博士論文（要約）

論文題目　Individual-based forest dynamics modeling of mixed conifer–broadleaf stands under selection system
（択伐施業下における針広混交林の個体ベース森林動態モデリング）

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Individual-based forest dynamics modeling of mixed conifer–broadleaf stands under selection system

択伐施業下における針広混交林の個体ベース森林動態モデリング

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Chapter 1

Introduction

1. Background

Prediction of forest dynamics has been one of the primary focuses of forest science since the inception of the discipline (Messier et al. 2003). Numerous models for predicting forest dynamics have been developed in the manner that meets social needs. Yield table, which has been developed from the 1700s, is likely the most traditional type of models that have been used to make growth and yield predictions of plantations (Weiskittel et al. 2011). Yield table has been widely applied to homogeneous areas, such as monospecific, even-aged, and reasonably young (<150 years) stands; however, it is unable to produce accurate predictions of the dynamics of structurally heterogeneous stands (Groot et al. 2004). In parallel with the recent increase in the public concern over uneven-aged forestry, spatially explicit, individual based models have received growing attention. This type of models allow for a wide range of conditions within single stands and thus offer the most viable approach for modelling uneven-aged stands (Coates et al. 2003, Groot et al. 2004, Weiskittel et al. 2011).

Many spatially explicit, individual-based models have been developed to investigate the effects of uneven-aged forestry on stand structures and yields (e.g. Rüger et al. 2007; Valle et al. 2007; Thorpe et al. 2010; Yasuda et al. 2013), but some common challenges remain to be solved. For example, Royo and Carson (2006) pointed out that the models typically lack to take into account the presence of understory vegetation, an important factor that affects tree recruitment. Also, despite many researches have documented interspecific difference in trees' competitive ability (Uriarte et al. 2010; Kunstler et al. 2012), individual-based models have almost invariably combined multiple species into groups in their parameter estimation process. Moreover, the models that explicitly incorporate tree mortality caused by logging practices are still scarce (Thorpe et al. 2010). Incorporating these factors into individual-based models will likely improve their prediction accuracy and range of application.

In this study, I overcome the above challenges by using neighborhood analyses based on hierarchical Bayesian modeling. Neighborhood analysis enables us to estimate the degree of interactions among plants (e.g. competition among trees, competition between trees and understory vegetation, and understory vegetation-mediated facilitation of tree recruitment by adult trees) by expressing them as functions of plant biomass (e.g. stem size, vegetation density), species identities, and the spatial configuration of individuals (Canham et al. 2004; Uriarte et al. 2004). As for Bayesian modeling, there is a growing body of evidence showing that this statistical approach could be a powerful means for quantifying fine-scale interactions among plant species in forests (Condit et al. 2006; Comita et al. 2010; Kunstler et al. 2012). Also, Bayesian approach provides a flexible modeling framework in which individual-based factors (e.g. effects of local logging intensity and species identity on tree demography) can be efficiently analyzed. By integrating the estimated Bayesian models and associate parameters, I developed a spatially explicit, individual-based model.

2. Study objectives

The objective of this study was to develop a spatially explicit, individual-based model and to explore forest dynamics under a variety of uneven-aged harvesting scenarios. Through its development, I conducted Bayesian modeling of trees' recruitment, growth, and mortality. In modeling tree recruitment, I explicitly analyzed the effects of understory vegetation on recruitment. As for tree growth, interspecific difference in competitive ability was quantified without combining multiple species. In modeling tree mortality, I investigated the influence of logging on residual tree's mortality in a spatially explicit manner.

My study was conducted in a mixed conifer–broadleaf forest in Hokkaido, northern Japan. The forest consists of multiple tree species with a range of sizes and has a heterogeneous configuration of individual trees. Forest floors are often covered by dwarf bamboos, which are perennial semi-woody plants that strongly inhibit tree regeneration (Abe et al. 2002; Noguchi and Yoshida 2004). As for silvicultural practices, single-tree selection has been widely conducted throughout Hokkaido for more than a century (Yoshida et al. 2006). Thus, forest in Hokkaido represents a good model system of which the basic and applied ecological background corresponds to my study objective. Several models have been previously developed for predicting the dynamics of mixed conifer–broadleaf mixed forests in Hokkaido (e.g. Ishibashi 1989a, 1989b; Yamamoto 1991; Yasuda et al. 2013). These studies have provided many pioneering outcomes; however, there is clearly a room left for further development, including the challenges stated above. My results offer novel methodologies for modeling forest dynamics using individual-based approach and provide new insights into single-tree selection management in Hokkaido.

