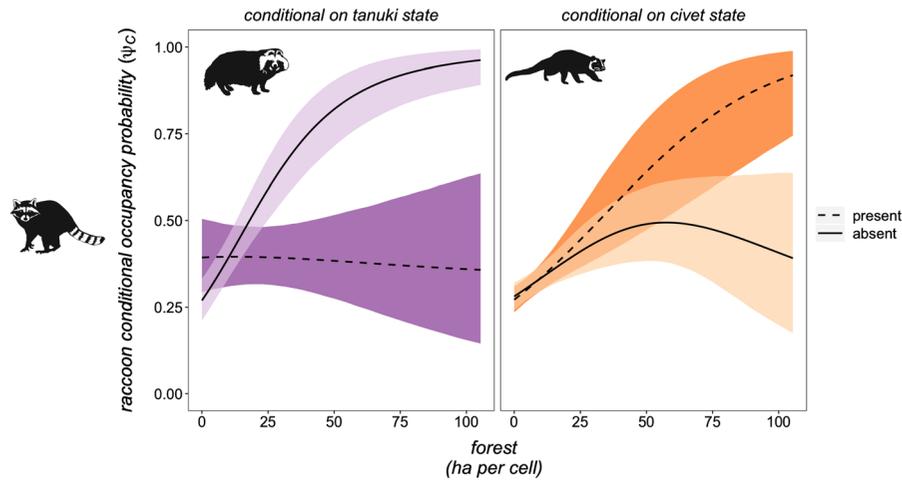


Fig. 3 Response curves for raccoon occupancy probability when tanuki (left) or civet (right) is either present or absent (i.e., conditional occupancy probability) over a range of forest cover values

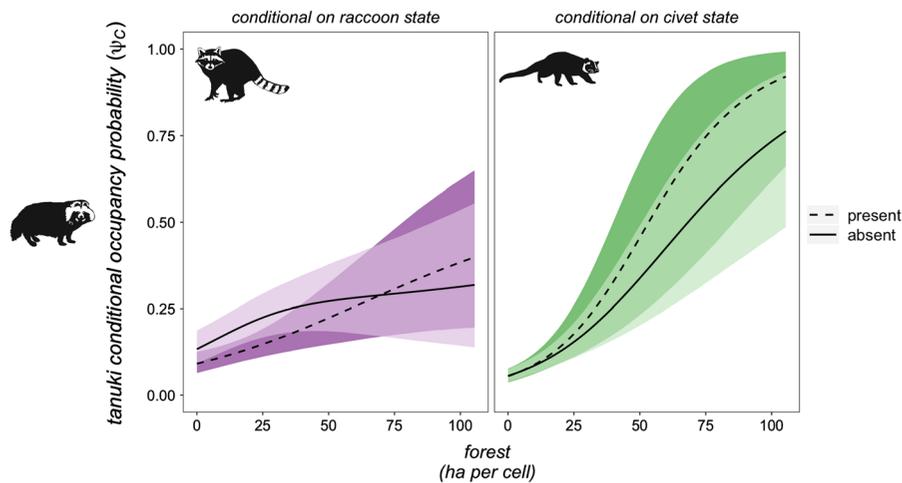


Fig. 4 Response curves for tanuki occupancy probability when raccoon (left) or civet (right) is either present or absent (i.e., conditional occupancy probability) over a range of forest cover values

for less populated areas when raccoons were absent (Fig. S5). Raccoon ψ_C rose with increasing wetland perimeter regardless of civet occupancy (Fig. S6), while civet ψ_C was generally higher for areas with more wetland when raccoons were absent (Fig. S7). A full account of the total observed occupancy states and year-to-year transitions that informed the model can be found in Table S2.

Geographic occupancy patterns of individual species

In general, ψ_M for all species was highest in the Kamakura region, further south in the Miura Peninsula, and in western Kanagawa (Fig. 5). Predictions for ψ_M were also made to areas that had no detection data and thus were not used to build the model—these cells lack grid outlines in Fig. 5. Raccoon ψ_M was higher throughout Kanagawa than the other two species, with high predictions west of Yokohama and throughout central Kanagawa. Tanuki ψ_M was highest in Kamakura, western Kanagawa, and just west of Yokohama.

