

Joint Modeling of Climate Niches for Adult and Juvenile Trees

Souparno GHOSH, Kai ZHU, Alan E. GELFAND, and James S. CLARK

Typical ecological gradient analysis for plant species considers variation in the response along a gradient of covariate values, for example, temperature or precipitation. Response is customarily modeled through the presence/absence or a suitable measure of abundance or both. Such analysis enables the creation of a *climate niche* or *range lim*its for the species using this covariate. Interest often extends to two climate covariates, thus seeking a climate niche in two-dimensional space. It also seeks to learn whether the niche changes over life stages of the species. For instance, is the niche for juveniles different from that for adults? Across the climate domain, where are seedlings relatively more or less abundant than adults? Adult abundance is measured through basal area, juvenile abundance through seedling counts. Our contribution is to describe a coherent modeling approach to address the foregoing objectives. We construct a hierarchical stochastic specification that jointly models juveniles and adults with regard to their two-dimensional climate niches. Joint modeling of the abundance response surfaces is proposed because seedlings and adults are living jointly, competitively and is justified through exploratory analysis. Joint modeling can be challenging when one response is counts and the other is area. We model adult abundance and then juvenile abundance driven by adult abundance. Due to excess zeroes over our study plots, we employ zeroinflated models for both adult and seedling abundance. We demonstrate the benefits of the joint modeling through out-of-sample predictive performance. Our abundance data come from the USDA Forest Service's Forest Inventory and Analysis dataset. Our climate data come from the 800 m resolution Parameter-elevation Regressions on Independent Slopes Model dataset. In order to extract a response to climate, we aggregate FIA plots to ecological subsections. At plot scale, micro-scale covariates explain variation in abundance; at a larger spatial scale, climate covariates can explain variation in abundance.

Key Words: Abundance; Basal area; Hierarchical model; Mean annual precipitation; Mean winter temperature; Zero-inflated models.

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Souparno Ghosh (⊠), Department of Mathematics & Statistics, Texas Tech University, Lubbock, TX, USA (E-mail: *souparno.ghosh@ttu.edu*). Kai Zhu, Nicholas School of the Environment, Duke University, Durham, NC, USA; Department of Global Ecology, Carnegie Institution for Science, Stanford, CA, USA; and Department of Biology, Stanford University, Stanford, CA, USA (E-mail: *kai.zhu@duke.edu*). Alan E. Gelfand, Department of Statistical Science, Duke University, Durham, NC, USA (E-mail: *alan@stat.duke.edu*). James S. Clark, Nicholas School of the Environment, Duke University, Durham, NC, USA (E-mail: *jimclark@duke.edu*).

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1. INTRODUCTION

A major problem in ecology is the development of species distribution models to understand the relationship between species presence/absence or abundance and climate variables. We consider species distribution models in the form of an abundance response surface for a species over a domain of climates. The response surface provides insight into climates that are more or perhaps less favorable for the species. Informally, the set of climates required for a species to develop is referred to as the *climate niche* for that species and the extremes associated with this niche are referred to as the *range limits* for that species. Importantly, climate requirements can change over the life stages of a species, hence, so might the associated response to climate surface.

Here, we consider two roughly defined life stages, seedling and adult, and propose joint modeling to develop joint abundance response surfaces for the two stages. Seedling abundance surfaces are modeled through zero-inflated models for seedling counts. In particular, to capture heavy tails in abundance counts, we employ a zero-inflated Poisson–gamma model. Adult abundance surfaces are modeled through zero-inflated models for basal areas. We introduce a point mass at 0 and also employ a *t*-distribution to model heavier-than-Gaussian right tails.

Altogether, we build a joint hierarchical model. Joint modeling is appropriate because seedlings and adults are related through competition and seed dispersal. Evidence of strength of dependence is illuminated in Sect. 3 below. However, to date, such joint modeling, with one response discrete and the other continuous, has not been implemented in the literature. Joint modeling enables us to clarify and quantify the nature of the dependence between the abundance distributions for the two life stages as well as to more appropriately capture the uncertainty in the response surfaces. We demonstrate the benefits of the joint modeling through out-of-sample predictive performance using root mean square predictive error (RMSPE).

Often, in plant ecology, the focus is on adult responses since adult responses are viewed as stronger than those for juveniles. Those studies which simultaneously model all life stages operate under the simplifying assumption that all life stages respond similarly to environmental stimuli (Collins and Carson 2004). However, such an assumption seems untenable since, for organisms, requirements and sensitivity to environmental factors change during their life cycle (Grubb 1977), encouraging formal investigation across different life stages of a species. Changes of distribution during the lifespan of a species are sometimes referred to as ontogenetic niche shifts (Chase and Leibold 2003). These shifts reflect changes in resource availability, requirements, and the tolerance of the organism to extrinsic factors at different stages of life. Customary terminology in this context suggests that a niche contraction occurs when species requirements are stricter in earlier stages and would be viewed as indicative of *recruitment failure*; a niche expansion occurs when the circumstances are reversed. Expansions are difficult to observe in practice because they would require extensive planting of seeds where adults are currently absent. Here, avoiding such terminology, we employ our response surfaces to investigate relative abundances of seedlings to adults across the climate domain; where are seedlings relatively more or less abundant than adults?

