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4 **Mast seeding, community dynamics, and tick-borne**

5 **disease risk in forest ecosystems**

6 by

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²⁸ **Table of contents**

²⁹ **1 Abstract**

³⁰ Tick-borne diseases are the most common vector-borne illnesses in the United States, with Lyme disease
³¹ being the most frequently reported. Due to a warming climate, the incidence rates of tick-borne
³² diseases are projected to increase — a risk exacerbated by the continued resilience of these diseases to
³³ the development of vaccines and treatments. Forecasting the risk of infection to prevent transmission
³⁴ in the first place remains the best approach for fighting tick-borne illnesses. Reservoir hosts, such
³⁵ as small mammals and deer, facilitate the transmission from the tick vector to humans with varying
³⁶ levels of success. Likewise, the population dynamics of reservoir host species may hinge on mast
³⁷ seeding events, or the synchronous, interannual variability in seed crop production within populations
³⁸ of perennial plants. The pulsed resource creates a trophic cascade through the food web that provides
³⁹ spatiotemporally separated niches for primary consumers of the mast. I explore the capacity of mast
⁴⁰ seeding events to explain, and therefore forecast, the distribution of ticks and the reservoir host species
⁴¹ that facilitate tick-borne diseases in the eastern United States. I estimate the historic mast seeding
⁴² events of individual trees with a state-space autoregressive model, synthesizing seed count data collected
⁴³ from sites for several decades. Based on these estimates, I determine the degree to which different genera
⁴⁴ of perennial plants affect reservoir host species, and in turn the degree to which different host species
⁴⁵ affect tick population dynamics.

⁴⁶ *Keywords:* blacklegged tick; Lyme disease; masting; pulsed-resource; resource-consumer interactions;
⁴⁷ tick-borne disease; tree seed production

⁴⁸ **2 Introduction**

⁴⁹ Resource pulses—temporally-variable influxes of nutrition in an ecosystem—travel through food webs
⁵⁰ like trophic cascades (Paine 1980, Ostfeld and Keesing 2000). Examples of pulsed-resources abound
⁵¹ across different ecosystems, yet all are characterized by low frequency, large magnitude, and short
⁵² duration relative to the timescale of their consumer (Yang et al. 2008). These episodic events, such as
⁵³ sudden marine upwellings (Bode et al. 1997) and El Niño downpours (Letnic et al. 2005), may provide
⁵⁴ stability and functionality within a variety of communities (McMeans et al. 2015).

⁵⁵ One such pulsed resource is mast seeding (Ostfeld and Keesing 2000). The behavior describes the
⁵⁶ synchronous, interannual variability in seed crop production within populations of perennial plants
⁵⁷ (Kelly 1994). Although the ultimate and proximate causes for the behavior remain unresolved, mast
⁵⁸ seeding seems to be linked to the relationship between weather cues and the allocation of resources
⁵⁹ towards reproduction (Pearse et al. 2016). The exact nature of this relationship depends on the species,

60 yet empirical studies have shown that high temperatures in the spring months correlate with high seed
61 crops (Sork 1993, Koenig et al. 1996). Indeed, Pérez-Ramos et al. (2015) found that colder spring
62 temperatures may reduce both the synchrony in pollen release and successful fertilization as well as
63 the overall size of the seed crop.

64 The resource pulse cascades through higher trophic levels, generating spatiotemporal structure in
65 the ecosystem that varies from year to year (Bergeron et al. 2011). Theoretical and empirical
66 evidence suggest that primary consumers—species that feed directly on the seed crop produced by
67 forests—experience the greatest effect from masting behavior (Mills and Doak 1993). The structure
68 created by masting is complex, however, as some primary consumers may anticipate the dynamic
69 resource availability, adjusting juvenile emergence with peak food abundance before a mast seeding
70 event (Boutin et al. 2006, White 2008). Therefore, anticipatory consumers grow their populations
71 in synchrony with the pulse-resource whereas reactionary consumers experience a lag (Bergeron et al.
72 2011). These temporally separated niches may promote species coexistence and ecosystem stability
73 (Loreau and de Mazancourt 2008).

74 Depending on the strength of the environmental cues, the pulsed nature of the resource may reverberate
75 beyond the level of primary producer [Paine1980]. An important example of such a phenomenon is
76 the degree to which mast seeding influences the spatiotemporal distribution of ticks (*Ixodes* spp.) and,
77 thus, tick-borne diseases. Tick populations rely on primary consumers of mast seeding such as small
78 mammals and deer (Granter et al. 2014). Not only do the consumers support tick populations, but
79 they also act as hosts facilitating the spread of tick-borne diseases across the parasite's different life
80 stages (Ostfeld et al. 2018).

81 Ticks pass through four life stages during their two-year lifespan – egg, larva, nymph, and adult. Upon
82 hatching in the summer, larvae and nymphs must consume a blood meal to develop into the next
83 stage (Granter et al. 2014). Likewise, an adult female feeds one last time before dropping from the
84 host, laying her eggs, and completing the cycle. As ticks hatch uninfected, it is during these feeding
85 bouts that the disease transmits from the host to the tick vector, and back again. The long-term
86 transmission of tick-borne diseases relies on the successful infection of hosts; however, different host
87 species have differential infection rates (LoGiudice et al. 2003). The most successful host species are

88 termed reservoir hosts. The primary hosts responsible for tick-borne diseases in eastern North America
89 are the white-footed mouse (*Peromyscus leucopus*), the deer mouse (*Peromyscus maniculatus*), the
90 masked shrew (*Sorex cinereus*), the short-tailed shrew (*Blarina brevicauda*), and the eastern chipmunk
91 (*Tamias striatus*; Barbour 2017, Ostfeld et al. 2018).

92 Tick-borne diseases are the most common vector-borne illnesses in the United States, with Lyme
93 disease being the most frequently reported (Dantas-Torres et al. 2012, Adrion et al. 2015) at an
94 estimated 30,000 new cases each year (Disease Control and Prevention) 2019b). Since ticks favor warm
95 temperatures, climate change will likely exacerbate the incidence of Lyme disease, by as much as 20
96 percent (Dumic and Severnini 2018). Thus far, we have had limited success in developing vaccines
97 and treatments for tick-borne diseases, and prevention remains the best approach for reducing their
98 incidence (Piesman and Eisen 2008). The disease is caused by the spirochete bacterium, *Borrelia*
99 *burgdorferi*, but relies on the interaction between hosts and the tick vector for transmission. A growing
100 body of research has prioritized determining the degree to which different wildlife species may act as
101 reservoirs of future zoonotic disease as a means of forecasting human disease risk (Karesh et al. 2012,
102 Han et al. 2015).

