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Nina K. Lany

Phoebe Zarnetske

Erin M. Schliep

Robert N. Schaeffer

Colin M. Orians

See next page for additional authors

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Authors

Nina K. Lany, Phoebe Zarnetske, Erin M. Schliep, Robert N. Schaeffer, Colin M. Orians, David A. Orwig, and Evan L. Preisser

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1 **Running title:** Spatio-temporal joint distribution model

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3 **Asymmetric biotic interactions and abiotic niche differences revealed by a dynamic joint**
4 **species distribution model**

5

6 N.K. Lany^{1,2}, P.L. Zarnetske^{1,2}, E.M. Schliep³, R.N. Schaeffer⁴, C.M. Orians⁴, D.A. Orwig⁵, E.L.
7 Preisser⁶

8

9 ¹Department of Forestry, Michigan State University, East Lansing, MI 48824 USA

10 ²Ecology, Evolutionary Biology, and Behavior Program, Michigan State University, East
11 Lansing, MI 48824 USA

12 ³Department of Statistics, University of Missouri, Columbia, MO 65211 USA

13 ⁴Department of Biology, Tufts University, Medford, MA 02155 USA

14 ⁵Harvard Forest, Harvard University, Petersham, MA 01366 USA

15 ⁶Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881 USA

16

17 **Corresponding author:** Nina K. Lany

18 480 Wilson Road, MSU Department of Forestry

19 East Lansing, MI 48862

20 Phone: (517) 355-7671, Fax: (517) 432-1143

21 email: lanynina@msu.edu

22

23 **Abstract:** A species' distribution and abundance are determined by abiotic conditions and biotic
24 interactions with other species in the community. Most species distribution models correlate the
25 occurrence of a single species with environmental variables only, and leave out biotic
26 interactions. To test the importance of biotic interactions on occurrence and abundance, we
27 compared a multivariate spatio-temporal model of the joint abundance of two invasive insects
28 that share a host plant - hemlock woolly adelgid (HWA; *Adelges tsugae*) and elongate hemlock
29 scale (EHS; *Fiorina externa*) - to independent models that do not account for dependence among
30 co-occurring species. The joint model revealed that HWA responded more strongly to abiotic
31 conditions than EHS. Additionally, HWA appeared to predispose stands to subsequent increase
32 of EHS, but HWA abundance was not strongly dependent on EHS abundance. This study
33 demonstrates how incorporating spatial and temporal dependence into a species distribution
34 model can reveal the dependence of a species' abundance on other species in the community.
35 Accounting for dependence among co-occurring species with a joint distribution model can also
36 improve estimation of the abiotic niche for species affected by interspecific interactions.

37 **Keywords:** *Adelges tsugae*, *Fiorinia externa*, invasive species, spatio-temporal species
38 distribution model, species interactions, *Tsuga canadensis*

39 **Introduction**

40 Ecologists have long sought to understand how abiotic conditions and biotic interactions
41 combine to determine a species' distribution and abundance (Grinnell 1917, Andrewartha and
42 Birch 1954, MacArthur 1972). The niche concept is often employed to conceptualize this
43 balance (Chase and Leibold 2003). The effect of the environment on a species, with an emphasis
44 on broad-scale abiotic conditions, has historically been associated with the Grinnellian niche
45 (Grinnell 1917), while the impact of a species on the environment and local interactions with

46 other species have been associated with the Eltonian niche (Elton 1927). Subsequent ecological
47 theory has integrated these paradigms to define a species' niche as the range of biotic
48 interactions and abiotic conditions under which a species has a positive population growth rate
49 (Hutchinson 1957, Chase and Leibold 2003). Hutchinson (1957) distinguished the "fundamental
50 niche" that encompasses the range of conditions under which a species could potentially exist
51 from the "realized niche" that encompasses the typically smaller range of conditions under which
52 a species can exist when competing with other species. The current definition additionally
53 acknowledges predation and mutualism, as well as dispersal limitation (Peterson et al. 2011).