There is a very large literature on species distribution models, explaining species presence and abundance, introducing notions like habitat models, climate envelopes, range limits, and niches, usually informally. Species distribution models study climate change impacts on forest biodiversity at regional scales (Botkin et al. 2007; Elith and Leathwick 2009; McMahon et al. 2011; Bellard et al. 2012), yet few consider responses from both juveniles/seedlings and adult trees (Bykova et al. 2012). A fundamental assumption for species distribution models is that species distributions are retained over life stages, that is, *niche conservatism* (Wiens and Graham 2005; Pearman et al. 2008; Wiens et al. 2010; Peterson 2011). Change in species distribution has been studied in the context of species invasion (Broennimann et al. 2007; Beaumont et al., 2009; Gallagher et al. 2010; Petitpierre et al. 2012) and evolution (Maiorano et al. 2013), but not at different life stages.

Again, ontogenetic shifts in environmental requirements for species occur when organisms provide different distributions at different life stages (again, Chase and Leibold 2003). Despite a large literature on such shifts in animals (reviewed by Werner and Gilliam 1984), there is little direct evidence for how it affects migration potential of plants (Young et al. 2005). Field experiments provide support for ontogenetic shifts in physiology (Parrish and Bazzaz 1985; Donovan and Ehleringer 1991; Cavender-Bares and Bazzaz 2000; Thomas and Winner 2002; Bansal and Germino 2010; Kulmatiski and Beard 2013), demography (Poorter 1999; Eriksson 2002; Miriti 2006; Warren and Bradford 2011), phenology (Yang and Rudolf 2010), and functional traits (Butterfield and Briggs 2011; Herault et al. 2011; Houter and Pons 2012; Palow et al. 2012) but few studies investigate biogeographic responses (Stohlgren et al. 1998; Quero et al. 2008; Urbieta et al. 2011).

For tree species, seedlings and adult trees are usually not part of the same analysis. Previous studies concentrate on either trees greater than a minimum diameter (e.g., Iverson and Prasad 1998; Canham and Thomas 2010) or on seedlings (e.g., Ibanez et al. 2008, 2009). Bertrand et al. (2011) consider modeling the probability of the presence of a species for each of its life stages as a function of environmental indicators. However, they model each life stage separately and consider only the presence/absence of the species, limiting opportunity to directly compare responses of large and small trees and to infer ontogenetic shifts.

Different metrics are used in the ecology literature to capture species abundance at different life stages. Biomass, captured through basal area, is appropriate for saplings and adults (henceforth just referred to as adults), while counts are appropriate for seedlings/juveniles since they have negligible biomass. As noted above, the standard approach in the literature is to specify separate models for each life stage. Again, we model different life stages simultaneously and develop a fully coherent inferential framework. None of the studies that we are aware of attempt to develop such an inferential framework for different life stages of plant species. Furthermore, none of the studies consider interaction between the environmental covariates to produce life stage appropriate abundance response surfaces over climate space for the species. Instead, they produce response curves for each life stage of the species for each of the climate covariates individually, and attempt to draw inference about distributional changes based on the location and scale of these curves obtained across the different life stages (Pyrke and Kirkpatrick 1994).

Again, we treat seedling count of a species in a plot as a measure of its juvenile abundance response to climate gradients, while the total basal area of the same species quantifies the



Figure 1. Histogram of observed adult and juvenile responses, aggregated to ecological subsection level, over the eastern US for \mathbf{a} LITU and \mathbf{b} QUAL.

adult abundance response with regard to the same factors. At our broad scale of climate conditions, a high percentage of zeros is observed, necessitating zero inflation. In addition, some geographic plots exhibit very large values for both abundance responses. So, a zero-inflated Poisson–gamma mixture model is proposed to accommodate such behavior in the seedling counts (see Ghosh et al. 2012 and references therein). To accommodate the same issues for the continuous adult responses, we propose a zero-inflated truncated *t*-distribution model for basal area. Figure 1 shows the histogram of aggregated basal area and of aggregated seedling counts at regional level (more precisely at ecological subsection level, see Sect. 2)

for two relatively abundant species, *Liriodendron tulipifera* (LITU, henceforth) and *Quercus alba* (QUAL, henceforth). At this geographical scale, 55 and 60 % of the areal units register the absence of LITU adults and juveniles, respectively, while QUAL adults and juveniles are absent in 22 and 31 % of the areal units, respectively. These reveal the potential need for zero inflation. Below, we show that our proposed zero-inflated joint model performs substantially better than standard ones, as measured by root mean square predictive error. We further show that our climate covariates alone cannot explain the heavy right tails in the figure. We will do better with a Poisson–gamma mixture and a *t* distribution with low d.f., respectively.