103 A better understanding of the population dynamics of competent reservoir host species as determined
104 by mast seeding pulsed-resources will improve our capacity to forecast the spatiotemporal distribution
105 of outbreaks of tick-borne diseases. Here, I assess the impacts mast seeding have on tick populations
106 through their connection with reservoir hosts. I ask:

- 107 • Which plants influence reservoir host populations by mast seeding?
- 108 • Which reservoir hosts are responsible for determining the dynamics of tick populations in the
109 eastern United States?
- 110 • What are the associated lag times between these processes?

111 **3 Methods**

112 **3.1 Data collection and study sites**

113 I leveraged two data networks to understand the nature of these processes: the Mast Inference and
114 Prediction (MASTIF, Clark et al. 2019) network and the National Ecological Observatory Network
115 (NEON, Ecological Observatory Network) 2018).

116 MASTIF is a long-term monitoring network with more than 500 plots across North America that collect
117 seed counts annually as well as basic tree metrics such as diameter at breast height (DBH), location,
118 species identification, canopy cover (grown in the open to grown in full shade), and maturation status.
119 Seed count data collected by the MASTIF network are used to fit a state-space autoregressive model
120 that predicts maturation and fecundity for individual trees over time. The synthesis generates a
121 posterior distribution across all sites, trees, and years to describe the spatiotemporal patterns of mast
122 seeding behavior. Typically, the model requires inputs of DBH as well as climate variables. I accessed
123 historical potential and actual evapotranspiration as well as temperature for the MASTIF field sites
124 from the NASA TerraClimate product (Abatzoglou et al. 2018) through Google Earth Engine (Gorelick
125 et al. 2017).

126 NEON is a continental-scale observation facility that collects long-term ecological, atmospheric, and
127 environmental data. Their methods are systematic and reproducible across approximately 80 field sites.
128 Here, I focus on their *woody plant vegetation structure*, *small mammal box trapping*, and *ticks sampled*
129 *using drag cloths* datasets as estimates for plant, small mammal, and tick abundance, respectively.
130 These data are collected on separate, often overlapping plots within a field site. Similar to MASTIF,
131 technicians at NEON collect basic tree metrics such as DBH, location, species identification, height, and
132 mortality status for all of the trees and woody shrubs ≥ 10 cm DBH within the plant abundance plots.
133 Small mammal abundance plots are organized with 100 box traps per plot. For each sampling bout,
134 technicians record the trap's location and catch status as well as the animal's species identification.
135 Although the small mammal traps capture an array of different species, I focus only on the competent
136 reservoir hosts in this region: the white-footed mouse (*P. leucopus*), the deer mouse (*P. maniculatus*),
137 the masked shrew (*S. cinereus*), the short-tailed shrew (*B. brevicauda*), and the eastern chipmunk (*T.*
138 *striatus*; Barbour 2017, Ostfeld et al. 2018). Tick abundance sampling involves dragging a $1m^2$ cloth

139 along the ground. The life stage (larva, nymph, or adult) of the ticks captured on the cloth is recorded.

140 Animals are sampled at regular intervals throughout the year.

141 I limited my study region to the eastern United States where the blacklegged tick (*Ixodes scapularis*)
142 is common (Disease Control and Prevention) [2019a](#)). I overlaid the MASTIF and NEON field sites
143 and found six regions, concentrated in the Northeast, where both sets of data are collected. These
144 sites allow for modeling at every stage (*i.e.* mast density to small mammal abundance, and small
145 mammal abundance to tick abundance). In order to incorporate as much data as possible, I included
146 an additional six field sites where only NEON data are collected. As the interannual mast behavior
147 of these regions is unknown, the additional sites supplement the stage of the model addressing the
148 effects of small mammal abundance on tick abundance. On the plant abundance plots overlapping a
149 MASTIF site, 48 species of woody plants from 29 genera (*Acer*, *Ailanthus*, *Betula*, *Carpinus*, *Carya*,
150 *Celtis*, *Cercis*, *Cornus*, *Diospyros*, *Fagus*, *Fraxinus*, *Ilex*, *Lindera*, *Liquidambar*, *Liriodendron*, *Juglans*,
151 *Magnolia*, *Nyssa*, *Ostrya*, *Oxydendrum*, *Picea*, *Pinus*, *Platanus*, *Prunus*, *Quercus*, *Robinia*, *Sassafras*,
152 *Tsuga*, and *Ulmus*) are present.

153 Within the NEON sites, there are multiple plots collecting data for each dataset (plant abundance,
154 small mammal abundance, and tick abundance). I paired up the different plots with each other by
155 proximity so that for the sites collecting both MASTIF and NEON data, there is a unique combination
156 of plant abundance, small mammal abundance, and tick abundance plots serving as an observational
157 unit. For the sites collecting only NEON data, the observational unit encompasses pairs of small
158 mammal abundance and tick abundance plots. Data collection for the NEON datasets began for most
159 of the sites within my study region in 2012 and continued until the end of my study period in 2018.