54 The distribution of a species can be interpreted as a projection of the realized niche onto
55 geographic space (Pulliam 2000, Peterson et al. 2011). Despite the connection between both the
56 biotic and abiotic components of a species niche and its geographic distribution, most species
57 distribution modeling approaches correlate the occurrence of a single species with broad-scale
58 environmental variables but omit biotic interactions. Because distribution and abundance often
59 depend on other species in the community, explicitly incorporating biotic interactions into
60 species distribution models is a research priority (Godsoe et al. 2015).

61 One way to accommodate biotic interactions is to model the joint distribution or
62 abundance of species in a community with a multivariate generalized linear model that estimates
63 the response of each co-occurring species to the abiotic environment. This approach explicitly
64 accounts for residual dependence among species that can arise from either shared responses to an
65 unmeasured covariate, or interactions among species (e.g. Ovaskainen et al. 2010, Pollock et al.
66 2014, Warton et al. 2015). Whereas the vast majority of species distribution models use static
67 binary occurrence data, a time-series of abundance data provides more information on dynamic
68 and density-dependent ecological processes (Pagel and Schurr 2012, Ehrlén and Morris 2015). In

69 addition, accounting for spatial autocorrelation can reflect underlying interactions among species
70 and improve the precision of parameter estimates (Dormann et al. 2007, Ovaskainen et al. 2016).

71 Here, we utilize a dynamic, spatially explicit joint species distribution model and long-
72 term, spatially explicit data on the abundance of two invasive insect herbivores that share a
73 common host plant – hemlock woolly adelgid (HWA; *Adelges tsugae*) and elongate hemlock
74 scale (EHS; *Fiorinia externa*) – to test the hypotheses that: 1) the abiotic niches of these co-
75 occurring species are different, and 2) the abundance of each of these species is dependent on
76 biotic interactions with the other. We explicitly compare joint vs. independent models.

77 **Methods**

78 In the eastern USA, eastern hemlock (*Tsuga canadensis*) is host plant to HWA and EHS.
79 HWA is a sessile xylem-feeding insect introduced to eastern North America from Japan and first
80 documented in 1951 that has severely impacted eastern hemlocks and threatens to extirpate the
81 species across its range (Orwig et al. 2012). EHS is also a sessile xylem-feeding insect
82 introduced from Japan in 1908 that preferentially feeds on eastern hemlock needles and rarely
83 kills its host tree (McClure 1980a). Fine-scale experiments have revealed exploitative
84 competition between HWA and EHS at the scale on individual branches (Preisser and Elkinton
85 2008) and large-scale observations suggest HWA may facilitate EHS (Preisser et al. 2008).

86 We assessed the abundance of HWA and EHS on five occasions over 14 years at 142
87 forest stands across a latitudinal transect encompassing 7,500 km² in Connecticut (CT) (Orwig
88 et al. 2002) and Massachusetts (MA) (Orwig et al. 2012). Stands were initially visited in 1997-
89 1998 (CT) or 2002-2004 (MA), and each one of these stands were subsequently re-visited in
90 2005, 2007, 2009 and 2011. In the initial year of sampling, each stand was given an ordinal score
91 representing the average infestation level of the stand (0 = 0 insects per meter of branch; 1 = 1-

92 10 insects/m; 2 = 11 – 100 insects/m; 3 = >100 insects/m). In subsequent years, 50 trees were
93 haphazardly selected in each stand for observation. Fewer than 50 trees were sampled per stand
94 in some highly-damaged stands, and stands impacted by logging or development during the
95 study period were not sampled post-disturbance, resulting in a total of 27,050 observations. The
96 median distance between pairs of stands was 56.7 km, and ranged from 0.2 to 165.2 km.

