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Modelling tree recruitment in relation to climate and competition in semi-natural *Larix-Picea-Abies* forests in northeast China

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ABSTRACT

Tree recruitment models are important tools for predicting forest dynamics, especially for long-term projections of future forest composition. However, as a highly variable, complicated, and largely stochastic process, tree recruitment remains difficult to accurately model. Traditional models neglect climatic variables and are not applicable to forest growth and yield projections under climatic change. In this study, we developed tree recruitment models including site condition, competition, and climate for semi-natural larch-spruce-fir forests under thinning treatments in northeast China. Negative binomial mixture models (zero-inflated and Hurdle models) and Poisson mixture models were compared, with the zero-inflated negative binomial model found to be the best model. Stand density variables (stem density or basal area) were found to be significant for all species categories (larch, conifers, and hardwoods). Additionally, site condition was found to be an important factor affecting recruitment. Four climatic variables, mean annual temperature, annual minimum temperature, growing season minimum temperature, and mean annual temperature divided by mean annual precipitation were found to be directly related to recruitment count. Variance analysis showed significant species-specific thinning effects on tree recruitment. Disentangling different sources of variation in tree recruitment will help further our understanding of the factors driving tree recruitment during climatic change.

1. Introduction

Tree recruitment and mortality are highly variable, complicated, and largely stochastic binary events, significantly affecting future forest stand dynamics (Vanclay, 1992; Li et al., 2011). In recent years, remarkable progress has been made in tree-mortality (or survival) modelling (Monserud, 1976; Vanclay, 1991; Monserud and Sterba, 1999; Bravo et al., 2001; Bravo-Oviedo et al., 2006). Despite these advances, tree recruitment remains neglected in growth and yield models as an explicit submodel mainly because of its poor performance (e.g., Cao, 2006; Bravo et al., 2008; Subedi and Sharma, 2011). However, standard forest growth and yield predictions will be biased without recruitment models, possibly weakening whole forest simulations, especially in multi-layered forests and over longer time scales (Andreassen, 1994; Weiskittel et al., 2011).

There are several approaches to modelling tree recruitment: Linear or nonlinear recruitment models, based on the least squares method, were initially developed (Shifley et al., 1993; Liang et al., 2005) and incorporated into standard forest models (Ferguson and Crookston, 1991; Monserud et al., 2004). It is challenging to accurately model recruitment through ordinary least squares methods as the estimated results will be biased since recruitment data inevitably includes a large proportion of zero counts and, as a result, are not Gaussian distributed. A two-stage conditional logistic model had been used by previous studies to overcome this problem, where logistic regression was used to model whether recruitment has occurred while observed recruitment counts could be fitted by least squares (Lexerød, 2005; Fortin and DeBlois, 2007; Bravo et al., 2008; Yang and Huang, 2015). However, inaccurate parameter estimations, caused by poorly defined stochastic structure, remained a major impediment for predicting recruitment (Affleck, 2006). Recently, these issues have been addressed through extensive modelling attempts such as negative binomial (NB) models, which were found to be flexible in fitting over-dispersed data while allowing for high variance and heterogeneity in the model (Yaacob et al., 2010). However, the NB model was unable to

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characterize data with a large number of zero counts, typical of tree regeneration inventory (Zhang et al., 2012). Therefore, more flexible count-data models should be considered, such as zero-inflated models (Lambert, 1992). Normally, binary logistic function was used for predicting whether a count occurs and Poisson or NB models used for describing positive counts (Karazsia and van Dulmen, 2008). For example, the Zero-inflated Poisson model (ZIP) and zero-inflated discrete Weibull (ZIW) have been applied in hardwood stands (Fortin and DeBlois, 2007). ZIP requires that the variance of positive counts be equal to the expectation, while in the ZIW model it is difficult to introduce additional parameters. The zero-inflated negative binomial model (ZINB) has been found to give more satisfactory results than ZIP (Zhang et al., 2012). Additionally, hurdle models have been found to be capable of dealing with over-dispersion by combining a left-truncated count component with a right-censored hurdle component (Mullahy, 1986). Similarly, the hurdle component of zero or nonzero was often fitted by logistic function while the truncated count component was employed using the Poisson model or negative binomial models (Zeileis et al., 2008). However, further validation of these models is necessary; using data from a wider range of sites, species, and growing conditions. In this context, negative binomial, Zero-inflated Poisson, Zero-inflated negative binomial, Hurdle-Poisson (HP), and Hurdle-negative binomial models (HNB) could all be considered candidates for modelling strategies to aid our understanding of such complex types of data.

Within-stand competition, species composition, and site quality have been quantified to explain recruitment in previous studies (Hann, 1980; Li et al., 2011; Yang and Huang, 2015). Within-stand competition determines establishment, growth, and survival of seedlings and, as a result, is often considered the most important factor affecting recruitment (Shifley et al., 1993; Lexerød, 2005; Bravo et al., 2008; Yang and Huang, 2015). As the most significant competition indicator, stand density is frequently used in recruitment studies and is typically expressed as stand basal area (Trasobares et al., 2004), stems per hectare (Lexerød, 2005; Lexerod and Eid, 2005), species basal area (Yang and Huang, 2015), or the stand quadratic mean diameter (Bravo et al., 2008; Zhang et al., 2012).