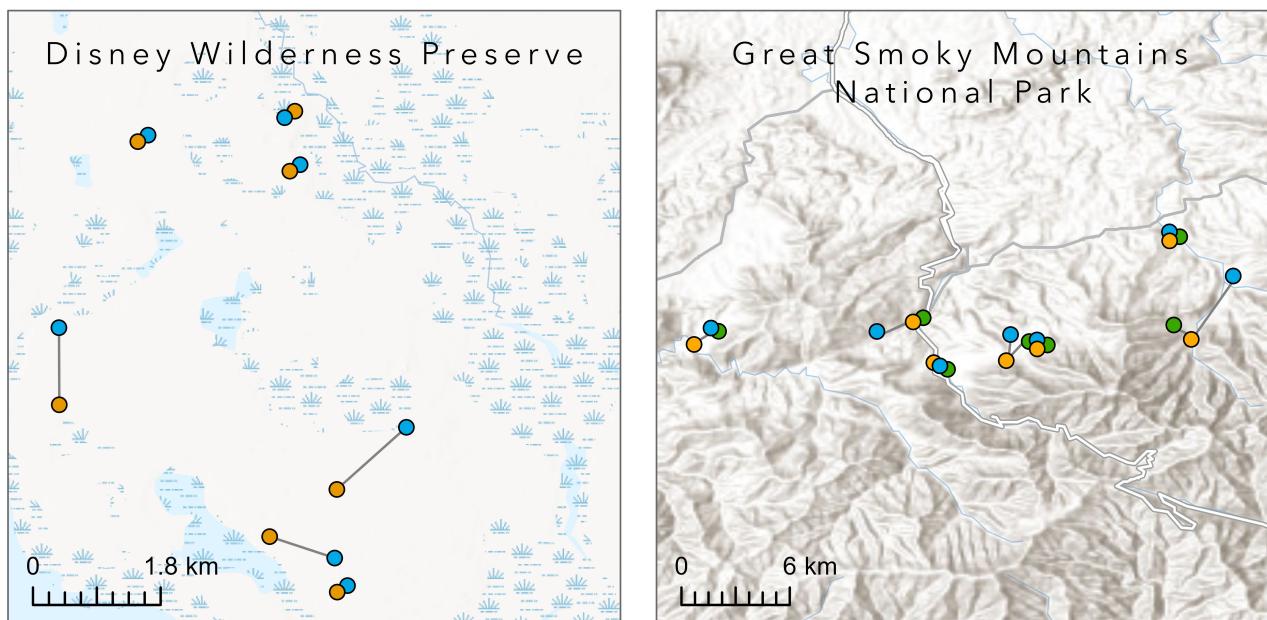
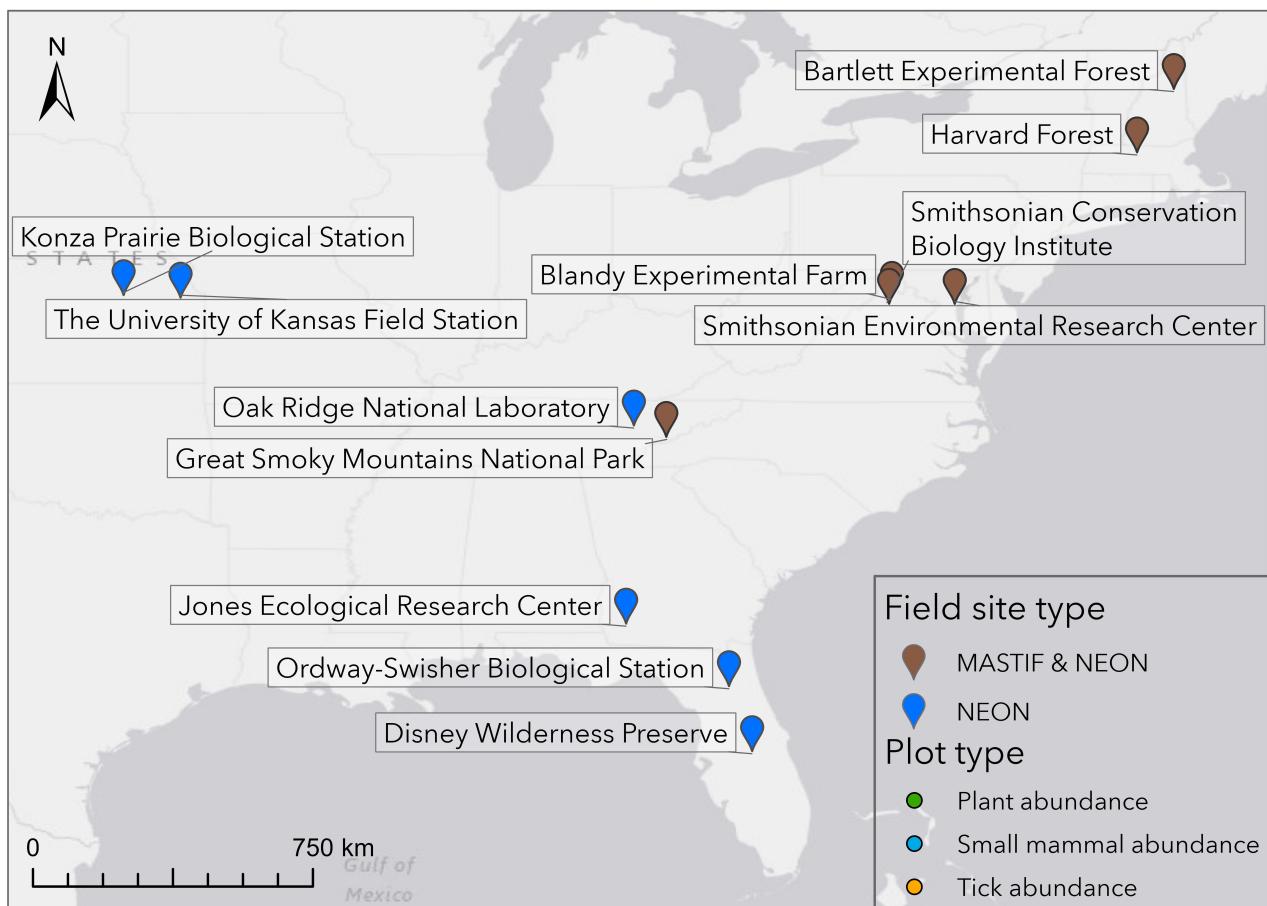


Figure 1: Map of the NEON and MASTIF field sites within the study region (top). Example of the plots making up an observational unit for a field site represented by just NEON (bottom left) and represented by both NEON and MASTIF (bottom right).

Table 1: The number of observational units (unique combination of plant-mammal-tick plots or mammal-tick plots) per field site. Field sites present in both the MASTIF and NEON networks are in bold.

Field site	Number of observational units
Bartlett Experimental Forest	6
Blandy Experimental Farm	4
Disney Wilderness Preserve	7
Great Smoky Mountains National Park	7
Harvard Forest	7
Jones Ecological Research Center	6
Konza Prairie Biological Station	6
Oak Ridge National Laboratory	6
Ordway-Swisher Biological Station	6
Smithsonian Conservation Biology Institute	6
Smithsonian Environmental Research Center	6
University of Kansas Field Station	6

160 3.2 Model design

161 3.2.1 Mast density

162 The MASTIF model is a state-space autoregressive model that estimates the mast density (seeds/unit
 163 area) of an individual tree per year as a function of DBH, canopy cover, and optional climate variables,
 164 recovering the latent parameters of maturation state and conditional fecundity in the process (Clark
 165 et al. 2019). Although the full MASTIF model includes parameters describing the shape of seed
 166 dispersal, I focused on the parameterization of maturation state, conditional fecundity, and actual
 167 fecundity. Therefore, I assume that all of the seeds stay within the site and available to consumers
 168 where they were produced, regardless of the dispersal characteristics of the tree.

169 I modeled the *maturation state*—the event that tree i can produce seed in year t —on the binomial
 170 distribution, where $\rho_{i,t} \in \{0, 1\}$, as a function of DBH. The covariate effects on the maturation
 171 probability are represented by the coefficients in β^v . I modeled the *conditional fecundity*—the number
 172 of seeds produced by tree i in year t given that the individual is mature ($\rho = 1$)—on a log-transformed
 173 normal distribution, where $\log \psi_{i,t} \sim \mathcal{N}(\mu_{i,t}, \sigma^2)$, as a function of DBH, canopy cover, surface deficit
 174 (surDefSite; the difference between potential evapotranspiration and actual evapotranspiration),
 175 spring minimum temperature (springTminSite; the minimum temperature between March and May,
 176 inclusive), and the anomalies of surface deficit (surDefAnom) and spring minimum temperature

(springTminAnom) from one year to the next. Coefficients in β^x describe the covariate effects of conditional fecundity. The *actual fecundity* $f_{i,t} = \psi_{i,t}\rho_{i,t} \geq 0$ is the product of conditional fecundity and maturation state. The site-level climate variables, surDefSite and springTminSite, give the model information on the spatial heterogeneity of water availability and spring temperature across the field sites. The anomalous climate variables, surDefAnom and springTminAnom, give the model information on the interannual changes in water availability and spring temperature. Both sets of variables are important predictors for masting behavior (Pearse et al. 2016). I modeled the different genera across all of the MASTIF sites separately, treating site as a random effect. When modeling a genus with more than one species present within the study region, I included species as an interactive term in both the maturation state and conditional fecundity models.