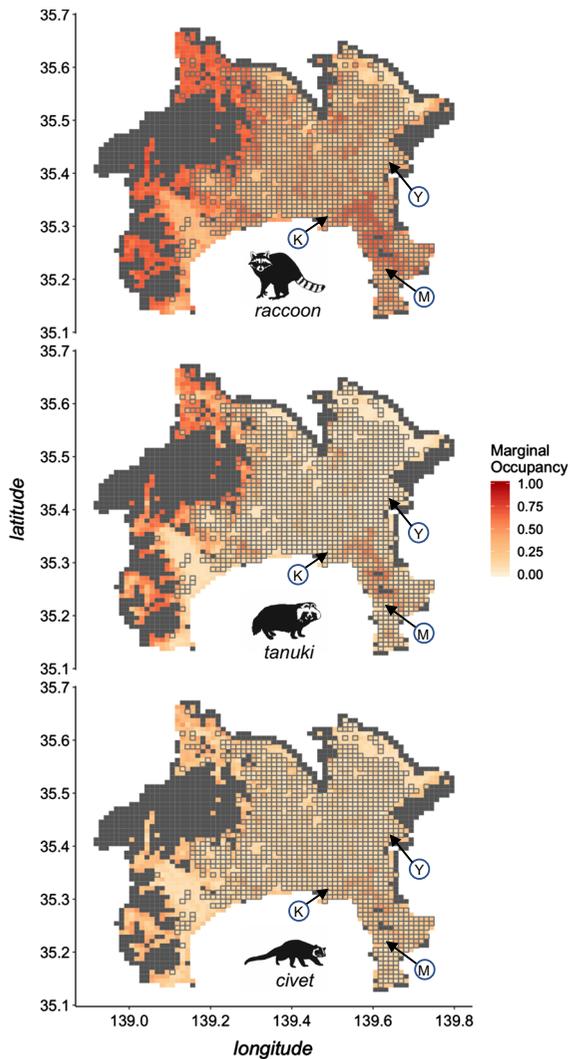


Fig. 5 Maps of marginal occupancy probability (ψ_M) throughout Kanagawa for all three carnivorans. Yokohama (Y), Kamakura (K), and Miura Peninsula (M) are labeled for reference. Areas used to train the model (cell outlines) are differentiated from those that lacked detection data and were predicted by the model (without outlines). Gray cells had missing data for at least one environmental variable and thus were not predicted

Civet ψ_M was generally low throughout the full study extent with some moderate values in Kamakura. Predicted ψ_M was very high for raccoons and tanuki in forested western areas. These areas, which lacked detection data, have forest cover values that are on average higher than those with detection data used to build the model (mean for cells with detection data: 16.8 ha, mean for projected areas: 44.2 ha; Fig. S9),

and they are also at a higher elevation than areas with detection data.

Discussion

We used a multispecies occupancy model to examine how patterns of co-occurrence between invasive and native species changed along environmental gradients. This framework allowed us to infer signals of competitive exclusion of native species by invasive ones, as well as how interactions between these species may be affected by the surrounding environment. In addition, we extended the static Rota et al. (2016) multispecies occupancy model to have temporal dependency by including a temporal autologistic parameter, enabling us to use multi-year detection data. Importantly, our results give us new insights into how invasive carnivorans interact with each other and native carnivorans of similar size and diet, and helped shed light on an assemblage that has been rarely examined using statistical modeling approaches. These insights led us to reconsider the hypothesis that raccoons competitively exclude tanuki (Abe et al. 2006; Kuriyama et al. 2018), and if confirmed with future field surveys could have global implications for the management of both species.

Interpreting the responses of individual species occupancy to the environment

Marginal occupancy probability for the three species was related to some environmental variables similarly and others differently, which helps increase our understanding of their habitat preferences when in sympatry. All species were more likely to be present in areas with forest cover, but in different degrees. Civets had the weakest response, but raccoons were associated with intermediate forest cover (i.e., secondary or disturbed forest) and tanuki with high forest cover (Fig. 2), which matches our expectations for these species (Abe et al. 2006; Kuriyama et al. 2018). Although all three carnivorans are known crop pests, agricultural extent lacked any strong associations with occupancy. The weak negative response for raccoons and civets may indicate that they prefer lower intensity farmland in a habitat mosaic, known as “satoyama” in Japan. Raccoon occupancy was more likely as wetland perimeter increased, which can be explained by their