3. Structure of dissertation

This thesis consists of 7 chapters. The first chapter is this *Introduction*. In chapters 2 to 5, by using Bayesina modeling approach, I estimated the forest's demographic parameters; that is, (chapters 2 and 3) recruitment rate, (4) growth rate, and (5) mortality. The titles of these chapters are as follows:

- Chapter 2 (Understory vegetation submodel): Modeling the effects of individual-tree size, distance, and species on understory vegetation based on neighborhood analysis
- Chapter 3 (Recruitment submodel): Mid-sized conifers indirectly facilitate tree recruitment via the suppression of understory vegetation in a mixed conifer–broadleaf forest
- Chapter 4 (Growth submodel): Bayesian modeling of neighborhood competition in uneven-aged mixed-species stands
- Chapter 5 (Mortality submodel): Individual-level analysis of damage to residual trees after single-tree selection harvesting in northern Japanese mixedwood stands

In chapter 6, we developed a spatially explicit, individual-based model by integrating these statistical models and explored forest dynamics under a variety of single-tree selection harvesting scenarios. The title of chapter 6 is as follows:

- Chapter 6 (Forest dynamics modeling): Irreversible transition of stand structures: anticipating harvesting-induced shifts by means of an empirically based forest dynamics model

Each chapter from 2 to 6 is written in a self-contained manner (i.e. each of them has its own *Introduction*, *Materials and methods*, *Results*, *Discussion*, and *Conclusions*) and thus is independently understandable. For the description for study site, however, I only stated at the *Materials and methods* section of chapter 2, because chapters 2 to 6 were conducted in the same study site. In chapter 7, I discussed the major findings and limitations of this dissertation as a whole.

Chapter 2 was published in Canadian Journal of Forest Research (S. Tatsumi and T. Owari, “Modeling the effects of individual-tree size, distance, and species on understory vegetation based on neighborhood analysis,” volume 43(11), pages 1006–1014, 2013), chapter 4 was published in Formath (S. Tatsumi, T. Owari, A. Ohkawa, Y. Nakagawa, “Bayesian modeling of neighborhood competition in uneven-aged mixed-species stands,” volume 12, pages 191–209, 2013), and chapter 5 is in press at Journal of Forest Research (S. Tatsumi, T. Owari, H. Kasahara, Y. Nakagawa, “Individual-level analysis of damage to residual trees after single-tree selection harvesting in northern Japanese mixedwood stands”).

第二章（chapter 2, pp. 5–21）の内容は、学術誌 Canadian Journal of Forest Research (S. Tatsumi and T. Owari, “Modeling the effects of individual-tree size, distance, and species on understory vegetation based on neighborhood analysis,” volume 43(11), pages 1006–1014, 2013) に掲載済みであり、インターネット公表に対する承諾が得られていない。

第三章（chapter 3, pp. 22–33）の内容は学術誌 Journal of Ecology に投稿予定のため、インターネットに公表できない。

Chapter 4. Growth submodel

Bayesian modeling of neighborhood competition in uneven-aged mixed-species stands

Keywords
Bayesian inference, distance-dependent analysis, interspecific variability, neighborhood competition index, tree growth

1. Introduction

Competitive interactions among individual trees are the primary factor that shapes stand structure (Curtis, 1970). In even-aged forestry, these interactions have been commonly described by stand-level indices such as stand density or stocking (Weiskittel et al., 2011). On another front, recent changes in management goals have led to a growing interest in uneven-aged mixed-species management. Such management encompasses a nearly infinite variation of species, sizes, and spatial configurations of residual trees (Papaik & Canham, 2006). Because of such structural heterogeneity, prediction of the competition in mixed-species forest calls for neighborhood analysis (Canham et al., 2006), in which the demography of component tree species is regulated by fine-scale spatial interactions (Canham & Uriarte, 2006).

Recent studies of neighborhood analysis have unexceptionally adopted maximum likelihood method for parameter estimation (Canham et al., 2004, 2006; Uriarte et al., 2004a, 2004b; Canham & Uriarte, 2006; Papaik & Canham, 2006; Coates et al., 2009). However, since mixed-species forest commonly consists of a few dozens to a few hundred of species (Vanclay, 1991), it is often prohibitively difficult to collect a sufficient amount of data to estimate the maximum likelihood (Coates et al., 2009). As a consequence, most previous studies have confined their target to major species that haSasample size larger than a prospectively defined threshold (Uriarte et al., 2004a, 2004b; Canham et al., 2006; Papaik & Canham, 2006). Yet, this methodological limitation hampers to reveal the competitive effects of minor species.