After recovering the parameters for the latent processes of maturation (β^v) and fecundity (β^x) from the MASTIF sites, I parameterized individual trees on the woody plant vegetation structure plots within the NEON sites and estimated their annual seed production. In doing so, I assume that individuals within a species modify their seed production in response to the climate in a similar manner based on geographic location.

3.2.2 Nutritional availability

As the mass rather than the number of seeds available is a better predictor of consumer behavior, I compiled information on the grams per seed for the species within my study region from the literature (Barclay and Earle 1974, Appendix: Table 2; Bonner et al. 2008). I multiplied the mast density (seeds/unit area) produced by each tree in each year by the seed weight (grams/seed), yielding an estimate for the mass of the mast (grams/unit area) produced in any given year. For the cases in which I could not find the seed weight for a given species, I used the average seed weight for that species' genus.

3.2.3 Determining lag time

Before assessing which masting species affect the population dynamics of reservoir host species, I must determine the degree to which the consumers anticipate or react to the pulsed resource (Smith and Reichman 1984). I fit a generative Generalized Joint Attribute Model (GJAM; Clark et al. 2017)

204 to estimate the response of the reservoir host species to the total mast density available to them in
205 time t and $t - 1$ (i.e. the mast density produced in the same year and from the year before the small
206 mammals were captured). I assumed a lag time of $t - 1$ when modeling the effect of host mammals on
207 tick populations (Ostfeld et al. 2018).

208 GJAM predicts species abundance on the community level and is based on a joint distribution of
209 parameters, predictors, and species responses. The parameters recovered by the model are of two
210 types: the matrices of coefficients between predictors and species responses, and the covariance matrix
211 between all of the species responses. The covariance matrix may account for sources of error unexplained
212 by the predictors, such as interactions between species and environmental gradients. Sensitivity of the
213 entire response matrix as well as sensitivities of individual species responses can be obtained from
214 the diagonals of the covariance matrix, allowing for a pairwise estimate of the degree to which each
215 predictor affects the response.

216 3.2.4 Determining sensitivity of different species and genera

217 Next, I modeled the response of the reservoir host species to the mast density produced by the different
218 genera of woody plants present within each plot. I deemed a host species to be anticipatory or
219 reactionary to the pulsed resource based on the strength of their sensitivity to the lag time from
220 the previous model and considered the mast produced by individuals from a genus in time t or time
221 $t - 1$ as the predictors accordingly. By accounting for the degree to which the host species might
222 anticipate the mast seeding event, the model is better able to determine the sensitivity of the different
223 tree genera to the reservoir hosts. Last, I modeled the different tick life stages as a response to the
224 reservoir host species abundance in time t . I included the effort in obtaining the data (number of box
225 traps for the small mammal sampling and area of cloth for the tick sampling) for all of the models.

226 4 Results

227 In determining the lag time between mast seeding and small mammal abundance, I found a significant
228 positive relationship between the mast density produced in time $t - 1$ and one of the most common small
229 mammals in my study region, the deer mouse (*P. maniculatus*). The eastern chipmunk (*T. striatus*)
230 and the short-tailed shrew (*B. brevicauda*) also showed a greater sensitivity to a lag time of one year

231 whereas the masked shrew (*S. cinereus*) and the white-footed mouse (*P. leucopus*) showed no lag time
 232 (Figure 2). Although these relationships were not significant, for some species (*P. leucopus*, *S. cinereus*,
 233 and *T. striatus*) they are substantiated by the literature (Smith and Reichman 1984, Bergeron et al.
 234 2011, Ostfeld et al. 2018).

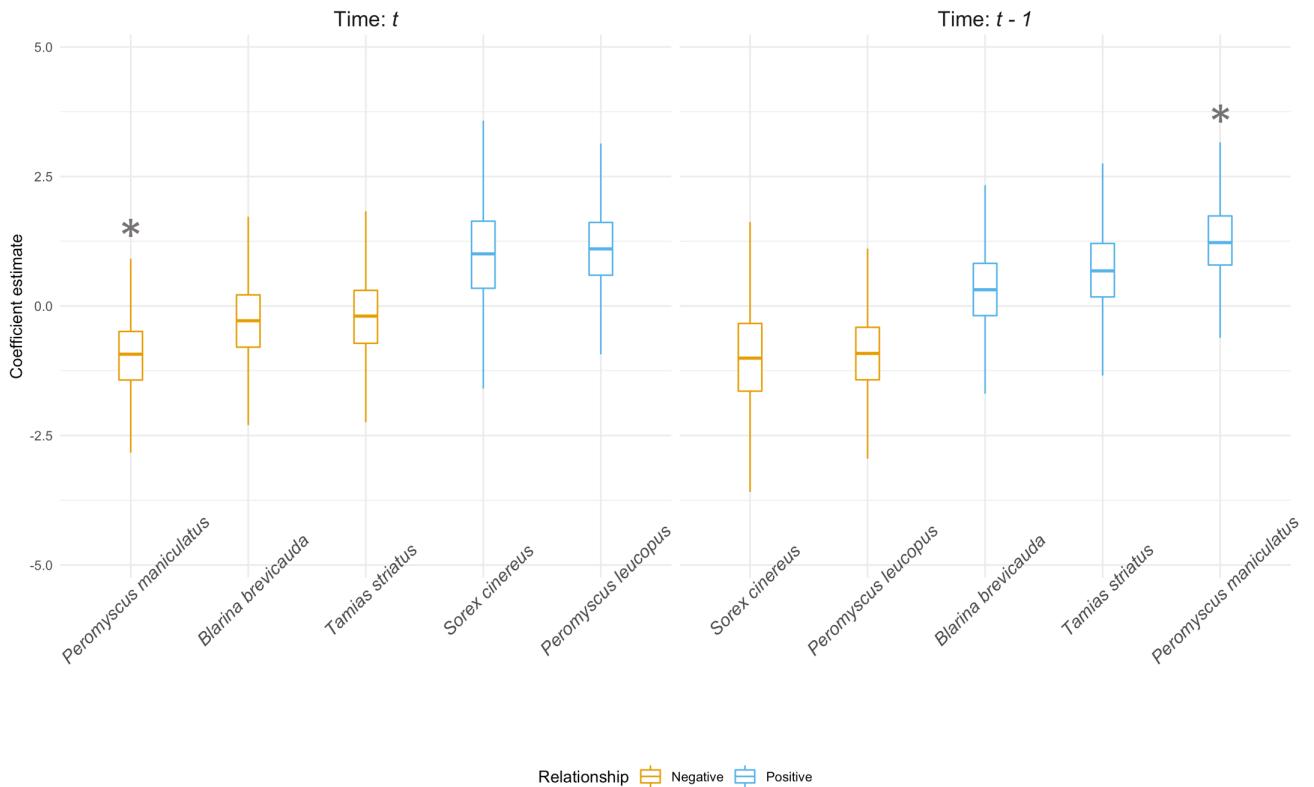


Figure 2: The distribution of coefficient estimates for the model determining the lag time associated with mast seeding events and small mammal populations. Orange indicates a negative relationship between the species and lag time. Blue indicates a positive correlation. Asterisk indicates significance at the 95% level.