propensity to hunt and forage along waterways (Zevuloff 2017). As this relationship was weaker than expected, it is perhaps worth exploring if other spatial metrics work as better predictors of raccoon occupancy. In contrast, civets had a strong negative response to wetland perimeter, likely because they are extremely arboreal with a high affinity for canopy trees (Rabinowitz 1991). It should be noted, however, that civets were found to consume freshwater prey in Chiba prefecture (Matsuo and Ochiai 2009), meaning that more work is needed to better determine their relationship with wetlands. All species responded negatively to human population density (Fig. 2), which was unexpected for these semi-urban species known to use anthropogenic resources. However, as all prefer to den in forest, perhaps suburban or rural areas with more nearby forest cover are associated with higher occupancy. The single detectability variable, number of trapping days, was not an important predictor for any species. This variable included many entries that were suspiciously high (i.e., 365 days), which may have resulted in poor explanatory power. Future surveys for trappers should provide more extensive instructions on how to measure effort. Finally, the temporal autologistic responses suggested that the relative site fidelity for raccoons may be low and for tanuki and civets higher, but confirmation of this would need long-term monitoring of occupied sites.

Although all species were highly predicted to occupy much of western Kanagawa (Fig. 5), these areas have higher elevation and forest cover values than the eastern areas used for model training, and thus have higher associated uncertainty (Fitzpatrick and Hargrove 2009). Although elevation was not considered explicitly as a variable in this model, it is likely linked to levels of agriculture, wetland, and human population density. If detection data from future surveys included high elevation forested areas, we would be better able to make more confident occupancy predictions for mountain areas and thus better inform invasive species management.

No evidence for competitive exclusion of tanuki by raccoon

Previous studies in Hokkaido and Chiba have suggested that raccoons may competitively exclude tanuki from suitable sites (Abe et al. 2006; Kuriyama

et al. 2018), but our results for Kanagawa show no evidence for this, and actually indicate the inverse could occur in some areas. We found that raccoon conditional occupancy had dramatically positive relationships with forest cover when tanuki were absent and civet present, yet lower conditional occupancy when tanuki were present and civets absent for all but the lowest forest cover values (Fig. 3). We also found no evidence that tanuki conditional occupancy in forest was affected negatively by raccoons or civets. Our results indicated that tanuki conditional occupancy increased with forest cover regardless of the presence or absence of either (Fig. 4). Although the model we used is correlative and thus cannot directly infer the mechanism driving co-occurrence patterns between these species, high trophic overlap and other ecological similarities make it likely co-occurrence leads to biotic interactions in this assemblage. Further, the model tended to overpredict raccoon-civet co-occurrence (Fig. S2), so the interpretation of these particular results come with some uncertainty.

One possible interpretation of the conditional occupancy results for raccoons is that tanuki are competitively excluding raccoons from heavily forested areas, but this is unlikely based on present knowledge. Although both in Hokkaido, Abe et al. (2006) suggested that raccoons may exclude tanuki from marginal woodlands which are part of their core home range areas, while Okabe and Agetsuma (2007) found evidence that direct competition was likely limited due to spatial and temporal differences in habitat use. It is also possible that shared resources exist only between raccoons and civets, but trophic similarity was found to be highest between tanuki and civets (Matsuo and Ochiai 2009), and civets were found to have positive associations with both raccoons and tanuki (Kuriyama et al. 2018). As we found that civets have a positive response to forest cover only when raccoons are present and tanuki absent, our results do seem to differ from those of Kuriyama et al. (2018). However, we used a model that allows for more focused insight into the relationships between co-occurrences and environmental predictor variables, and the associations we concentrate on here apply mainly to forested areas and not to the entire landscape. Regardless, similar modeling studies should be undertaken both in other regions of Japan and parts of the world where both species are invasive (i.e., Europe; Duscher et al. 2017) to determine if

associations between these carnivorans in forest actually differ between regions. The possibility remains that one or more variables we have not accounted for are driving these differences, such as microhabitat factors, as Okabe and Agetsuma (2007) found positive associations with understory ferns for both raccoons and tanuki. Further, although we did not examine three-way interactions in this study, it would be interesting to explore in future research if any spatial or environmental differences exist between sites occupied by all three species and those occupied by one or two species.