One approach for overcoming the problem of minor species is Bayesian inference with Markov chain Monte Carlo (MCMC) method. By using Bayesian inference, the interspecific variability can be represented as a random effect. Such representation has already been occasionally used within the framework of generalized linear mixed models (GLMM; e.g. Akasaka and Takamura, 2010; Suzuki, 2011), but not in complex models including neighborhood competition models. Bayesian inference may largely relax the limitation in sample size and avoid excluding the minor species from analysis.

In this chapter, I develop a Bayesian model for neighborhood competition in uneven-aged mixed-species stands. My specific objectives are to address the following questions: (1) When the interspecific variability is expressed as a random effect in neighborhood analysis, would the parameters be successfully estimated by Bayesian inference? (2) If so, would such approach be superior to the previous approaches in terms of statistical performance? (3) Is there a significant difference in competitive effects among species, including minor ones?

2. Materials and methods

See Materials and methods in Chapter 2 for a description on study site.

2.1. Data

I used inventory data collected from 16 permanent plots that are located across the study site. In the permanent plots, all trees ≥ 5.0 cm diameters at breast height (DBH) have been measured at 4–6 year intervals. Spatial positions (x-y coordinates) of living trees and dead trees (snags, logs, and stumps) were mapped in 2008–2011. I only used the recently measured DBH data for the analysis. To avoid edge effects, I excluded target trees (“target trees” are the trees of which their DBH growth are used as a response variable; described below in detail) that were within 10 m of the edge of the plot. In total, there were 1744 measurements for DBH of target trees (872 measurements for DBH growth) and 30987 measurements for DBH of neighboring trees (“neighboring trees” are trees that exert competitive effect on target trees; note that each neighboring tree corresponds to multiple target trees; Table 4.1). A total of 39 species and species groups were observed for neighboring trees (including other species). Only those individuals located within 10 m of a target tree were considered potential neighbors. I selected this range based on results of preliminary analyses and to ensure sufficient number of target trees in the dataset with complete mapped neighbors.

2.2. Statistical modeling

In the analysis, the DBH growth of *A. sachalinensis* (the most dominant species in the study site; $n = 872$) was used as the response variable. The DBH growth was defined as the difference in DBH between two measurements. I analyzed the DBH growth of target tree as a function of its initial DBH and competitive effect of neighboring trees, using the differential form of the Gomperz growth function:

$$[1] \quad ObsGrowth \sim Norm(TrueGrowth, {\sigma_1}^2)$$

$$\ln(TrueGrowth) \sim Norm(\ln(MeanGrowth), {\sigma_2}^2)$$

$$MeanGrowth = \exp(\alpha_1 + \alpha_2 \cdot TrgDBH + \ln(TrgDBH) + NCI + \ln(Yrs) + R_{plot})$$

where $ObsGrowth$ is the observed DBH growth of a target tree (cm), $TrueGrowth$ is the DBH growth of a target tree without measurement error, $MeanGrowth$ is the expected DBH growth of a target tree without process error, $TrgDBH$ is the initial DBH of a target tree (cm), NCI is Neighborhood Competition Index (Eq. 2), Yrs is the number of years between two measurements, R_{plot} is a random effect for permanent plots, and α_1 and α_2 are parameters. I assumed that $ObsGrowth$ is distributed normally with mean $TrueGrowth$ and variance ${\sigma_1}^2$

because there were some negative DBH growths in the dataset, indicating that there was certain amount of measurement error. I have set $TrueGrowth$ to be distributed log-normally with mean $MeanGrowth$ and variance ${\sigma_2}^2$ to represent process error. $\ln(Yrs)$ is an offset variable.