235 After partitioning the effect of the mast seeding events across the different plant genera, I found scant
 236 evidence for which genera of trees are driving the dynamics of small mammal abundance (Figure 3).
 237 Only three plant genera showed a significant effect on small mammal species: a negative effect of
 238 sweetgum (*Liquidambar*) on *B. brevicauda*, a negative effect of locust (*Robinia*) on *P. maniculatus*, and
 239 a negative effect of hickory (*Carya*) on *T. striatus*. I found no evidence to suggest that the population
 240 dynamics of individual host species affects any of the mobile tick life stages (Figure 4).

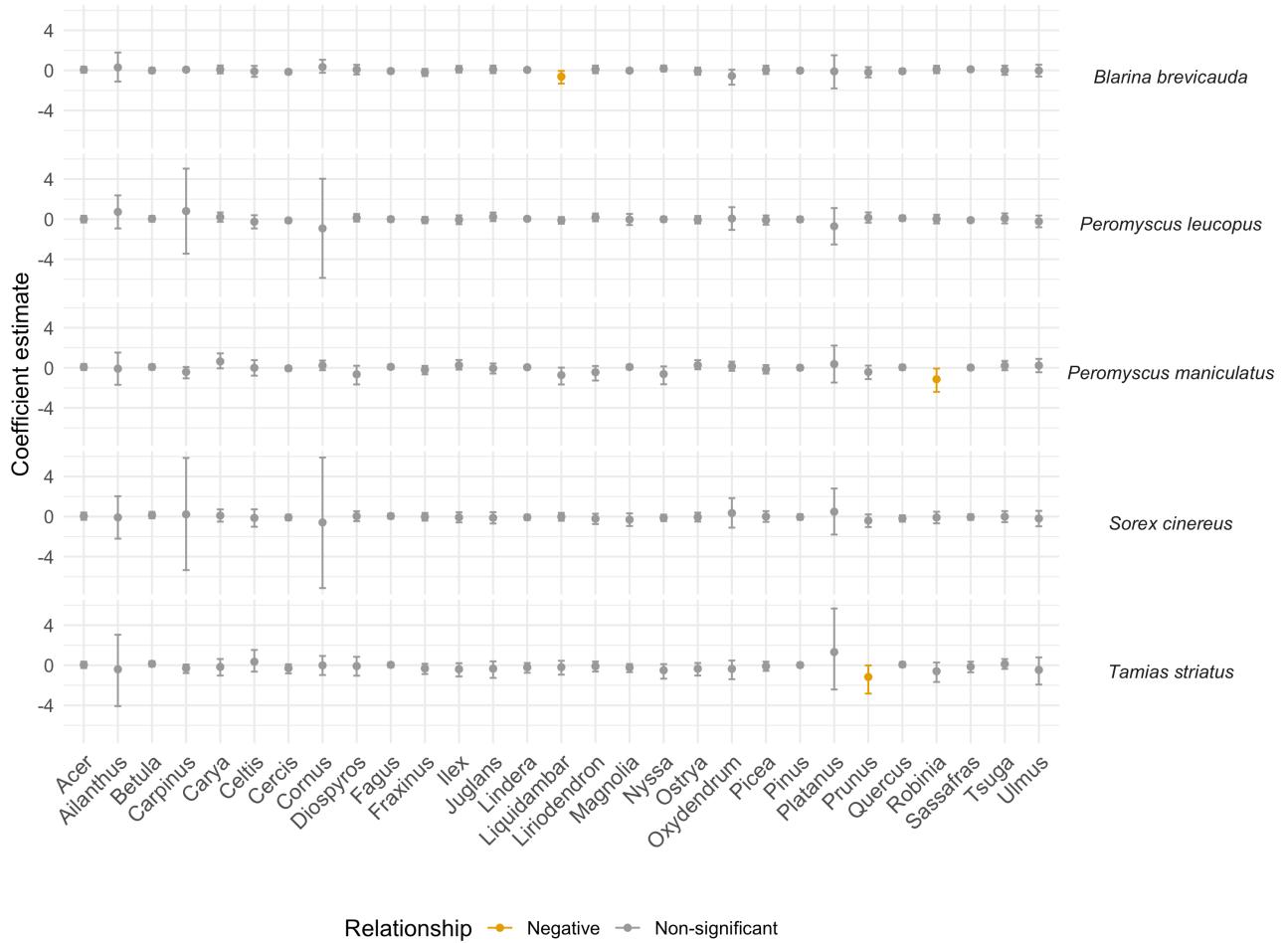


Figure 3: Credible intervals at the 95% level of coefficient estimates for the model determining the sensitivity of small mammal species to mast produced by different plant genera.