97 Daily temperature and precipitation data were obtained for each stand from 1996 to 2011
98 by interpolating 4 km² resolution climate data at the centroid of each eastern hemlock stand
99 (PRISM Climate Group). For each stand-year, we calculated three weather variables known to
100 affect HWA and EHS abundance: minimum temperature during the winter preceding the
101 growing season, maximum summer temperature during the growing season, and total
102 precipitation during the interval April 1 – September 30. We expect a positive relationship
103 between winter temperature and insect abundance due to winter mortality (Cheah 2017) and
104 between summer temperature and abundance due to the effects of temperature on development
105 rate (Salom et al. 2002). Extremely warm summer temperatures, however, cause mortality for
106 EHS (McClure 1989) and HWA during diapause (Sussky and Elkinton 2015). Heavy rains
107 dislodge adelgid and scale insects (McClure 1989) and insects also benefit from feeding on
108 drought-stressed trees (Koricheva et al. 1998), resulting in a negative relationship with summer
109 precipitation. Minimum winter temperatures ranged from -12.4 to -28.4 °C, and were negatively
110 correlated with latitude ($r = -0.78$, Appendix S1: Figure S1). Summer precipitation ranged from
111 422.7 to 1187.3 mm, and maximum summer temperature ranged from 30.0 to 38.5 °C. Neither
112 summer precipitation ($r = -0.07$) nor summer temperature ($r = -0.11$) was strongly correlated
113 with latitude, but both showed high inter-annual variation (Appendix S1: Figure S1). The

114 greatest correlation between covariates occurred between summer temperature and precipitation
115 ($r = 0.54$). Data are archived at the Environmental Data Initiative (Orwig et al. 2017).

116 We modeled the joint abundance of the two insects with a multivariate generalized linear
117 model with probit link function following the methods we developed in Schliep et al. (2018).
118 We extended the probit link function to accomodate ordinal abundance categories by assuming
119 that for each species s on tree j in stand i and time t , the observed ordinal abundance $Y^{(s)}_{i,t,j}$
120 resulted from a thresholding process on a latent (or *unobserved true*) multivariate Gaussian
121 abundance $Z^{(s)}_{i,t,j}$. Here, $s = 1$ for HWA and $s = 2$ for EHS. Because the same trees were not
122 sampled between years, we used a hierarchical structure to infer the stand-level mean ($\mathbf{K}_{i,t}$) of the
123 latent bivariate abundance $\mathbf{Z}_{i,j,t}$ for each insect species in each year, such that $\mathbf{Z}_{i,j,t} \sim$ Multivariate
124 Normal ($\mathbf{K}^{(s)}_{i,t}, \Omega_i$). Larger values of $\mathbf{K}_{i,t}$ indicate higher abundance of a species in a particular
125 stand and year, while lower values indicate lower abundance. Tree-level dependence between
126 species, the scale at which these species interact (Preisser and Elkinton 2008), was modeled with
127 a 2x2 covariance matrix (Ω_i) for each stand. The **diagonals $\Omega_{1,1}$ and $\Omega_{2,2}$ describe the variance in**
128 **abundance of each species on individual trees within a stand across all years, and the off-**
129 **diagonal $\Omega_{1,2} = \Omega_{2,1}$ describes the within-stand covariance in abundance between the two species.**

130 We defined the mean latent abundance of each species as $\mathbf{K}_{i,t} = \boldsymbol{\alpha}_t + \boldsymbol{\beta}\mathbf{X}_{i,t} + \boldsymbol{\rho}\mathbf{K}_{i,t-1} +$
131 $\boldsymbol{\eta}_{i,t}$, using the species- and year-specific random intercept $\boldsymbol{\alpha}_t$, to capture variability across years
132 and account for northward range expansion over the study period (see Schliep et al. 2018 for
133 discussion of why a temporal random effect is necessary for these data), the term $\boldsymbol{\beta}\mathbf{X}_{i,t}$ to
134 incorporate abiotic conditions specific to each stand-year, a lag-1 vector auto-regressive process
135 $\boldsymbol{\rho}\mathbf{K}_{i,t-1}$ to capture temporal dependence, and a spatially correlated error term $\boldsymbol{\eta}_{i,t}$ to capture spatial
136 dependence. $\mathbf{X}_{i,t}$ included weather-related covariates specific to each stand-year as both linear