The format of the paper is as follows. Section 2 describes the data we work with. Section 3 details the model specification. Section 4 provides the analysis of the data, while Sect. 5 concludes with a brief summary.

2. DETAILS OF THE DATASET

The USDA Forest Service's Forest Inventory and Analysis (FIA) program is the primary source for information about the extent, condition, status, and trends of forest resources in the United States (Smith et al. 2009). FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships across the United States, resulting in a national sample intensity of one plot per 2428 ha (Bechtold et al. 2005). Satellite imagery is used to stratify the population (in an attempt to increase the precision of population estimates) and to establish permanent inventory plots in forest land uses. Forested land is defined as areas at least 10 % covered by tree species, at least 0.4 ha in size, and at least 36.6 m wide. FIA inventory plots that are established in forested conditions consist of four 7.2 m fixed radius subplots. Three of these subplots are arranged in a triangular configuration with one subplot in the center (Bechtold et al. 2005). All trees (standing live and dead) with a diameter at breast height (dbh) of at least 12.7 cm, are inventoried on forested subplots. Within each subplot, a 2.07-m-radius microplot offset 3.66 m from subplot center is established. Within each microplot, all live tree seedlings are tallied according to species.

In this analysis, FIA data were extracted from the most recent annual inventories (1999 to 2008) in 31 eastern states for a total of 43,396 inventory plots (available online, http://fia.fs.fed.us/, from FIADataBase version 4.0, extracted on March 16, 2010). To compare species abundance in different life stages, we adopted the FIA guideline to divide the data into two size classes: (1) seedling (dbh < 2.54 cm) and (2) tree (dbh \geq 2.54 cm). For each species, we extracted the seedling count and tree basal area in each plot. The condition delineation in the FIA database was used to identify fully forested plots that have both the seedling and tree survey. Thus, for every species we have 43,396 zero or non-zero complete seedling count or tree basal area records. In other words, the zero record in our dataset is a "true zero" (Martin et al. 2005), indicating that the plot was sampled, but no individual (seedling or tree) was found.

This region covers climate conditions varying from hot and moist in the region adjacent to the Gulf of Mexico to cold and dry in the region adjacent to the Great Lakes system. Species response over such a broad geographic domain, hence climate domain, has not been available before. In particular, the climate data in this study were extracted from the 800 m resolution Parameter-elevation Regressions on Independent Slopes Model (PRISM) dataset (available online, http://www.prism.oregonstate.edu/). PRISM is recognized as a high quality spatial climate dataset, employing a sophisticated interpolation, using meteorological station data, to produce digital grid estimates of climatic parameters, with consideration of location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position, and orographic effectiveness of the terrain (Daly et al. 2008).

In each plot, corresponding to the FIA measurement, we used the climate data from the previous year to create the climatic covariates. Again, we build climate niches over two climate dimensions so we extracted two illustrative choices, the mean annual precipitation (mm) and the mean winter temperature (°C), defined as the average of January, February, and March maximum and minimum monthly values.

Canham and Thomas (2010) assert that climate does not matter with regard to inter-plot variation of abundance for plots in close proximity, that variation in abundance at plot level depends more on micro-scale covariates like soil moisture, nutrient availability, and so on. Regional climatological covariates are smoothed over a broad geographical area leading to a misalignment between climate and plot-level plant abundance data. Consequently, abundance varies along climate gradients at regional scales (Iverson and Prasad 1998), but not at plot scales (Canham and Thomas 2010). We, therefore, follow the idea similar to Iverson and Prasad (1998) to aggregate plot-level FIA data to a scale more compatible with regional climate data (Zhu et al. 2014).

More precisely, we use the concept of ecological subsections, as created in the FIA database (and shown in Fig. 2a). These subsections define regions of unique ecological characteristics that differ from neighboring units across the United States (Cleland et al. 1997). Within this national framework, the ecological subsection is specifically defined as an area of similar surficial geology, lithology, geomorphic process, soil groups, subregional climate, and potential natural communities, and its boundaries usually correspond with discrete changes in geomorphology (Keys et al. 2007). In our study area of the eastern United States, there are 427 ecological subsections, as described in detail by McNab et al. (2007). The ecological subsections are not of the same size since they aggregate varying numbers of plots.

With regard to the responses, we aggregated the plot-level data (n = 43,396) to the ecological subsection level (n = 427) by summing the seedling counts and tree basal areas. Environmental variables were obtained by averaging precipitation and temperature of plots within each ecological subsection. The resultant covariates ranged from approximately 500 to 1700 mm/year for precipitation, from roughly -10 to 20° C for temperature (Fig. 2b and 2c). The sampling area of an ecological subsection was considered as the total area of plots within that region, not its actual geographic area.