To analyze the competitive effect of neighboring trees, I used NCI, an index in which the competitive effect of neighboring trees is predicted as a function of its DBH, distance from the target tree, and its species (Canham *et al.*, 2004). The total competitive effect of neighbors is the sum of individual neighbors ($i = 1, 2, \ldots, n$) found within 10 m of a target tree (Canham *et al.*, 2004):

$$NCI = \sum_{i=1}^{n} \beta_{si} \cdot \exp(\gamma_1 \cdot \ln(ngbDBH_i) + \gamma_2 \cdot Dist_i) \tag{2}$$

where $ngbDBH$ is the DBH of a neighboring tree (cm), $Dist$ is the distance from the target tree to a neighboring tree (m), and β_s, γ_1, and γ_2 are parameters.

Table 4.1. Species and sample size of neighboring trees.

Species	n	Species	n
Abies sachalinensis	13933	*Fraxinus lanuginosa*	298
Taxus cuspidata	2007	*Picea glehnii*	295
Tilia japonica	1448	*Acer japonicum*	281
Sorbus commixta var. *rufoferruginea*	1393	*Betula maximowicziana*	243
Acer mono var. *mayrii Koidz*	1111	*Styrax obassia*	226
Ostrya japonica	940	*Acer ukurunduense*	121
Eleutherococcus sciadophylloides	859	*Phellodendron amurense*	84
Picea jezoensis	774	*Cercidiphyllum japonicum*	60
Prunus ssiori	745	*Hydrangea paniculata*	60
Magnolia obovata	741	*Fraxinus mandshurica* var. *japonica*	27
Aria alnifolia	731	*Morus australis*	25
Tilia maximowicziana	730	*Juglans mandshurica* var. *sachalinensis*	12
Acer palmatum var. *amoenum*	654	*Euonymus oxyphyllus*	10
Kalopanax pictus	628	*Syringa reticulata*	9
Acer mono Maxim	482	*Salix bakko*	8
Prunus spp.*	474	*Maackia amurensis*	6
Swida controversa	441	*Carpinus cordata*	5
Ulmus spp.**	379	*Picrasma quassioides*	5
Quercus crispula	366	Other species (Unidentified	21
Magnolia kobus var. *borealis*	355	Total	30987

* *P. sargentii* and *P. maximowiczii.* ** *U. laciniata* and *U. davidiana*

Here, the net competitive effect of an individual neighbor is multiplied by the species-specific parameter β_s, which is estimated for each species s. Previous studies assumed that there is no interspecific similarity in competitive effect, and thus estimated β_s independently from one species to another (i.e. β_s was expressed as a fixed effect; Canham *et al.*; 2004, Canham & Uriarte, 2006; Papaik & Canham, 2006; Coates *et al.*, 2009; Uriarte *et al.*, 2009). I define a model based on this assumption 'model 1'. A new approach based on using random effect, on the other hand, assumes that all species exert basically similar competitive effect with only slight differences. I define a model based on this assumption 'model 2'. Finally, as a control test, 'model 3' assumes that there is no interspecific difference in competitive effect.

Based on the above assumptions, the prior distributions for β_s were as follows:

Model 1

[3a] $$\beta_s \sim Norm(0, 10^2), \forall_s$$

Model 2

[3b] $$\beta_s \sim Norm(\mu, {\sigma_3}^2), \forall_s$$

$$\mu \sim Norm(0, 10^2)$$

$$\sigma_3 \sim Unif(0, 10^4)$$

Model 3

[3c] $$\beta_s = 1, \forall_s$$

Priors for β_s in model 1 and μ in model 2 were noninformative normal distributions, while those of β_s in model 2 were normal distributions with mean μ and variance ${\sigma_3}^2$. β_s in model 3 were 1. The variance parameter σ_3 is referred to as a hyperparameter of which prior distributions (i.e. hyperprior distributions) were noninformative uniform distributions.

The priors for fixed-effect parameters α_1, α_2, γ_1, and γ_2 were noninformative normal distributions [$Norm(0, 10^2)$]; those for random-effect parameter R_{plot} were normal distributions with variance ${\sigma_4}^2$ [$Norm(0, {\sigma_4}^2)$]; those for variance parameters $1/{\sigma_1}^2$ and $1/{\sigma_2}^2$ were noninformative gamma distributions [$Gamma(1, 10^{-3})$]; and those for variance parameters σ_4 were noninformative uniform distributions [$Unif(0, 10^4)$].

