

Mast seeding, community dynamics, and tick-born...

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Mast seeding, community dynamics, and tick-borne disease risk in forest ecosystems by Taylor Minich Dr. James S. Clark, Advisor November 1, 2019 Master’s project proposal

submitted in partial fulfillment of the requirements for the Master of Forestry and Master of Environmental Management degrees in the Nicholas School of the Environment of Duke University of contents

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Abstract Tick-borne diseases are the most common vector-borne illnesses in the United States, with Lyme disease being the most

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frequently reported. Due to a warming climate, the incidence rates of tick-borne diseases are projected to increase – a risk exacerbated by the continued resilience of these diseases to

the development of vaccines and treatments. Forecasting the risk of infection to prevent

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transmission in the first place remains the best approach for fighting tick-borne illnesses. Reservoir hosts, such as small mammals and deer, facilitate the transmission from the tick vector to humans with varying levels of success. Likewise, the

population dynamics of reservoir host species may hinge on mast seeding events, or the synchronous, interannual

variability in seed   crop   production   within   populations of perennial plants.

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The pulsed resource creates a trophic cascade through the food web that provides spatiotemporally separated niches for primary consumers of the mast. I explore the capacity of mast seeding events to explain, and therefore forecast, the distribution of ticks and the reservoir host species that facilitate

tick-borne diseases in the   eastern   United States.   I estimate   the

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historic mast seeding events of individual trees with a state-space autoregressive model, synthesizing seed count data collected from sites for several decades. Based on these estimates, I determine the degree to which different genera of perennial plants affect reservoir host species, and in turn the degree to which different host species affect tick population dynamics. Keywords: blacklegged tick; Lyme disease; masting; pulsed-resource; resource-consumer interactions; tick-borne disease; tree seed production 2 Intro duction Resource pulses—temporally-variable influxes of nutrition in an ecosystem—travel through food webs like trophic cascades (Paine 1980, Ostfeld and Keesing 2000). Examples of pulsed-resources abound across different ecosystems, yet all are characterized by

low frequency, large magnitude, and short duration relative to the timescale of their

14

consumer

(Yang et al. 2008). These   episodic   events,

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such as sudden marine upwellings (Bode et al. 1997) and El Niño downpours (Letnic et al. 2005), may provide stability and functionality within a variety of communities (McMeans et al. 2015). One such pulsed resource is mast seeding (Ostfeld and Keesing 2000). The behavior describes the synchronous, interannual

variability in seed   crop   production   within   populations of perennial plants

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(Kelly 1994). Although the ultimate and proximate causes for the behavior remain unresolved, mast seeding seems to be linked to

the relationship between weather cues and

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the

allocation of resources towards reproduction (Pearse et al. 2016). The

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exact nature of this relationship depends on the species, 1 yet empirical studies have shown that

high temperatures in the spring months

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correlate with high seed crops (Sork 1993,

Koenig et al. 1996). Indeed, Pérez-Ramos et al.

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(2015) found that colder spring temperatures may reduce both the

8

synchrony in pollen release and successful fertilization as well as the overall size of the seed crop. The resource pulse cascades through higher trophic levels, generating spatiotemporal structure in the ecosystem that varies from year to year (Bergeron

et al. 2011). Theoretical and empirical evidence suggest that

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primary consumers—species that feed directly on the seed crop produced by forests—experience the greatest effect from masting behavior (Mills and Doak 1993). The structure created by masting is complex, however, as some primary consumers may anticipate the dynamic resource availability, adjusting juvenile emergence with peak food abundance before a mast seeding event (Boutin et al. 2006, White 2008). Therefore, anticipatory consumers grow their populations in synchrony with the pulse-resource whereas reactionary consumers experience a lag (Bergeron et al. 2011). These temporally separated niches may promote species coexistence and ecosystem stability

(Loreau and de Mazancourt 2008). Depending on the strength of the environmental cues, the