3. MODEL DETAILS

3.1. JOINT MODEL SPECIFICATION

Let Y_i and Z_i , respectively, denote the cumulative seedling count and cumulative basal area in ecological subsection i, i = 1, 2, ..., n(n = 427). We build our joint specification



Figure 2. **a** Map of 427 ecological subsections spread across the 31 states of the eastern United States with a spatial map of **b** annual average precipitation and **c** mean winter temperature at ecological subsection scale.

by modeling Z_i and then Y_i given Z_i . Again, because both responses contain a considerable number of zeros, we propose to model the former as a zero-inflated Poisson–gamma mixture and the latter as a zero-inflated truncated *t*-distribution. The seedling model has two sources of zeros, one coming from a Bernoulli occurrence model, reflecting the climate suitability of the ecological subsection, and the other obtained from the Poisson abundance model, reflecting random absence.

Similarly, we model basal area as a zero-inflated truncated distribution. To provide a distributional specification, we performed an exploratory data analysis on the basal area data, regressing the observed non-zero basal area density values (observed total basal area in an ecological subsection scaled by the number of plots in that ecological subsection) on temperature and precipitation, for a collection of species. For two illustrative species, LITU and QUAL, probability plots of the residuals obtained for a standard normal distribution and for a *t* distribution with 3 d.f. are shown in Fig. 3.¹ We see that the t_3 -distribution

¹A heavier than normal tail is needed which we capture through a *t* distribution with low d.f. We use d.f.=3 in the sequel but there is little sensitivity to this choice.



Figure 3. Probability plots of the residuals obtained for non-zero basal area responses, standard normal and t_3 , for a LITU b QUAL.

better captures the heavier right tail of the residuals which, in turn, helps with regard to potential under-prediction of large basal areas in the dataset. The left truncation of the t_3 will automatically handle the left tail.

We denote the climate covariates, here, temperature and precipitation observed in ecological subsection *i*, by \mathbf{x}_i , with the area of that subsection denoted by $A_i = n_i |A|$ recorded in hectares, where |A| is the common plot area (for seedlings this is 0.0054 ha, for basal area it is 0.0672 ha) and n_i is the number of plots in ecological subsection *i*.

First, we model the Z_i . In fact, we assume

$$Z_i = 0 \text{ with probability } p_z$$

= $n_i |A| \tilde{w}_i$ with probability $1 - p_z$, (1)

where $w_i \in \mathbb{R}^1$ is a latent variable with $\tilde{w}_i = \text{Max}(0, w_i)$. From (1), the w_i and \tilde{w}_i are interpreted as *per hectare* basal area, with |A| denoting here the common plot area for adult responses. We model $w_i \sim t_v(\mu_i^{(w)}, \sigma^{(w)})$, i.e., as a t-distribution with v = 3 d.f., location $\mu_i^{(w)}$ and scale $\sigma^{(w)}$. Evidently, $(1 - p_z)|A|E(\tilde{w}_i)$ is the *per plot* expected basal area for ecological subsection *i*, while we can think of $|A|\mu_i^{(w)}$ as a *latent per plot* expected basal area for that subsection. We model $\mu_i^{(w)} \equiv h(\mathbf{x}_i, \boldsymbol{\beta}) = \beta_0 + \beta_1$ temperature_{*i*} + β_2 precipitation_{*i*} + β_3 temperature²_{*i*} + β_4 precipitation²_{*i*} + β_5 temperature_{*i*} × precipitation_{*i*}.

Why do we choose this form? Exploratory analysis yielding the contour plots of the loess smoothed per hectare basal area surface (shown in Fig. 4a for LITU and Fig. 4c for QUAL) and the loess smoothed log seedling abundance (shown in Fig. 4b for LITU and Fig. 4d for QUAL) vs. the climate covariates is performed. Fig. 4a and c motivate a quadratic form in the covariates for the mean per hectare basal area surface.² The bounding polygon is the convex hull of available temperature and precipitation combinations over the region. Under this formulation, the probability of the absence of basal area is given by

 $^{^{2}}$ More complex surfaces over climate space could be examined but, illustratively, we confine ourselves to quadratics here.



Figure 4. Loess smoothed abundance surfaces in the climate space for \mathbf{a} basal area per hectare for LITU \mathbf{b} logarithm of per hectare seedling abundance for LITU \mathbf{c} basal area per hectare for QUAL \mathbf{d} logarithm of per hectare seedling abundance for QUAL.

$$P(Z_i = 0) = p_z + (1 - p_z)P(w_i \le 0),$$

clarifying the zero-inflation role of p_z .