Regarding tanuki conditional occupancy, differences in diel behavior that prevent direct interactions may help explain these results. Okabe and Agetsuma (2007) observed that raccoons and tanuki likely segregate behaviorally through partitioning of activity time, as tanuki may be more diurnal than raccoons regardless of raccoon presence, possibly limiting direct competition for shared resources. Such temporal partitioning would not explain why raccoon conditional occupancy responds negatively when tanuki are present as forest cover increases, but raccoons may avoid areas with signs of tanuki (e.g., scent marks) while the inverse may not be true. It is also possible that there were general or regional biases towards releasing tanuki and civets while exterminating raccoons, though as all are considered agricultural pests in this area such a bias is unlikely. If this occurred, we might see a bias towards higher occupancy probability for tanuki and/or civet for some ranges of predictor variables when raccoons are absent. We see such patterns with forest cover and human population density, but the differences between conditional probabilities were not extreme. Lastly, although it may seem from these raccoon conditional occupancy results that civets could be mediating raccoon exclusion from deep forest, this is unlikely given that tanuki conditional occupancy was unaffected by civet presence (Fig. 4).

Management implications

These results have potential management implications that may help prioritize invasive raccoon mitigation efforts. Our results show that forested areas occupied by tanuki may be deterrents against raccoon establishment. Tanuki are considered crop pests in parts of Japan and thus are sometimes culled, but keeping their

numbers intact may help reduce the number of suitable denning sites for raccoons. For places such as Europe where both species are invasive, focusing on areas with low tanuki density may be an efficient management strategy for raccoon eradication. Our results also show that civet presence may to some extent predict raccoon presence (in agreement with Kuriyama et al. 2018), meaning that civets could be used as an indicator species to aid raccoon management in Japan. Although masked palm civets are not found in other areas of the world invaded by the raccoon, future research on different carnivoran assemblages in these areas may uncover other possible indicator species.

More field research is needed to confirm whether the co-occurrence patterns predicted in this study, or for that matter the density relationships modeled by Kuriyama et al. (2018), indeed translate to actual interactions on the ground. But as this assemblage of carnivorans shares many traits and life history characteristics, and as this modeling approach that examines how co-occurrence is shaped by the environment is more explicitly mechanistic than other MSDMs that rely on covariances of model residuals, we think it is a real possibility that the observed co-occurrence patterns reflect species interactions that can help guide raccoon management. But without new field data, evaluation of the relationships between co-occurrence with raccoons and environment variables are difficult because we lack good detection data for this region before the raccoon invasion. In addition to field validation in our current study region, it is also needed in more mountainous areas to determine where elevation may limit the raccoon's range and help focus management resources. All new field validation work can also potentially uncover any variables missing from this study that can help explain the species associations we found.

Future directions

As we demonstrated in this study, multispecies occupancy models that explicitly account for species interactions and can model co-occurrence as a function of environmental variables can lead to great insights in ecology, particularly for species with low detectability and interactions that are difficult to observe in nature. We used these models to find evidence for competitive exclusion, which is not

possible with models that cannot estimate occupancy probabilities conditional on other species. We were also able to examine the response of co-occurrence along environment gradients, and future studies using this modeling framework could conduct field validation along transects of forest fragmentation, for example, to determine if the interactions inferred from the model hold true as the environment changes across space. In addition to our implementation of temporal dependence, more extensions to the modeling framework will allow for a greater diversity of ecological questions to be pursued. For example, a recent study presented an implementation of this model that emulates the classic MacKenzie et al. (2003) model and estimates colonization and extinction probabilities (Fidino et al. 2019). As interpreting co-occurrence as a direct proxy for interactions runs the risk of extending the inference too far in some cases (Morales-Castilla et al. 2015), future studies should address field validation of model results in order to better select which models are most ecologically realistic. In addition, including other kinds of information on species interactions into these models, such as from food webs or interaction networks, should aid the interpretation of co-occurrence patterns and help shed light on the underlying mechanisms.

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Data accessibility The detection data used in this study are archived in the Knowledge Network for Biocomplexity repository (<https://doi.org/10.5063/F1X34VS1>).

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