2.3. Parameter estimation and model selection

I conducted sampling from the marginal posterior distributions by the MCMC method by means of WinBUGS 1.4.3 (Lunn *et al.*, 2000) via the R2WinBUGS package (Sturtz *et al.*, 2005) in R 2.15.0 (R Development Core Team, 2012). For each model (model 1–3), I obtained the posterior samples by three independent MCMC samplings, in each of which 4000 values were sampled with a five-step interval after 1000 burn-in MCMC steps. The convergence of

MCMC calculations was confirmed by evaluating Gelman and Rubin's $\hat{R}$ (Gelman *et al.*, 2004) for all parameters. For model selection, I used the Deviance Information Criterion (DIC; Spiegelhalter *et al.*, 2002), a generalization of the Beyesian Information Criterion (BIC).

Since β_s in model 1 did not converge in our preliminary analysis ($\hat{R} > 1.1$), I combined the species with small sample sizes into o*ther species* only when analyzing model 1. I gradually increased the threshold of the sample size from 100 at intervals of 100 (i.e. 100, 200, 300, …).

3. Results

3.1. Model selection and goodness of fit

All the model parameters adequately converged ($\hat{R} < 1.1$; β_s in model 1 converged when the threshold of sample size was 700; I hereinafter refer to the species that has a sample size smaller than 700 as minor species). Model 2, the model in which interspecific variability was represented as a random effect, was selected as the best model (Table 4.2). Neither model 1 nor model 3 was assessed to have substantial support ($\Delta\mathrm{DIC} > 10.0$; Spiegelhalter *et al.*, 2002; McCarthy, 2007). The best model (model 2) and its associated parameter estimates (Table 4.3) provided an acceptable fit to the data ($R^2 = 0.48$; Fig. 4.1).

3.2. Effects of neighboring tree characteristics on NCI

NCI in the best model increased with increasing DBH of neighbors and with decreasing distance between target tree and neighbors (Fig. 4.2). For instance, a neighbor with 40 cm DBH and 80 cm DBH had 14.5 times and 35.3 times a larger competitive effect than a neighbor with 5 cm DBH, respectively. Likewise, a neighbor located 5 m and 10 m away from a target tree had 0.16 times and 0.02 times a larger competitive effect than a neighbor 0.1 m away, respectively. As for interspecific variability (β_s), if the 95% credible interval of β_s of a focal species did not overlap the mean value of μ, that specie was considered to have significant difference with other species. A smaller β_s value represents a larger competitive effect the focal species exerts. There was a distinct evidence for interspecific variability, although the number of species that showed significant differences was small; only *A. sachalinensis, Ostrya japonica*, and *Magnolia obovata* (Table 4.3, Fig. 4.3). *A. sachalinensis* exerted the largest competitive effect (mean $\beta_s = -0.0066$); whereas *Ostrya japonica* exerted the smallest (mean $\beta_s = -0.0010$). None of the minor species showed significant difference.

4. Discussion

4.1. Parameter estimation by Bayesian inference and goodness of fit

My results showed that parameters within complex neighborhood models with random effects can be successfully estimated by Bayesian inference. Besides, predictive accuracy of the fitted model ($R^2 = 0.48$) was the highest among the studies that used maximum likelihood method; the mean R^2 values in previous studies were 0.09 (Uriarte *et al.*, 2004a), 0.26 (Uriarte *et al.*, 2004b), 0.22 (Canham *et al.*, 2004), 0.33 (Papaik & Canham, 2006).

Table 4.2. DIC and ΔDIC of alternate models. ΔDIC is defined as the difference from the lowest DIC.

Model	Description	DIC	ΔDIC
1	Interspecific variability as fixed effect	4621.9	21.7
2	Interspecific variability as radom effect	4600.2	0
3	No interspecific variability	4689.0	88.8

Table 4.3. The means and quantiles (2.5% and 97.5%) of posterior distributions of fixed-effect parameters and variances.

Parameter	Mean	2.5%	97.5%
α_1	-3.94	-4.16	-3.71
α_2 ($\times 10^{-2}$)	-2.01	-2.34	-1.67
γ_1	1.29	1.04	1.49
γ_2 ($\times 10^{-1}$)	3.73	4.63	3.00
σ_1 ($\times 10^{-1}$)	2.36	2.00	2.77
σ_2 ($\times 10^{-1}$)	5.12	4.71	5.53
σ_3 ($\times 10^{-3}$)	2.93	1.01	7.36
σ_4 ($\times 10^{-1}$)	2.69	1.70	4.19