Turning to the seedling abundances, let $G(y_i|A_i\lambda_i)$ denote the Poisson mass function associated with the count random variable Y_i . The associated zero-inflated distribution is then defined as

$$\pi(y_i | p_{y,i}, \lambda_i) = p_{y,i} \delta_{\{0\}} + (1 - p_{y,i}) G(y_i | A_i \lambda_i).$$
⁽²⁾

Here, $\delta_{\{0\}}$ is the delta function at 0 and $(1 - p_{y,i})\lambda_i$ is the expected number of seedlings *per hectare* in ecological subsection *i*. We can think of $(1 - p_{y,i})|A|\lambda_i$ as the expected number of seedlings *per plot* in ecological subsection *i*, where now |A| is the common plot area for seedlings. Given \mathbf{x}_i and w_i , λ_i is assumed to follow a Gamma distribution with mean $\mu_i^{(y)}$ and variance $b\mu_i^{(y)}$ denoted as $\lambda_i \sim \text{Gamma}(\mu_i^{(y)}/b, b)$, where $\log \mu_i^{(y)} = \theta_0 + \theta_1$ temperature_{*i*} + θ_2 precipitation_{*i*} + θ_3 temperature²_{*i*} + θ_4 precipitation²_{*i*} + θ_5 temperature_{*i*} × precipitation_{*i*} + $\eta \tilde{w}_i$. Again, we propose a quadratic specification, now motivated by Fig. 4b for LITU and Fig. 4d for QUAL.



Figure 5. Residual plot of fitted log seedling abundance vs. basal area per hectare a LITU b QUAL.

Note that we use \tilde{w}_i in this specification since this is the *actual* adult basal area at ecological subsection *i* that is affecting seedling abundance and η is the coefficient that joins the basal area surface to the seedling abundance surface. Here, we might consider introducing a transformation of basal area into the mean for log seedling abundance. However, Fig. 5 presents a plot of the residuals from log seedling abundance for the positive abundances under the foregoing mean specification vs. basal area per hectare. There is nothing to suggest need for more than a linear term in basal area.

With regard to spatial dependence among the residuals obtained at the ecological subsection level, we ran Moran's I test for both non-zero basal area density (as obtained in Fig. 3) and non-zero log seedling abundance (as obtained in Fig. 5) for both LITU and QUAL. We used a weight matrix with 1s denoting the four nearest neighbors for each ecological subsection in the computation of Moran's I. For the four tests, the smallest p-value was 0.11 indicating no need to include spatial autocorrelation in the model.

Returning to p_y , for a set of 25 species, using simple 2 × 2 tables over the 427 ecological subregions (not shown), the probability of the presence of seedlings given the presence of adults ranged from 0.71 to 0.96. This again supports the need for joint model but, furthermore, suggests that, for the Bernoulli occurrence model, we can posit a logit specification for p_y in basal area, $logit(p_{y_i}(w_i; \alpha)) = \alpha_0 + \alpha_1 \delta_{\{\tilde{w}_i > 0\}}$. We have investigated inclusion of the climate covariates in both p_z and p_y ; overfitting arises yielding very badly behaved model fitting.

3.2. PRIORS AND MODEL FITTING

We specify a Normal(0, 100) prior on the each of the regression parameters β , θ , η , α_0 and α_1 . p_z is assumed to follow Uniform(0,1) distribution. Once again w_i is interpreted a latent per hectare basal area and hence can be unrestricted. Model fitting is done through Markov chain Monte Carlo. We achieve well-behaved MCMC with better acceptance if we center the prior of $\sigma^{(w)}$ properly. To that end, we estimate the variance of the residuals obtained during the exploratory data analysis. We then propose a Gamma prior on $\sigma^{(w)}$ which is centered at this empirical residual variance but with large uncertainty (prior variance is set at 100).

To facilitate computation, we introduce auxiliary binary variables $r_i \sim \text{Bernoulli}(p_z)$ in the basal area model (1). That is,

$$Z_i = 0 \text{ if } r_i = 1$$

= $\tilde{w}_i \text{ if } r_i = 0.$ (3)

In other words, $P(Z_i = 0 | r_i = 1) = p_z$ but if $r_i = 0$ we can still have $Z_i = 0$. In particular, whenever $Z_i > 0$, the associated $r_i = 0$. For the $Z_i = 0$, we can have $r_i = 0$ or 1 and we update r_i , i.e., $r_i | Z_i = 0$ from its full conditional distribution, a Bernoulli $(\frac{p_z}{p_z + (1 - p_z)P(w_i \le 0)})$. The full conditional of p_z is given by Beta $(\sum_{i=1}^n r_i + 1, n - \sum_{i=1}^n r_i + 1)$.

The latent w_i 's are updated as follows. When $r_i = 1$, we update w_i from its full conditional given by

 $[Y_i | \boldsymbol{\alpha}, \boldsymbol{\theta}, \eta, \mathbf{x}_i, w_i] [w_i | \mathbf{x}_i, \boldsymbol{\beta}, \sigma^{(w)}]$, with the first term obtained after marginalizing over λ_i . When $r_i = 0$ we write

$$w_i = u_i \text{ if } z_i = 0$$
$$= z_i / A_i \text{ if } z_i > 0$$

So, the u_i 's enter into the model as parameters and are drawn from truncated t_3 full conditionals. Once the w_i 's are updated, β and $\sigma^{(w)}$ are updated from their full conditionals using the current values of the w_i 's. We update θ by first integrating out the λ_i s and then drawing from $p(\theta|\eta, \alpha, \{Y_i\}, \{w_i\}, \{Z_i\})$. η, α_0 and α_1 are updated in similar fashion. Three parallel chains were run and convergence was assessed using the Gelman–Rubin criterion (Gelman and Rubin 1992). For the FIA analyses presented below, their \hat{R} statistic ranged from 1.0002 (for α_1 for both LITU and QUAL) to 1.026 (for p_z associated with LITU).