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pulsed nature of the resource may reverberate beyond the level of primary producer [Paine1980]. An important example of such a phenomenon is the degree to which mast seeding influences the spatiotemporal distribution of ticks (Ixodes spp.) and, thus, tick-borne diseases. Tick populations rely on primary consumers of mast seeding such as small mammals and deer (Granter et al. 2014). Not only do the consumers support tick populations, but they also act as hosts facilitating the spread of tick-borne diseases across the parasite’s different life stages (Ostfeld et al. 2018). Ticks pass through four life stages during their two-year lifespan – egg, larva, nymph, and adult. Upon hatching in the summer,

larvae and nymphs must consume a blood meal to develop into the next stage

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(Granter et al. 2014). Likewise, an adult female feeds one last time before dropping from the host, laying her eggs, and completing the cycle. As ticks hatch uninfected, it is during these feeding bouts that the disease transmits

from the host to the tick vector, and

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back again. The long-term

transmission of tick-borne diseases relies on the

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successful infection of hosts; however, different host species have differential

infection rates (LoGiudice et al. 2003). The most successful host

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species are 2 termed reservoir hosts. The primary hosts responsible for tick-borne diseases in eastern

North America are the white-footed mouse (Peromyscus leucopus), the deer mouse (Peromyscus maniculatus),

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the masked shrew (*Sorex cinereus*), the short-tailed shrew (*Blarina brevicauda*), and the eastern chipmunk (*Tamias striatus*); 13

Barbour 2017, Ostfeld et al. 2018).

Tick-borne diseases are the most common vector-borne illnesses in the United States, with Lyme disease being the most 9

frequently reported

(Dantas-Torres et al. 2012, Adrion et al. 33

2015) at an estimated 30,000 new cases each year (Disease Control and Prevention) 2019b). Since ticks favor warm temperatures, climate change will likely exacerbate the incidence of Lyme disease, by as much as 20 percent (Dumic and Severnini 2018). Thus far, we have had limited success in developing vaccines and treatments for

tick-borne diseases, and prevention remains the best approach for 6

reducing their incidence (Piesman and Eisen 2008). The

disease is caused by the spirochete bacterium, *Borrelia burgdorferi*, but relies on the 23

interaction between hosts and the tick vector for transmission. A growing body of research has prioritized determining the degree to which different wildlife species may act as reservoirs of future zoonotic disease as a means of forecasting human disease risk (Karesh et al. 2012, Han et al. 2015).

A better understanding of the population dynamics of competent reservoir host species 26

as determined by mast seeding pulsed-resources will improve our capacity to forecast the spatiotemporal distribution of outbreaks of tick-borne diseases. Here, I assess the impacts mast seeding have on tick populations through their

connection with reservoir hosts. I ask: • Which plants influence reservoir host populations by mast seeding? • Which reservoir hosts are responsible for determining the

dynamics of tick populations in the eastern United States? • What are

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the associated lag times between these processes? 3 3 Metho ds 3.1 Data collection and study sites I leveraged two data networks to understand the nature of these processes: the Mast Inference and Prediction (MASTIF, Clark et al. 2019) network and

the National Ecological Observatory Network (NEON, Ecological Observatory Network)

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

from the NASA TerraClimate product (Abatzoglou et al. 2018)

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through

Google Earth Engine (Gorelick et al. 2017).

2

NEON is a continental-scale observation facility that collects long-term ecological, atmospheric, and environmental data. Their methods are systematic and reproducible across approximately 80 field sites. Here, I focus on their woody plant vegetation structure, small mammal box trapping, and ticks sampled using drag cloths datasets as estimates for plant, small mammal, and tick abundance, respectively. These data are collected on separate, often overlapping plots within a field site. Similar to MASTIF, technicians at NEON collect basic tree metrics such as DBH, location, species identification, height, and mortality status for all of the trees and woody shrubs ≥ 10 cm DBH within the plant abundance plots. Small mammal abundance plots are organized with 100 box traps per plot. For each sampling bout, technicians record the trap’s location

and catch status as well as the animal's species identification. Although the small mammal traps capture an array of different species, I focus only on the competent reservoir hosts in this region:

the white-footed mouse (*P. leucopus*), the deer mouse (*P. maniculatus*), the

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masked shrew (*S. cinereus*), the short-tailed shrew (*B. brevicauda*), and the eastern chipmunk (*T. striatus*;