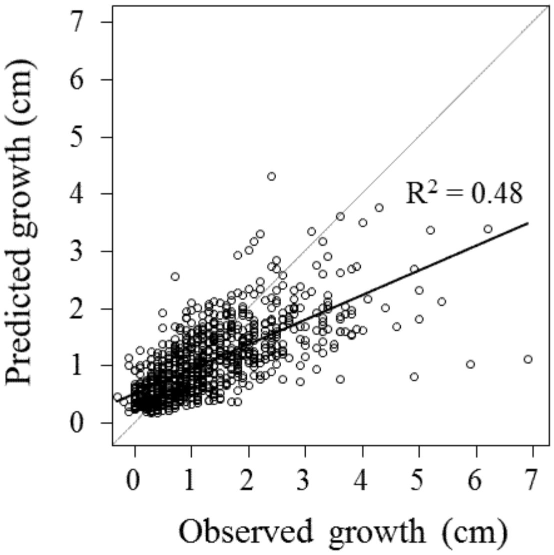

Figure 4.1. Relationship between observed growth and predicted growth (n=872). The growth is defined as the difference in DBH between two measurements with 4–6 year interval.

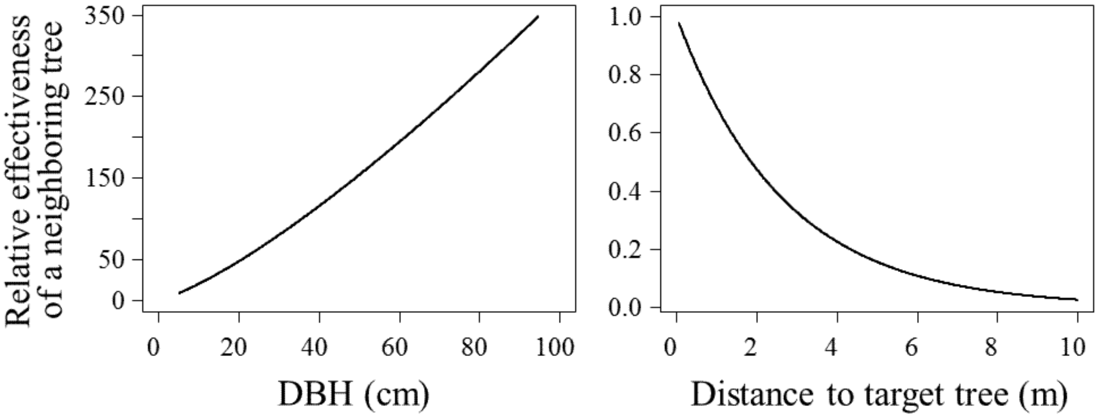

Figure 4.2. The effect of a neighboring tree DBH (left) and distance between a neighbor and a target tree (right) on the relative competitive effectiveness of that neighboring tree [expressed as exp (γ1·ln[ngbDBH*i*]) and exsp (γ2·Dist*i*), respectively; parameter estimates can be found in Table 4.4].

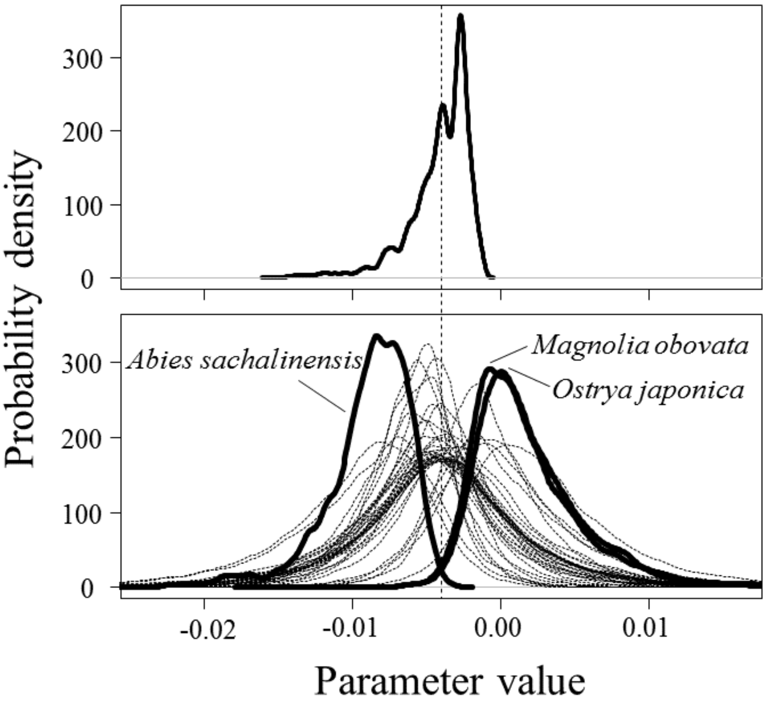

Figure 4.3. Posterior distributions of parameters μ (above) and β_s (below). The vertical dashed line represents the mean value of μ. The solid bold and dotted curves in below correspond to the posterior distributions of which 95% credible interval do and do not include the mean μ value.