3.3. RESPONSE SURFACE ESTIMATION

The fitting procedure described in Sects. 3.1 and 3.2 produces samples from the joint posterior of $\Omega = \{w_i\}, \theta, \eta, \beta, \sigma_w^2, \alpha_0, \alpha_1, p_z | \{Y_i\}, \{Z_i\}$. The set of samples enables a posterior sample of response surfaces. We overlay a fine grid of cells on the climate space from which we calculate a posterior median surface by taking the median value for each cell. Hence, after the model fitting, we obtain two posterior predictive *median* abundance response surfaces, one for adults and one for seedlings, over $\mathbf{x} =$ (temperature, precipitation). In displaying these surfaces, we confine the domain to the convex hull of observed temperature and precipitation in our study region. We prefer posterior median surfaces to posterior mean surfaces due to the right skewness that occurs to the mean when we exponentiate the log abundance surfaces.

More explicitly, with regard to adults, for each posterior realization of β , we obtain an intensity surface, using $h(\mathbf{x}; \beta)$ below (1) evaluated at each \mathbf{x}_j . Next, with a posterior draw of $\sigma^{(w)}$ we can use the t_3 distribution to draw a w surface, hence a \tilde{w} surface. With B posterior draws we obtain B such surfaces. Taking the median at each \mathbf{x}_j , we obtain the *median basal area per hectare* response surface.

For the response surface for the seedlings, we need to marginalize $[\lambda | \theta, \eta, \mathbf{x}, w]$ over w to obtain the corresponding median surface. To that end, once we generate a realization of

the \tilde{w} for a particular \mathbf{x}_j (as above), we plug that into the expression for $\mu^{(y)}$ given below (2), along with posterior realizations of $\boldsymbol{\theta}$. Then, with a draw of *b*, using the gamma distribution, we obtain a predictive realization of λ . Doing this across the \mathbf{x}_j , we obtain a posterior λ surface. Then, with *B* posterior draws we obtain *B* such surfaces. Taking the median at each \mathbf{x}_j , we obtain the *median number of seedlings per hectare* response surface.

4. ANALYSIS OF FIA DATA

For a collection of 25 species, the FIA dataset was randomly partitioned into a training set, containing 382 observations with the remaining 45 observations included in a test dataset to cross-validate the predictive ability of the posited model. We use posterior predictive medians, \tilde{Y}_i and \tilde{Z}_i , as point estimates of the predicted seedling and basal area abundance, respectively, at the areal level. To further justify the joint modeling through the inclusion of basal area in the seedling model, for each species we report the associated root mean square predictive error associated seedling abundance for two models, one with basal area as a covariate (the joint model) and the other without basal area as a covariate (the independence model). The RMSPEs are defined as follows:

$$RMSPE_{joint\ model} = \left(\frac{1}{|T|} \sum_{j \in T} (Y_{j,obs} - \tilde{Y}_{j,joint})^2\right)^{1/2}$$
$$RMSPE_{independence\ model} = \left(\frac{1}{|T|} \sum_{j \in T} (Y_{j,obs} - \tilde{Y}_{j,independence})^2\right)^{1/2},$$

where *T* is the set of data points belonging to the test dataset, |T| is the cardinality of the test dataset, $Y_{.,obs}$ is the observed seedling abundance, $\tilde{Y}_{.,joint}$ and $\tilde{Y}_{.,independence}$ are the posterior predictive medians of seedling abundance obtained from the joint model and independence model, respectively. The results, shown in Table 1, suggest that inclusion of basal area in the seedling model significantly improves predictive performance for seedling abundance for the illustrative two species. Table A1, in the appendix, further suggests that the joint model provides substantially improved predictive performance for almost all species, reaching as much as 55 % for *Pinus strobus*.

LITU is considered to be relatively widespread; however, its adults do not perform well under suboptimal moisture conditions. They respond better to moderately moist, well

Table 1. Root mean square predictive error associated with predicting seedling abundance for the joint model and the independence model.

Species name	RMSPE for seedling model including basal area	RMSPE for seedling model without basal area
Liriodendron tulipifera	56.46	89.02
Quercus alba	106.09	193.78

drained, and loose textured soil. LITU rarely does well in very wet or very dry situations (McCarthy 1933; Della-Bianca and Olson 1961). The juveniles need adequate soil moisture to survive and become established. Seedling development is better in well-drained mineral soil with sufficient availability of soil moisture. Extreme moisture conditions (too wet or too dry) are detrimental to seedling development (McAlpine 1961).