137 and quadratic terms: minimum winter temperature, maximum summer temperature, and summer
138 precipitation. All covariates were mean centered and standardized. β was the 2 x 7 (linear and
139 quadratic forms of each of the three predictor variables, plus the intercept) matrix of coefficients
140 that described the response to abiotic conditions unique to each species and allowed comparison
141 of the abiotic niche for each species. Inter- and intra-specific temporal dependence was modeled
142 with the 2x2 lag-1 autoregressive matrix ρ . The off-diagonal elements of the parameter matrix ρ
143 ($\rho_{1,2}$ and $\rho_{2,1}$) described temporal dependence between species. For example, positive estimates
144 of the off-diagonal parameter $\rho_{1,2}$ would indicate that average stand-level EHS latent abundance
145 at time $t-1$ made a stand more susceptible to infestation by HWA at time t . Importantly, temporal
146 dependence between species can be directional because the ρ matrix is not necessarily
147 symmetric. Spatially-correlated dependence within and among species not accounted for by
148 model terms was captured with a linear model of coregionalization for the error term $\eta_{i,t}$. This
149 permitted estimation of the effective range (the distance at which residual spatial correlation
150 dropped below 0.05) for each species (Schliep et al. 2018). A large estimated effective range
151 would indicate that important predictor variable(s) may be missing from the model.

152 We obtained inference in a Bayesian framework with non-informative and conjugate
153 priors, and calculated marginal rank probability scores (RPS) to assess model fit (Schliep et al.
154 2018). We used the function 'Multivariate.Ordinal.Spatial.ModelX' available in the online
155 supplement for Schliep et al. (2018). We evaluated evidence for the hypothesis that there is a
156 difference in the abiotic niches of two species by comparing posterior estimates of the β
157 coefficients. To evaluate whether biotic interactions between the two insects mediate distribution
158 and abundance (hypothesis 2), we evaluated the posterior estimates of $\rho_{1,2}$ and $\rho_{2,1}$. In addition,
159 we specified independent models that did not include biotic interactions by setting the

160 parameters that describe temporal ($\rho_{1,2}$ and $\rho_{2,1}$), spatial (in the error term $\boldsymbol{\eta}_{i,t}$), and tree-level
161 ($\boldsymbol{\Omega}_{1,2} = \boldsymbol{\Omega}_{2,1}$ for each stand) dependence between species to zero. We compared the effective range
162 of residual spatial correlation for each species from the joint model that accounts for dependence
163 among species *vs.* independent models of the abundance of each species that do not account for
164 dependence. Narrower credible intervals for the β coefficients and smaller effective ranges in the
165 dependent *vs.* independent model would indicate a better-specified, more robust model (Barry
166 and Elith 2006). Markov chain Monte Carlo was run for 10,000 iterations and the first 2,000
167 were discarded as burn-in. No issues of convergence were detected in any of the models. An R
168 script that runs the joint and independent models is provided in Appendix S2.

169 **Results**

170 The posterior mean of latent abundance of each species varied from year-to-year and also
171 with latitude (Figure 1). In the joint model, HWA abundance was positively associated with
172 minimum winter temperature as both linear and quadratic terms (Figure 2). HWA abundance was
173 negatively associated with summer precipitation and positively associated with the square of
174 summer precipitation (Figure 2). HWA abundance increased linearly according to maximum
175 summer temperature (Figure 2). EHS abundance was positively and linearly associated with
176 minimum winter temperature, but none of the other posterior coefficient estimates describing the
177 abiotic niche for EHS were significantly different than zero according to the 95% credible
178 intervals (Appendix S1: Table S1).