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Barbour 2017, Ostfeld et al. 2018). Tick abundance sampling involves dragging a 1m2 cloth 4 along the ground. The life stage (larva, nymph, or adult) of the ticks captured on the cloth is recorded. Animals are sampled at regular intervals throughout the year. I limited my study region to the

eastern United States where the blacklegged tick (*Ixodes scapularis*)

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is common (Disease Control and Prevention) 2019a). I overlaid the MASTIF and NEON field sites and found six regions, concentrated in the Northeast, where both sets of data are collected. These sites allow for modeling at every stage (i.e. mast density to small mammal abundance, and small mammal abundance to tick abundance). In order to incorporate as much data as possible, I included an additional six field sites where only NEON data are collected. As the interannual mast behavior of these regions is unknown, the additional sites supplement the stage of the model addressing the effects of small mammal abundance on tick abundance. On the plant abundance plots overlapping a MASTIF site, 48 species of woody plants from 29 genera (*Acer*, *Ailanthus*, *Betula*, *Carpinus*, *Carya*, *Celtis*, *Cercis*, *Cornus*, *Diospyros*, *Fagus*, *Fraxinus*, *Ilex*, *Lindera*, *Liquidambar*, *Liriodendron*, *Juglans*, *Magnolia*, *Nyssa*, *Ostrya*, *Oxydendrum*, *Picea*, *Pinus*, *Platanus*, *Prunus*, *Quercus*, *Robinia*, *Sassafras*, *Tsuga*, and *Ulmus*) are present. Within the NEON sites, there are multiple plots collecting data for each dataset (plant abundance, small mammal abundance, and tick abundance). I paired up the different plots with each other by proximity so that for the sites collecting both MASTIF and NEON data, there is a unique combination of plant abundance, small mammal abundance, and tick abundance plots serving as an observational unit. For the sites collecting only NEON data, the observational unit encompasses pairs of small mammal abundance and tick abundance plots. Data collection for the NEON datasets began for most of the sites within my study region in 2012 and continued until the end of my study period in 2018. 5 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). 6 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 6 160 161 162 163 164 165 166 167 168 169 170 171 172 173 174 175 176 3.2 Model design 3.2.1 Mast density The MASTIF model is a state-space autoregressive model that estimates the mast density (seeds/unit area) of an individual tree per year as a function of DBH, canopy cover, and optional climate variables, recovering the latent parameters of maturation state and conditional fecundity in the process (Clark et al. 2019). Although the full MASTIF model includes parameters describing the shape of seed dispersal, I focused on the parameterization of maturation state, conditional fecundity, and actual fecundity. Therefore, I assume that all of the seeds stay within the site and available to consumers where they were produced, regardless of the dispersal characteristics of the tree. I modeled the maturation state

—the event that tree  $i$  can produce seed in year  $t$ — on the

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binomial distribution, where  $p_{i,t} \in \{0, 1\}$ , as a function of DBH. The covariate effects on the maturation probability are represented by the coefficients in  $\beta_v$ . I modeled the conditional fecundity—the number of seeds produced by tree  $i$  in year  $t$  given that the individual is mature ( $p = 1$ )—on a log-transformed normal distribution, where  $\log \psi_{i,t} \sim N(\mu_{i,t}, \sigma^2)$ , as a function of DBH, canopy cover, surface deficit ( $\text{surDefSite}$ ; the difference between potential evapotranspiration and actual evapotranspiration), spring minimum temperature ( $\text{springTminSite}$ ; the minimum temperature between March and May, inclusive), and the anomalies of surface deficit ( $\text{surDefAnom}$ ) and spring minimum temperature 7 ( $\text{springTminAnom}$ ) from one year to the next. Coefficients in  $\beta_x$  describe the covariate effects of conditional fecundity. The actual fecundity  $f_{i,t} = \psi_{i,t} p_{i,t}$

,  $t \geq 0$  is the product of conditional fecundity and maturation

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state. The site-level climate variables,  $\text{surDefSite}$  and  $\text{springTminSite}$ , give the model information on the spatial heterogeneity of water availability and spring temperature across the field sites. The anomalous climate variables,  $\text{surDefAnom}$  and  $\text{springTminAnom}$ , 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 ( $\beta_v$ ) and fecundity ( $\beta_x$ ) from the MASTIF sites, I parameterized individual trees

on the woody plant vegetation structure plots within the NEON sites and

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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