QUAL is an important lumber tree and is widespread across eastern North America. It is found from southwestern Maine to southeastern Minnesota all the way south to northern Florida and eastern Texas. The optimum range for QUAL is in the Ohio Valley and the central part of the Mississippi Valley (Minckler 1965). QUAL adults grow best on moderately dry slopes with shallow soils (Della-Bianca and Olson 1961). Preferred temperature for germination is between 10 to 16°C (Bell 1975). However, soil moisture is not a critical determinant of seedling survival and seedlings persist equally well in dry and moist sites provided they have access to adequate sunlight (Minckler 1965).

As noted in Sect. 1, at ecological subsection level, the LITU basal area and seedling count data includes 55 and 60 % zeroes, respectively. For QUAL, the percentages of zeros for basal area and seedling counts are about 22 and 31 %, respectively.

In Fig. 6, we present the contour plots of the posterior predictive median abundance surfaces for the two life stages and for the two species, restricted to the convex hull of the observed locations in climate space. Figure 6a shows the posterior predictive median surface of the basal area per hectare of LITU adults. The circles indicate the locations (in the climate space) where LITU adults were observed. Figure 6b is the posterior predictive median seedling count per hectare for LITU juveniles, again with the circles indicating the climate coordinates of the occurrence of LITU juveniles. Figure 6c, d mimics Fig. 6a, b), but now for QUAL adults and juveniles, respectively.

For the LITU adult abundance response surface (Fig. 6a), wetter and moderate temperatures are preferred. Elliptical contours are suggested, i.e., constancy of gradients on ellipses within the convex hull. The magnitudes of the contours suggest diminished performance of LITU adults under too moist or too dry moisture conditions, in agreement with the foregoing findings of McCarthy 1933 and Della-Bianca and Olson (1961). The contours associated with the abundance surface for LITU juveniles (Fig. 6b) suggest their preference for moderate temperature and more average precipitation, a temperate climate. The completed elliptical contours suggest that the abundance surface drops off in all directions from temperate climate within the observed set of locations. This is in accord with the above-mentioned stricter moisture requirements for LITU juveniles to develop.

Turning to the ratio plot (Fig. 7), the intent is to provide a visual comparison between the previous two plots. Again the more variability we see in the ratio surface, the more difference there is between the abundance surfaces for the two life stages, the more evidence of ontogenetic shift in climate requirements. Figure 7a shows the contour plot of the logarithm of the ratio of posterior predictive median of seedling counts per hectare to that of the basal area per hectare for LITU. We see that the most favorable ratio for juveniles is associated with lower to average precipitation regions in climate space, while for adults the ratio is most favorable for wetter conditions.

The highest intensity for the responses of QUAL adults occurs in the north-east corner of the convex hull (Fig. 6c) indicating a preference for warm and wet climate conditions, in



Figure 6. Contour plots of the posterior predictive medians of \mathbf{a} basal area per hectare for LITU adults, \mathbf{b} log seedling counts per hectare for LITU juveniles, \mathbf{c} basal area per hectare for QUAL adults, \mathbf{d} log seedling counts per hectare for QUAL juveniles. The *circles* indicate the occurrences of adult and juvenile responses in the convex hull of the observed climate space.



Figure 7. The contour plot of the logarithm of posterior predictive median ratio of the juvenile abundance to that of the adult abundance for **a** LITU and **b** QUAL.

agreement with the foregoing ecological habitat discussion. Rough constancy of gradients on ellipses within the climate convex hull is suggested by the contours. The contours associated with QUAL juveniles (Fig. 6d) imply a saddle surface. It seems that juveniles do well in



Figure 8. Plot of logarithm of median predicted responses and logarithm observed responses for **a** LITU adults **b** LITU juveniles **c** QUAL adults and **d** QUAL juveniles for the test dataset. The solid line is the 45° line.

both dry and moist sites provided the temperature ranges between 7 to 12°C. A slight preference for moist sites is also indicated. This finding concurs with Minckler (1961) who documented 98 % seedling survival when available soil moisture was 19 % of oven dry soil weight as against 87 % survival at 3 % available soil moisture. While the surfaces appear quite different, overall, they reveal that both QUAL adults and juveniles are more abundant in the warm and relatively moist climate.

As for the ratio plot for QUAL (Fig. 7b), we see a considerable difference compared with Fig. 7a for LITU. In Fig. 7b, again we see a relatively strong preference of adults for temperate climate. However, the climate requirement for both stages does not change widely. There is much more difference in the life stage abundance surfaces for LITU. We would assert that there is much stronger evidence for an ontogenetic climate shift for LITU.

Plots of the logarithm posterior predictive medians of abundances vs. logarithm of observed non-zero abundances for both life stage for both species are provided in Fig. 8.