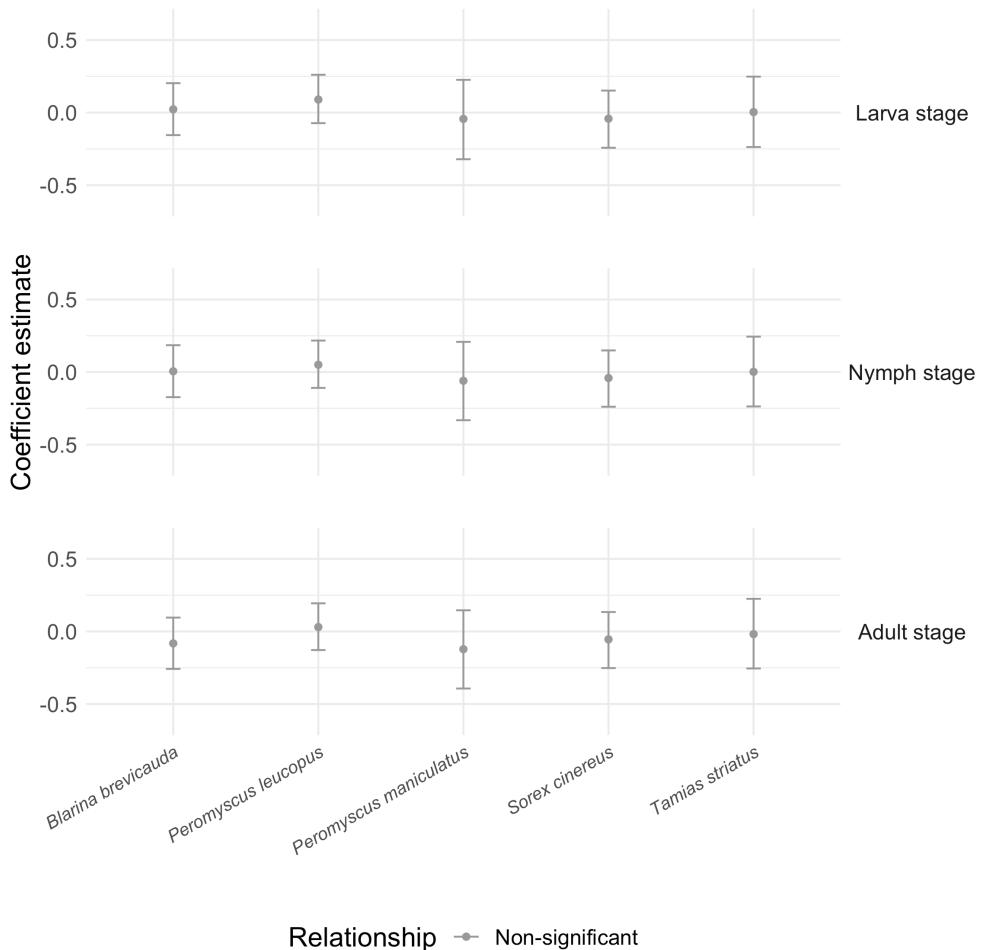


Figure 4: Credible intervals at the 95% level of coefficient estimates for the model determining the sensitivity of tick life stages to small mammal abundance.

241 5 Discussion

242 Tracking the effect of the pulsed resource of mast seeding on tick populations and their reservoir hosts
 243 involves one small food chain amongst a broader and more complex food web. Such an analysis can
 244 only consider bottom-up forces (*i.e.* where primary control is held by resources) on the community and
 245 neglects entirely top-down forces (*i.e.* where primary control is held by predators) as well as competitive
 246 exclusion within a trophic level (Hardin 1960, Power 1992). Incorporating as many predictors as
 247 possible into a model, however, limits its simplicity (and therefore utility) and introduces a host of
 248 other issues such as overfitting and collinearity between predictors (Wold et al. 1984, Hawkins 2004).
 249 Bearing this in mind, it is important to determine whether the lack of significant connections between

250 mast seeding and tick populations is accurate or rather a consequence of poor model performance.

251 Like other Bayesian models, GJAM makes use of Gibbs sampling, a Markov chain Monte Carlo (MCMC)
252 algorithm, to determine the marginal distribution of the parameters (Gelfand [2000](#), Clark et al. [2017](#)).
253 With any MCMC approach, it is important to make sure that the chains have converged on a singular
254 coefficient estimate, even if the uncertainty associated with the estimate is large. Moreover, GJAM
255 sets aside some of the data to determine how well the observations align with the predictions of the
256 parameter estimates. Both the convergence of the MCMC chains and the comparison of predicted
257 *vs* observed data are important indicators of model performance. All of the models showed complete
258 convergence and a good fit between predicted *vs* observed data (Appendix: Figures 5-8). Even though
259 the models performed well, they could have found a paucity of evidence for these processes for two
260 reasons: the connection between the different trophic levels was weaker than expected or there were
261 insufficient data to determine the connection.

262 The competent reservoir host species for tick-borne diseases in the eastern United States are all
263 generalist consumers (Ostfeld et al. [2018](#)). In times of resource scarcity, generalist consumers,
264 unlike their specialist counterparts, can undergo *diet switching*, or a dynamic altering of their diet
265 in response to the environment (Polis and Strong [1996](#)). Indeed, some generalist consumers (such as
266 *P. leucopus*) alter not only their diet but also their trophic level, removing themselves further from
267 the pulsed resource of mast seeding (Shaner and Macko [2011](#)). In non-mast years, the reservoir host
268 species can turn to other sources of food to sustain their populations, which diminishes the strength
269 of bottom-up forces on a community. Indeed, the weak trophic interactions may be important in
270 promoting community persistence and stability (McCann et al. [1998](#)). Weak trophic interactions
271 limit our ability to predict how other trophic levels react to mast seeding events, especially when the
272 strength of the resource pulse is partitioned across different groups of plants or community types.

273 When it comes to forecasting the spatiotemporal distribution of tick abundance and Lyme disease risk,
274 understanding the patterns of mast seeding events may not be enough. The strength of the pulsed
275 resource diminishes as it travels through the population dynamics of generalist consumers. Moreover,
276 using reservoir host species abundance as a predictor for tick abundance presents its own challenges
277 (Vu Hai et al. [2014](#)). Ticks have been known to expand their list of reservoir host species over time as

278 communities are altered by culling programs (Jaenson et al. 2012). The spread of tick-borne diseases
279 can depend more on the biodiversity of the entire community than the abundance of individual species
280 (Levi et al. 2016). The populations of host species are also in a state of flux as they respond to
281 climate change, anthropogenic modification of the landscape, and the introduciton of invasive species.
282 The multitude, interactivity, and complexity of variables affecting tick-borne diseases place robust
283 forecasting of disease risk beyond current human understanding (Dantas-Torres 2015). Additional
284 research into new and innovative approaches for predicting tick-borne disease risk are necessary to
285 ensure its success. One such approach that shows promise uses prevalence of Lyme disease in our
286 canine companions as a proxy for prevalence in humans, thereby removing the predictor from the
287 complexity of multi-trophic interactions (Watson et al. 2017). Until we develop vaccines or treatments
288 for Lyme disease and other tick-borne illnesses, forecasting risk and preventing the spread of infection
289 remains our only option in the fight against tick-borne diseases.