30

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) 8 to estimate the

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

is based on a joint distribution of parameters, predictors, and species responses. The parameters

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recovered by the model are of

two types: the matrices of coefficients between predictors and species responses, and the covariance matrix between all of the species responses. The covariance matrix may account for sources of error unexplained by the predictors, such as interactions between species and environmental gradients. Sensitivity of the entire response matrix as well as sensitivities of individual species responses can be obtained from the diagonals of the covariance matrix, allowing for a pairwise estimate of the degree to which each predictor affects the response. 3.2.4 Determining sensitivity of different species and genera Next, I modeled the response of the reservoir host species to the mast density produced by the different genera of woody plants present within each plot. I deemed a host species to be anticipatory or reactionary to the pulsed resource based on the strength of their sensitivity to the lag time from the previous model and considered the mast produced by individuals from a genus in time  $t$  or time  $t - 1$  as the predictors accordingly. By accounting for the degree to which the host species might anticipate the mast seeding event, the model is better able to determine the sensitivity of the different tree

genera to the reservoir hosts. Last, I modeled the different tick life stages as a response to the reservoir host species abundance in time t. I included the effort in obtaining the data (number of box traps for the small mammal sampling and area of cloth for the tick sampling) for all of the models. 4 Results In determining the lag time between mast seeding and small mammal abundance, I found a significant positive relationship between the mast density produced in time t-1 and one

of the most common small mammals in my study region, the deer mouse

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(P. maniculatus).

The eastern chipmunk (T. striatus) and the short-tailed shrew (B. brevicauda)

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also showed a greater sensitivity to a lag time of one year 9 whereas the

masked shrew (S. cinereus) and the

16

white-footed mouse (P. leucopus) showed no

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lag time (Figure 2). Although these relationships were not significant, for some species (P. leucopus, S. cinereus, and T. striatus) they are substantiated by the literature (Smith and Reichman 1984,

Bergeron et al. 2011, Ostfeld et al. 2018). Figure 2: The distribution of

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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. After partitioning the effect of the mast seeding events across the different plant genera, I found scant evidence for which genera of trees are driving the dynamics of small mammal abundance (Figure 3). Only three plant genera showed a significant effect on small mammal species: a negative effect of sweetgum (Liquidambar) on B. brevicauda, a negative effect of locust (Robinia) on P. maniculatus, and a negative effect of hickory (Carya) on T. striatus. I found no evidence to suggest that the population dynamics of individual host species affects any of the mobile tick life stages (Figure 4). 10 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. 11 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. 5 Discussion Tracking the effect of the pulsed resource of mast seeding on tick populations and their reservoir hosts involves one small food chain amongst a broader and more complex food web. Such an analysis can only consider bottom-up forces (i.e. where primary control is held by resources) on the community and neglects entirely top-down forces (i.e. where primary control is held by predators) as well as competitive exclusion within a trophic level (Hardin 1960, Power 1992). Incorporating as many predictors as possible into a model, however, limits its simplicity (and therefore utility) and introduces a host of other issues such as overfitting and collinearity between predictors (Wold et al. 1984, Hawkins 2004). Bearing this in mind, it is important to determine whether the lack of significant connections between 12 mast seeding and tick populations is accurate or rather a consequence of poor model performance. Like other Bayesian models, GJAM makes

**use of Gibbs sampling,** a **Markov chain Monte Carlo (MCMC)** algorithm, to determine **the**  
marginal distribution **of the**

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parameters (Gelfand 2000, Clark et al. 2017). With any MCMC approach, it is important to make sure that the chains have converged on a singular coefficient estimate, even if the uncertainty associated with the estimate is large. Moreover, GJAM sets aside some of the data to determine how well the observations align with the predictions of the parameter estimates. Both the convergence of the MCMC chains and the comparison of predicted vs observed data are important indicators of model performance. All of the models showed complete convergence and a good fit between predicted vs observed data (Appendix: Figures 5-8). Even though the models performed well, they could have found a paucity of evidence for these processes for two reasons: the connection between the different trophic levels was weaker than expected or there were insufficient data to determine the connection. The competent reservoir host species for