179 We found evidence for dependence between HWA and EHS. Both parameters that
180 describe temporal dependence between the species ($\rho_{1,2}$ and $\rho_{2,1}$) had positive posterior means
181 (Figure 3), indicating that higher EHS abundance at time $t-1$ was associated with higher HWA
182 abundance at the subsequent time step, and *vice versa*. Zero was in the posterior credible interval

183 for $\rho_{2,1}$ (Appendix S1: Table S1), and the probability that $\rho_{2,1} > 0$ was 9.966. After accounting for
184 all other model parameters, tree-level covariance across all years between the latent abundance
185 of the two species ($\Omega_{1,2}$) was largely not significant from zero for the majority of eastern
186 hemlock stands (118 of 142, Appendix S1: Figure S2). For the rest of the stands however, we did
187 detect positive tree-level covariance in 19 stands, while five were negative. There was greater
188 variability in abundance of both species among trees in southern stands ($\Omega_{1,1}$ and $\Omega_{2,2}$), especially
189 for HWA (Appendix S1: Figure S2). There was positive spatial dependence between the two
190 species at the stand level, and the effective range of residual spatial correlation was larger for
191 EHS than for HWA (29.3 vs. 2.9 km, Figure 3).

192 Modeling the abundance of the two species jointly had a larger effect on EHS-specific
193 parameters than on HWA-specific parameters. Posterior estimates for EHS tended to have
194 narrower credible intervals in the joint distribution model (Figure 2), and the effective range of
195 EHS residual spatial correlation was smaller in the joint model than in the independent model
196 (26.7 km vs. 87.6 km, Figure 2). For HWA, however, the posterior coefficient estimates and the
197 width of the credible intervals (Figure 2), as well as the effective range (Figure 2), were very
198 similar in the independent vs. joint models. Marginal RPS did not indicate problems with lack of
199 model fit, and were similar between the joint and independent models (Appendix S1: Figure S3).

200 **Discussion**

201 This study provides some of the first evidence that simultaneously modeling the
202 abundance of multiple species in a community with a spatio-temporal joint species distribution
203 model can indicate the degree to which a species' distribution and abundance are dependent on
204 biotic interactions with other species (but see Schliep et al. 2018). Our study also illustrates how
205 this approach can improve estimation of the abiotic niche of species whose abundance is

206 dependent on other species. Analyses revealed differences in the abiotic niches of EHS and
207 HWA. The positive relationship between minimum winter temperature and abundance was
208 quadratic for HWA and linear for EHS. Therefore, we expect directional increases in winter
209 temperature to benefit HWA more than EHS. Recent studies align with this expectation, showing
210 that colder winter temperatures reduce HWA populations (Cheah 2017). HWA abundance was
211 sensitive to abiotic conditions during the growing season, but EHS abundance was not. Higher
212 HWA abundance was associated with extremely dry summers, perhaps because sap-sucking
213 insects perform well when trees are water-stressed (Koricheva et al. 1998). HWA abundance was
214 also positively associated with maximum summer temperatures – a pattern consistent with the
215 ways temperature regulates development rate, an important life history characteristic for HWA
216 (Salom et al. 2002). Taken together, these findings indicated that HWA was sensitive to
217 extremes in abiotic conditions that may become more common as climate changes.

218 Hemlock woolly adelgid appeared to predispose stands to subsequent increase of EHS,
219 but HWA abundance was not strongly dependent on EHS abundance. Evidence for dependence
220 of EHS on HWA was found in the positive stand-level temporal dependence between the species
221 ($\rho_{2,1}$, although the posterior credible interval for this parameter contained zero), and in the
222 increased effective range of residual spatial autocorrelation combined with lower precision of
223 parameter (β) estimates in the independent model, which does not account for dependence
224 between species. Temporal dependence of HWA on EHS ($\rho_{1,2}$) was also positive, but the
225 effective range and precision of the posterior distribution of the β parameters were very similar
226 in the independent vs. joint models for HWA. This asymmetric interaction is consistent with
227 patterns observed after a single time step of sampling these eastern hemlock stands (initial year
228 vs. 2005, Preisser et al. 2008) but differs from a fine-scale experiment in which HWA showed

229 reduced colonization on branches that were previously colonized by EHS, while EHS settlement
230 was unaffected by previous HWA colonization (Miller-Pierce and Preisser 2012).