290 **6 Appendix**

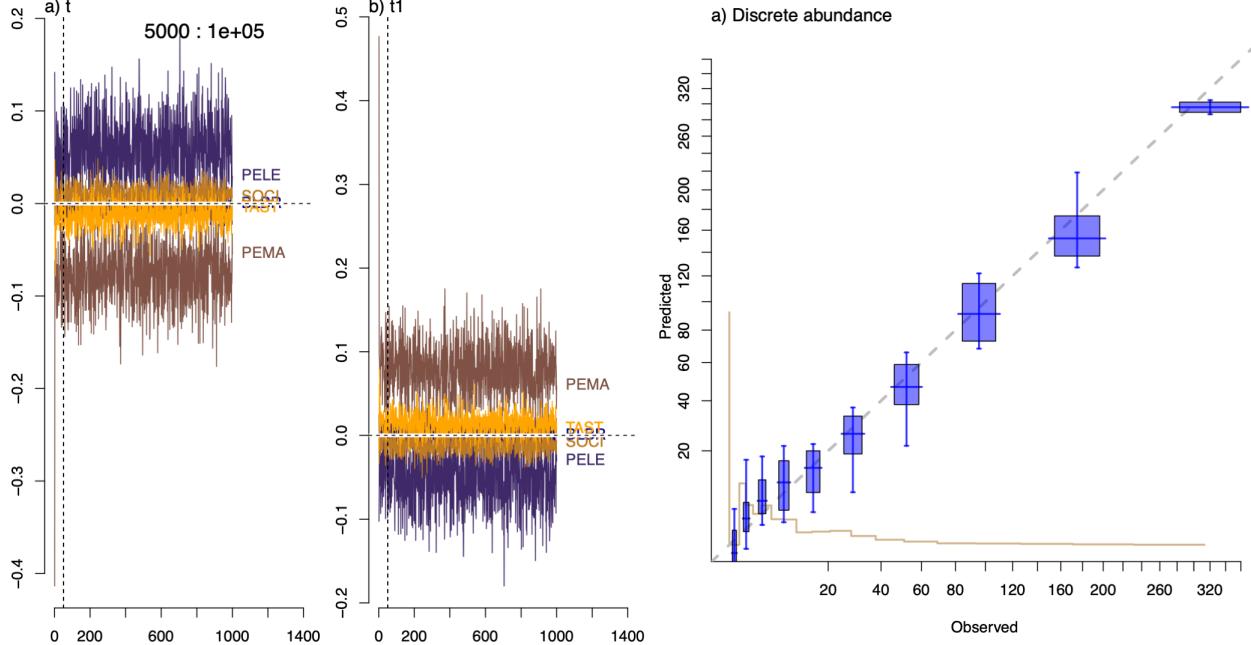


Figure 5: MCMC chains (left) and Predicted vs Observed (right) for model determining lag time

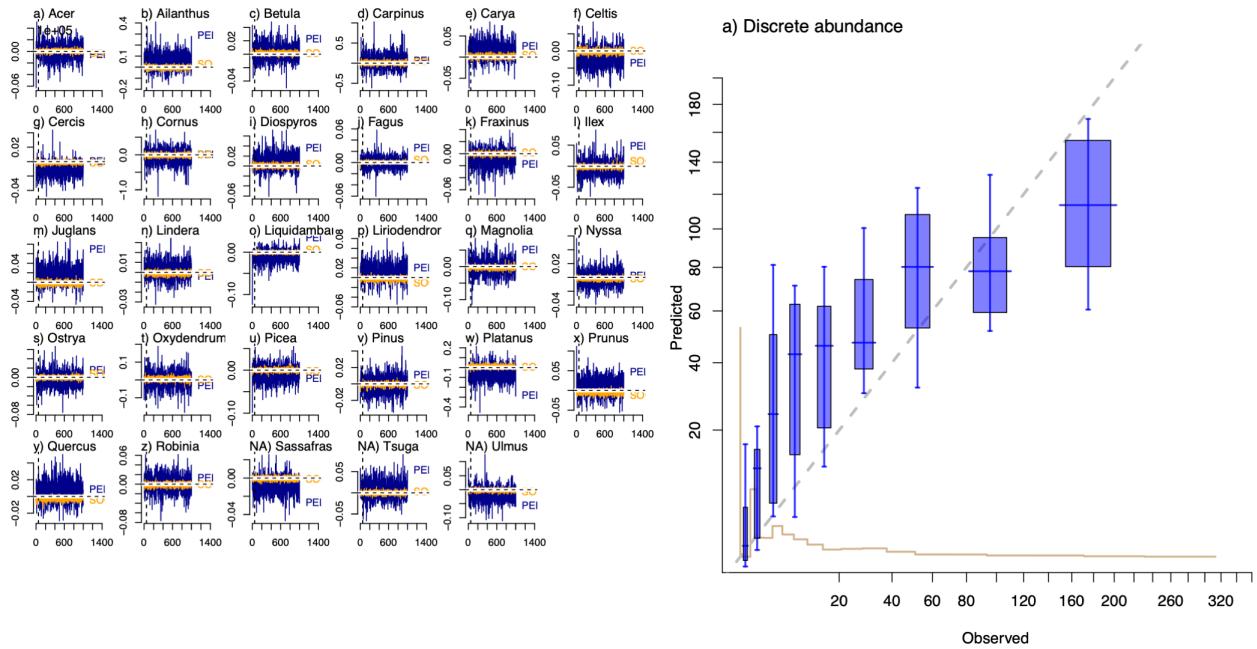


Figure 6: MCMC chains (left) and Predicted vs Observed (right) for model determining effect of plant genera on small mammal species with lag time $t - 1$

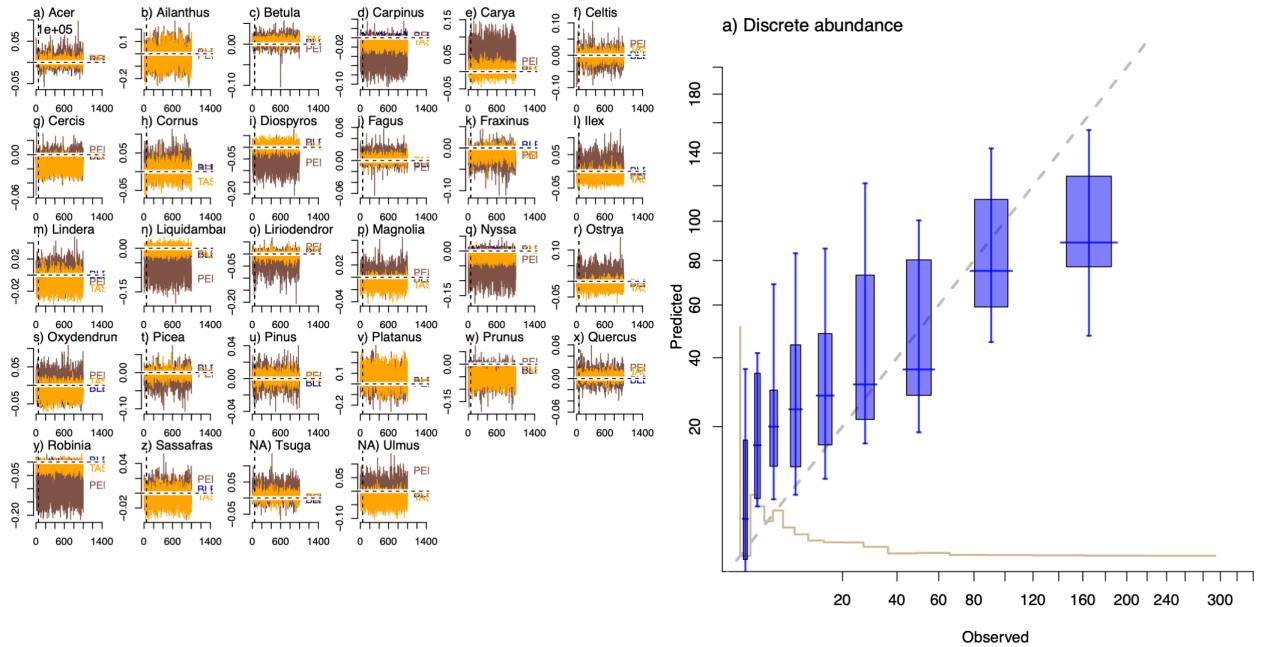


Figure 7: MCMC chains (left) and Predicted vs Observed (right) for model determining effect of plant genera on small mammal species with lag time t