**tick-borne diseases in the** eastern **United States are**

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all generalist consumers (Ostfeld et al. 2018). In times of resource scarcity, generalist consumers, unlike their specialist counterparts, can undergo diet switching, or a dynamic altering of their diet in response to the environment (Polis and Strong 1996). Indeed, some generalist consumers (such as *P. leucopus*) alter not only their diet but also their trophic level, removing themselves further from the pulsed resource of mast seeding (Shaner and Macko 2011). In non-mast years, the reservoir host species can turn to other sources of food to sustain their populations, which diminishes the strength of bottom-up forces on a community. Indeed, the

**weak trophic** interactions **may be important in promoting community persistence and stability**  
**(McCann et al. 1998).**

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Weak trophic interactions limit our ability to predict how other trophic levels react to mast seeding events, especially when the strength of the resource pulse is partitioned across different groups of plants or community types. When it comes to forecasting the spatiotemporal distribution of tick abundance and Lyme disease risk, understanding the patterns of mast seeding events may not be enough. The strength of the pulsed resource diminishes as it travels through the population dynamics of generalist consumers. Moreover, using reservoir host species abundance as a predictor for tick abundance presents its own challenges (Vu Hai et al. 2014). Ticks have been known to expand their list of reservoir host species over time as 13 communities are altered by culling programs (Jaenson et al. 2012). The spread of tick-borne diseases can depend more on the biodiversity of the entire community than the abundance of individual species (Levi et al. 2016). The populations of host species are also in a state of flux as they respond to climate change, anthropogenic modification of the landscape, and the introduction of invasive species. The multitude, interactivity, and complexity of variables affecting tick-borne diseases place robust forecasting of disease risk beyond current human understanding (Dantas-Torres 2015). Additional research into new and innovative approaches for predicting tick-borne disease risk are necessary to ensure its success. One such approach that shows promise uses prevalence of Lyme disease in our canine companions as a proxy for prevalence in humans, thereby removing the predictor from the complexity of multi-trophic interactions (Watson et al. 2017). Until we develop vaccines or treatments

for Lyme disease and other tick-borne illnesses,

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forecasting risk and preventing the spread of infection remains our only option in the fight against tick-borne diseases. 14  
290 6 App endix 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  $t - 1$  15 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 16 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. Species Seed weight (g/seed) *Abies fraseri* 0.02211 *Acer negundo* 0.04022 *Acer pensylvanicum*  
0.03711 *Acer rubrum* 0.07722 *Acer saccharum* 0.06211 *Ailanthus altissima* 0.00822 *Amelanchier laevis* 0.00622 *Betula*  
*alleghaniensis* 0.00111 *Betula lenta* 0.000811 *Betula papyrifera* 0.000311 *Carpinus caroliniana* 0.02611 *Carya cordiformis*  
6.63011 *Carya ovata* 4.40011 *Celtis occidentalis* 0.10022 *Cercis canadensis* 0.03222 *Cornus florida* 0.10011 *Diospyros*  
*virginiana* 0.37822 *Fagus grandifolia* 0.26011 *Fraxinus americana* 0.04522 *Fraxinus pennsylvanica* 0.03211 *Ilex opaca*  
0.01611 *Juglans nigra* 11.30001 *Juniperus virginiana* 0.01011 *Lindera benzoin* 0.10011 *Liquidambar styraciflua* 0.00611  
*Liriodendron tulipifera* 0.03211 *Magnolia fraseri* 0.10011 *Nyssa sylvatica* 0.58011 *Ostrya virginiana* 0.01511 *Oxydendrum*  
*arboreum* 0.000111 *Paulownia tomentosa* 0.000211 *Picea glauca* 0.00411 *Pinus rigida* 0.02711 *Pinus strobus* 0.01711  
*Pinus taeda* 0.00711 *Pinus virginiana* 0.00811 *Platanus occidentalis* 0.00422 *Prunus pensylvanica* 0.02811 *Quercus alba*  
3.54011 *Quercus coccinea* 1.93011 *Quercus montana* 1.80011 *Quercus rubra* 3.63011 *Quercus velutina* 1.85011 *Robinia*  
*pseudoacacia* 0.01911 *Sassafras albidum* 0.09111 *Sorbus americana* 0.03211 *Tsuga canadensis* 0.00211 *Ulmus americana*

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