Parameters	Posterior summary for LITU	Posterior summary for QUAL
β_0	1.08 (0.92, 1.25)	1.65 (1.47, 1.82)
β_1	-0.04 (-0.23, 0.14)	0.28 (0.05, 0.53)
β_2	0.39 (0.24, 0.56)	0.23 (0.01, 0.46)
β_3	-0.48(-0.60, -0.36)	-1.59(-1.77, -1.42)
β_4	-0.34(-0.51, -0.16)	-0.09(-0.39, 1.93)
β5	0.44 (0.21, 0.66)	0.39 (-0.01, 0.78)
σ_w	0.62 (0.05, 1.92)	0.73 (0.06, 1.88)
p_z	0.03(0.002, 0.05)	0.0001 (0.00002, 0.0003)
θ_0	4.68(4.65, 4.73)	4.79 (4.74 4.83)
θ_1	1.09 (1.03, 1.16)	0.39 (0.31 0.49)
θ_2	-0.48(-0.53, -0.39)	-0.38(-0.420.37)
θ_3	-1.23(-1.31, -1.16)	-0.73(-0.79, -0.65)
θ_4	-0.19(-0.25, -0.14)	0.37 (0.33 0.47)
θ_5	0.31 (0.20, 0.42)	$-0.008(-0.07\ 0.04)$
η	0.31 (0.29, 0.35)	0.30 (0.27 0.32)
α_0	3.08 (1.98, 4.25)	2.69 (1.28 4.09)
α1	-4.97 (-6.26, -3.68)	-4.62 (-6.05 -3.17)

Table 2. Posterior mean and 95 % credible interval (in parenthesis) for the model parameters for LITU and QUAL.

These plots are over the 45 ecological subsections that constituted the test dataset. They reveal a noisy fit for basal area with a somewhat better fit for seedling counts.

We present the post-convergence posterior summaries for the model parameters for LITU and QUAL in Table 2. Although direct interpretation of the model parameters is difficult in the presence of the interaction term, the significant negativity of the quadratic terms provide further justification for the specification of quadratic mean surface model for both the adult and juveniles responses. Perhaps more importantly, the strong significance of η for LITU and for QUAL suggests the importance of using basal area to explain seedling counts. Moreover, the significant large negative values of α_1 for the two species have an expected interpretation; more basal area implies less chance of seedling absence. These α 's further reveal the importance of specifying a joint model for adult and juvenile presences.

Finally, Table 2 shows that p_z is negligible for QUAL while explaining only 3 % of zeros for LITU. It seems that, in accordance with the findings of Canham and Thomas (2010), at subsection scale, the climate covariates are adequate predictors of species occurrence. So, perhaps for these species, zero inflation was not needed but we would not have learned this without fitting our models and it might be more important for other species.

5. SUMMARY

We have developed a joint model for abundance at two life stages for trees, basal area for adult trees and counts for seedlings, in response to climate, characterized by average precipitation and mean winter temperature. We have argued for the need and demonstrated the benefit of formulating a joint model. We have shown how these abundance response surfaces can be employed to investigate change in distribution between the two life stages. We have illustrated this for two species, revealing different climatic requirements of adult specimens as compared to their juvenile counterparts.

Future work will plan to provide a user friendly R-package to make this model fitting more accessible to ecologists. In this context, ecologists will be able to extract readily interpreted niches from the posterior predictive median surfaces (as in Fig. 6) by suitable thresholding of temperature and precipitation. A further future objective will be to investigate alternative climate predictors as well as the possible extension to include a third predictor in specifying adult and juvenile response surfaces. We also can look at the effect of aggregation, starting at plot level and building larger areal units, in terms of strength of climate signals.

More generally, we have proposed a framework that can jointly model zero-inflated continuous and count data. Other applications of such modeling are possible. For instance, over multiple geographic regions and over time, we can jointly model the number of precipitation events (in a year) exceeding a certain threshold and average annual precipitation. Such joint model can inform us not only about the increase in the frequency of extreme events over time but also about the magnitude of these extreme events.

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APPENDIX: RSMPES FOR 25 SPECIES

See Table 3.

RMSPE for seedling RMSPE for seedling Species name model without basal model including basal area area Liriodendron tulipifera 56.46 89.02 106.09 193.78 **Ouercus** alba Pinus taeda 106.10 110.18 Fraxinus americana 119.57 129.79 Fraxinus nigra 197.24 260.73 Liquidambar styraciflua 94.46 137.81 Larix laricina 31.2 43.86 Amelanchier medik 42.59 52.34 Nyssa sylvatica 55.91 66.10 Pinus strobus 39.19 89.62 47.46 Quercus velutina 34.6 Sassafras albidum 75.02 82.3 Ulmus alata 47.8 48.81 Ulmus americana 58.39 63.84 Ulmus rubra 23.68 35.05 Ostrya virginiana 79.05 105.93 Carya glabra 29.85 40.20 144.48 231.34 Populus tremuloides

Table 3. Root mean square predictive error associated with predicting seedling abundance for the joint model and the independence model.

Species name	RMSPE for seedling model including	RMSPE for seedling model without basal
	basal area	area
Prunus serotina	61.59	74.19
Carpinus caroliniana	71.06	87.62
Crataegus L.	19.14	22.03
Carya alba	43.58	62.88
Carya ovata	11.99	17.04
Acer negundo	16.97	23.93
Cercis canadensis	20.85	22.47

Table 3. (Continued)

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