231 One interpretation of the result that HWA appeared to predispose stands to subsequent
232 increase of EHS is that commensalism expanded the realized niche of EHS. The commensalism
233 could have resulted from indirect interactions mediated by herbivore-induced changes in eastern
234 hemlock primary and secondary metabolism. For instance, high HWA abundance could have
235 facilitated EHS establishment and reproduction, as HWA infestation can increase foliar nitrogen
236 levels (Soltis et al. 2015), an important factor determining EHS survival and fecundity (McClure
237 1980b). Another possibility is that HWA herbivory activates the salicylic acid (SA) defense
238 pathway (Schaeffer et al. *In Press*), and thus compromises the ability of the host to activate the
239 jasmonic acid (JA) defense pathway in response to subsequent EHS herbivory. Negative ‘cross
240 talk’ in plant signaling pathways can inhibit plants from activating the JA pathway following
241 induction of the SA pathway (Thaler et al. 2012), with downstream changes in metabolites and
242 within-plant resource allocation that affect herbivores (Schweiger et al. 2014). Further research
243 by Pezet *et al.* (2013) supports this interpretation – while HWA feeding (but not EHS) led to
244 elevated methyl salicylate, EHS feeding more strongly increased green leaf volatiles. Green leaf
245 volatiles can prime defenses and coordinate with the JA pathway to confer herbivore resistance
246 (Christensen et al. 2013).

247 Commensalism could explain the long time period between EHS arrival and range
248 expansion if EHS was unable to establish in new areas until HWA invasion made stands suitable
249 for EHS infestation. An additional explanation is that EHS expanded northward more slowly
250 because Allee effects had a stronger effect on EHS than on HWA (Taylor and Hastings 2005).
251 The sexual reproduction strategy of EHS likely required a greater number of individuals to

252 disperse to a site in order to overcome negative density-dependence at very small population
253 size, slowing expansion. EHS may also be a poorer disperser than HWA. EHS and HWA have
254 similar dispersal kernels in the absence of wind, but HWA crawlers are active earlier spring
255 when winds are strong and frequent (McClure 1989). Also, HWA produces 15 times more eggs
256 per female than EHS (McClure 1989). These alternative explanations, however, cannot fully
257 account for higher EHS abundance following a time step in which HWA abundance was higher.

258 It is important to highlight that although the joint species distribution model better
259 described the ecology of this system, RPS indicated that the joint and independent models fit the
260 data equally well. This result was expected because both models split the residual error into
261 spatial and non-spatial correlation structures. The joint model captured dependence among
262 species with model parameters, while the independent model captured that dependence as
263 unexplained error that exhibited spatial correlation structure. The joint model better attributed
264 variation in the abundance of each species to specific elements that were hypothesized to affect
265 abundance *a priori*. Specifying a model that directly mapped to hypotheses about how the
266 ecological system works was more informative than capturing those ecological processes with
267 spatially-correlated errors that do not identify a specific process. However, the similarity of RPS
268 between the two models adds to the evidence that when data are not available to fully specify a
269 model containing all of the components hypothesized to strongly affect a system (which is often
270 the case in ecological studies), accounting for spatial correlation of residual error can improve
271 the robustness, fit, and predictive ability of species distribution models (Record et al. 2013).

272 This study demonstrates the benefits of accounting for biotic interactions with spatio-
273 temporal joint species distribution models implemented in a multivariate generalized linear
274 modeling framework. Accounting for spatial and temporal dependence among species improved

275 the precision of parameter estimates describing the abiotic niche for a species whose abundance
276 was highly dependent on interactions with another species in the community. Correctly
277 estimating the parameters that describe the abiotic niche of a species, and discovering whether
278 the distribution and abundance of a species is highly dependent on other species in the
279 community, are essential for tackling fundamental ecological questions, for making predictions
280 under climate change scenarios, and for conservation aims. Dynamic joint distribution models
281 such as the one presented here can help infer the underlying ecological processes that lead to
282 pattern and guide the design of future research.