Significant climatic effects on tree recruitment have also been detected (Gehrig-Fasel et al., 2007; Batllori et al., 2009). Recruitment studies have typically been established at latitudinal or altitudinal extremes (arctic or alpine tree line) where temperature is often a limiting factor. Although the relationship between climate and recruitment derived from narrow geographic gradients of tree line forests is not necessarily reflective of boreal or temperate forests, temperature conditions associated with water availability were found to be an important determining factor affecting tree recruitment in these areas (Stephenson, 1990; Ibáñez et al., 2007; Lenoir et al., 2009; Vitasse et al., 2012). Furthermore, different recruitment responses to climate suggests tree recruitment also depends on species-specific traits and environmental constraints (Batllori et al., 2009; Hofgaard et al., 2009); possibly increasing tree recruitment variability and uncertainty under recent climatic change (Walther, 2003; Bravo et al., 2008; Lenoir et al., 2009).

By manipulating stand basal area and stem density, thinning has a significant effect on inter-tree competition, affecting tree recruitment (Albrecht and McCarthy, 2006; Kuehne et al., 2015). However, the stochasticity of recruitment response to thinning treatments has also increased significantly as a result of climatic change (Bravo et al., 2008). Additionally, elevation, aspect, and slope (as site specific surrogates of air temperature, solar radiation, soil moisture and temperature, and nutrients) are important factors describing the influence of site condition on tree recruitment (Körner, 2007; Stage and Salas, 2007; Alves et al., 2010). As a result, understanding the confounding effects of climate and thinning-induced stand density on recruitment under different site conditions is increasing important given increased climatic uncertainty over the coming decades. Nevertheless, disentangling all possible drivers of recruitment is difficult given the nature of recruitment data and potential for confounding explanatory variables of local scale environmental conditions, thinning treatments, and large scale climatic variables.

In this study, semi-natural larch-spruce-fir forests in northeast China were investigated from 1987 to 2012 in order to (1) develop and compare the NB, ZIP, ZINB, HP, and HNB models for predicting tree recruitment; and (2) examine the effects of climate, competition, and site condition on tree recruitment.

2. Materials and methods

2.1. Sample plots and measurements

Recruitment data were collected from the Jingouling Experimental Forest Farm run by the Wangqing Forestry Bureau, in Jilin Province, located in the middle lower hill region of the Changbai Mountains in northeast China (130°5′-130°20′E, 43°17′-43°25′N). Within the study area, elevation ranges from 550 m to 1100 m asl, with annual rainfall from 600 to 700 mm, and a mean annual temperature of 3.9 °C. Mean monthly maximum and minimum temperatures are 22 °C and −32 °C, respectively, with a 120 day growing season. Dark brown soils are the dominant soil type throughout the study area.

Stands in the study area were originally Changbai larch (*Larix olgensis* A. Henry) forests planted in clear-cut areas between 1962 and 1964 with some fir (*Abies*), spruce (*Picea*) and broad-leaved trees remaining, with most stands developing into mixed forests (semi-natural larch-spruce-fir forest) when thinning experiments were initiated in 1987 (Lei et al., 2007). Tree species in the study area consisted of Changbai larch, Jezo spruce (*Picea jezoensis* var. *microsperma* (Lindl.) Cheng et L. K. Fu), Manchurian fir (*Abies nephrolepis* (Trautv. ex Maxim.) Maxim.), Korean pine (*Pinus koraiensis Siebold & Zucc*), Asian white birch (*Betula platyphylla* Sukaczev), Ussuri poplar (*Populus ussuriensis* Kom.), ribbed birch (*Betula costata* Trautv.), amur linden (*Tilia amurensis* Rupr.), elm (*Ulmus propinqua* Koidz.), maple (*Acer mono* Maxim.), manchurian ash (*Fraxinus mandshurica* Rupr.), and amur cork (*Phellodendron amurense* Rupr.).

Twenty rectangular permanent plots were established, ranging in area from 0.0775 to 0.25 ha. Treatments were arranged in five blocks in a randomized block design for three thinning intensities ranked according to the percentage of basal area removed: Light (LT, 20%), moderate (MT, 30%), heavy (HT, 40%) and a control (CT, 0%). Thinning from below was adopted (Lei et al., 2007).

Tree species and diameter at breast height (DBH) for stems with DBH $\geqslant$ 5 cm were investigated every two to three years from 1987 to 2012. Owing to the small sample size, some species were grouped into three categories: two softwoods, (1) shade-intolerant larch (Changbai larch) and (2) shade-tolerant conifers (spruce, fir, and Korean pine); and (3) all hardwood species, according to their growth traits. Detailed information on larch-spruce-fir stands during establishment is shown in Table 1. In this study, only data with 5-year intervals was used, which consisted of 319 measurements.

2.2. Model development

2.2.1. Candidate variables selection

Tree recruitment, the number of saplings with DBH $\geqslant$ 5 cm may be related to stand characteristics, site conditions, and