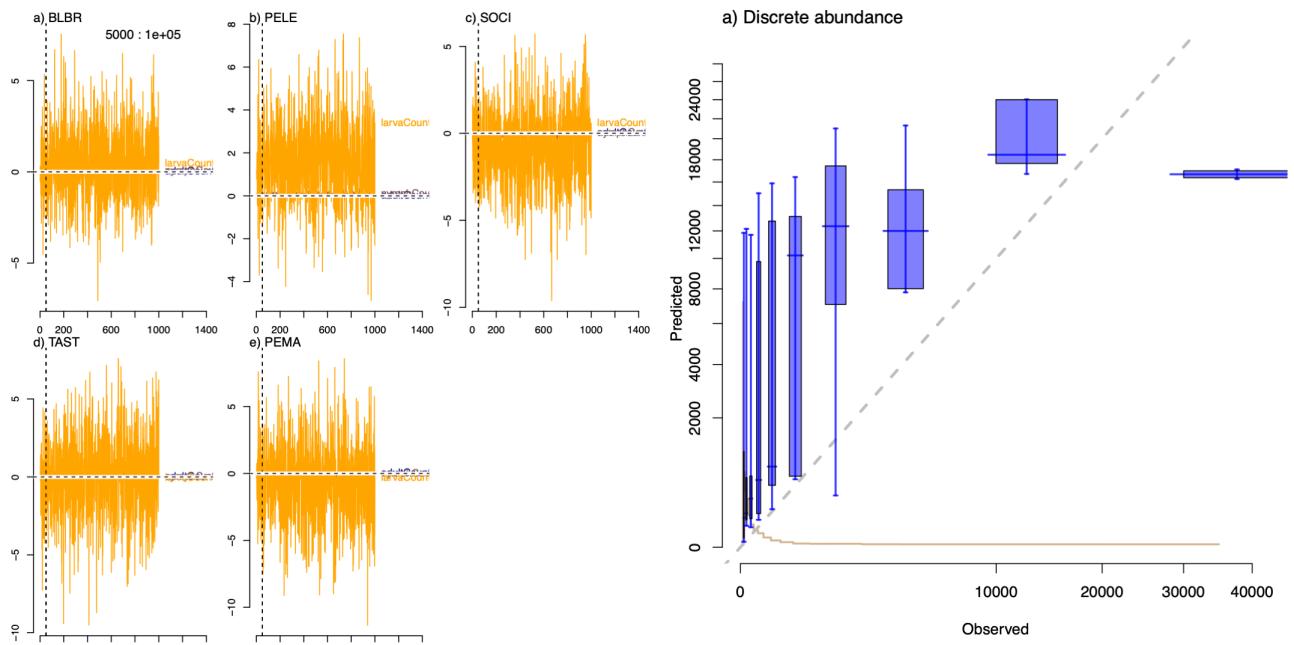


Figure 8: MCMC chains (left) and Predicted vs Observed (right) for model determining effect of small mammal species on tick life stages

Table 2: The number of observational units (unique combination of plant-mammal-tick plots or mammal-tick plots) per field site. Field sites present in both the MASTIF and NEON networks are in bold.

<i>Species</i>	Seed weight (g/seed)
<i>Abies fraseri</i>	0.0221 ¹
<i>Acer negundo</i>	0.0402 ²
<i>Acer pensylvanicum</i>	0.0371 ¹
<i>Acer rubrum</i>	0.0772 ²
<i>Acer saccharum</i>	0.0621 ¹
<i>Ailanthus altissima</i>	0.0082 ²
<i>Amelanchier laevis</i>	0.0062 ²
<i>Betula alleghaniensis</i>	0.0011 ¹
<i>Betula lenta</i>	0.00081 ¹
<i>Betula papyrifera</i>	0.00031 ¹
<i>Carpinus caroliniana</i>	0.0261 ¹
<i>Carya cordiformis</i>	6.6301 ¹
<i>Carya ovata</i>	4.4001 ¹
<i>Celtis occidentalis</i>	0.1002 ²
<i>Cercis canadensis</i>	0.0322 ²
<i>Cornus florida</i>	0.1001 ¹
<i>Diospyros virginiana</i>	0.3782 ²
<i>Fagus grandifolia</i>	0.2601 ¹
<i>Fraxinus americana</i>	0.0452 ²
<i>Fraxinus pennsylvanica</i>	0.0321 ¹
<i>Ilex opaca</i>	0.0161 ¹
<i>Juglans nigra</i>	11.3000 ¹
<i>Juniperus virginiana</i>	0.0101 ¹
<i>Lindera benzoin</i>	0.1001 ¹
<i>Liquidambar styraciflua</i>	0.0061 ¹
<i>Liriodendron tulipifera</i>	0.0321 ¹
<i>Magnolia fraseri</i>	0.1001 ¹
<i>Nyssa sylvatica</i>	0.5801 ¹
<i>Ostrya virginiana</i>	0.0151 ¹
<i>Oxydendrum arboreum</i>	0.00011 ¹
<i>Paulownia tomentosa</i>	0.00021 ¹
<i>Picea glauca</i>	0.0041 ¹
<i>Pinus rigida</i>	0.0271 ¹
<i>Pinus strobus</i>	0.0171 ¹
<i>Pinus taeda</i>	0.0071 ¹
<i>Pinus virginiana</i>	0.0081 ¹
<i>Platanus occidentalis</i>	0.0042 ²
<i>Prunus pensylvanica</i>	0.0281 ¹
<i>Quercus alba</i>	3.5401 ¹
<i>Quercus coccinea</i>	1.9301 ¹
<i>Quercus montana</i>	1.8001 ¹
<i>Quercus rubra</i>	3.6301 ¹
<i>Quercus velutina</i>	1.8501 ¹
<i>Robinia pseudoacacia</i>	0.0191 ¹
<i>Sassafras albidum</i>	0.0911 ¹
<i>Sorbus americana</i>	0.0321 ¹
<i>Tsuga canadensis</i>	0.0021 ¹
<i>Ulmus americana</i>	0.0061 ¹
<i>Ulmus rubra</i>	0.0111 ¹

¹ Bonner 2008

² Barclay 1974

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