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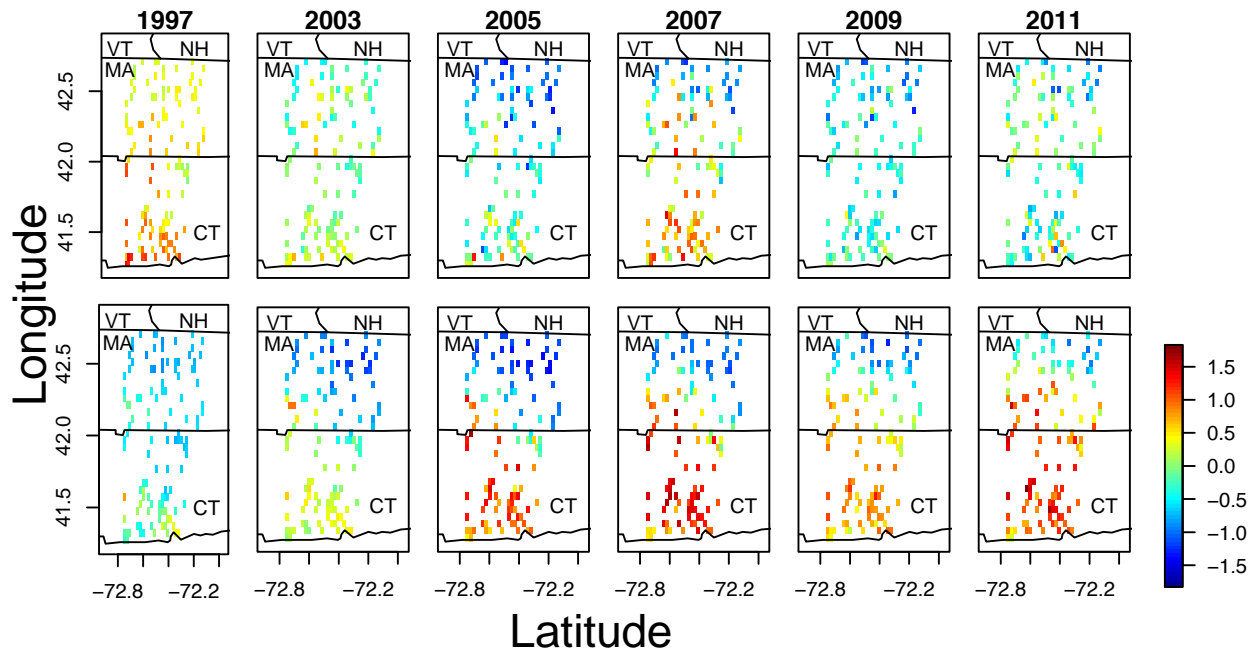
391 **Figure 1.** Posterior mean of hemlock woolly adelgid (upper) and elongate hemlock scale (lower)
392 latent abundance over time at 142 eastern hemlock stands located along a 165 km transect in
393 Connecticut (CT) and Massachusetts (MA), USA. .

394

395 **Figure 2.** Posterior distributions of model coefficients from joint vs. independent models of
396 hemlock woolly adelgid (HWA) and elongate hemlock scale (EHS) abundance in Connecticut
397 and Massachusetts, USA (1997-2011). Parameters describing the abiotic niche of each species
398 (β) are shown in A). Although HWA abundance appeared independent of EHS abundance (the
399 red and blue distributions were similar), including information on HWA abundance improved the
400 precision of model parameters for EHS (red distributions were wider than blue distributions).
401 Parameters describing temporal dependence are shown in B). Independent distribution models
402 were specified by setting all parameters that describe dependence between species to zero. In C),
403 the spatial extent of EHS effective range (ϕ_{EHS}) shrank considerably in the joint model that
404 included HWA abundance. However, the effective range of HWA (ϕ_{HWA}) was similar in the
405 independent vs. joint models.

406

407 .



408
409 **Figure 1.**