4.2. Factors that contributed to the high predictive accuracy

There are three possible factors which supported the high accuracy: (1) Because we did not exclude minor species with small sample sizes in our best model (model 2); (2) because previous studies have made an erroneous assumption in which the interspecific variability of competitive effect is independent of one another; (3) because previous studies failed to allow for uncertainty such as plot effects (R_{plot}).

4.2.1. Factor 1: Efficient use of minor species data

Previous studies excluded minor species from analysis, which is inevitable in analyses based on maximum likelihood method. Also in my analysis of model 1 (the model in which each species had independent β_s), species with small sample size were to be combined necessarily in order to converge the parameters. However, such exclusion or grouping commonly reduces the information that original data hold. In the best model (model 2), on the other hand, I efficiently included the minor species' data to the analysis. I assume that such effective utilization of data information made the resultant models more accurate.

4.2.2. Factor 2: Representing interspecific variability as a random effect

The above assumption of efficient data utilization is further supported by the results of model selection (Table 4.2). In model selection, DIC were smaller in ascending order from model 2, model 1, to model 3. This result suggests that although there is a clear evidence for interspecific variability, the species-specific effects are not independent to each other, but rather have somewhat of similarity.

This evidence is also indicated from the estimated β_s value, in which its variation was smaller than previously reported. In previous studies, β_s varied among species dramatically: For example, the effect of some species had dozens of times larger the competitive effect of other species, whereas some species had completely none effect (i.e. $\beta_s = 0$; Uriarte *et al*., 2004a, Uriarte *et al*., 2004b, Canham *et al*., 2006, Papaik & Canham, 2006). In this study, on the other hand, the largest β_s was only 6.6 times larger than the smallest β_s (-0.0066 for *A. sachalinensis* and -0.0010 for *O. japonica*). Besides, only three species had statistically significant difference with other species (Fig. 4.3), and none of them were minor species. These results indicate that previous studies based on maximum likelihood method have overestimated the differences, due to the erroneous assumption that the species-specific effects are independent.

4.2.3. Factor3: Allowance of uncertainties

The problems of overestimation in previous studies may be also attributed to the failure of allowing uncertainties in resources and how individual use resources. Clark *et al*. (2003) suggests that these failures result in biased estimates and inaccurate confidence intervals. They also indicate that some results suggested by traditional methods can be an artifact to the assumption that all individuals respond identically. Since tree growth and competition are a noisy process that reflects both the history of individual trees and environmental variation

(Clark *et al*., 2003; Uriarte *et al*., 2004b), it is important to properly model the resource levels that cannot be precisely known.

5. Conclusions

My result indicated that Bayesian inference enables to estimate the parameters of neighborhood competition models in which the interspecific variability is expressed as a random effect. Based on a model selection using DIC, the model that represented interspecific variability as a random effect was superior to other models that represented it as a fixed effect or that had no interspecific variability. This result suggests that although there was a clear evidence for interspecific variability, all species including minor ones exert measurably similar competitive effects.

There is a potential for further model development. I assumed that the competitive impact a target tree suffers is independent of its size and of the difference in size between neighbors. A model based on such assumption is called “two-sided competition models” (Weiskittel *et al.,* 2001). However, previous studies adopted “one-sided completion models”, in which only larger neighbors exert competitive effect (Weiskittel *et al.*, 2001), or included an additional parameter that allows the competitive effect of neighbors to decline as target tree size increases (Canham *et al*., 2006; Uriarte *et al.*, 2004a, 2004b; Papaik & Canham, 2006; Coates *et al.,* 2009)). While the two-sided competition model afforded us computational simplicity, future research could examine alternative models which may contribute to higher accuracy.

第五章（chapter 5, pp. 43–62）の内容は、学術誌 Journal of Forest Research (S. Tatsumi, T. Owari, H. Kasahara, Y. Nakagawa, “Individual-level analysis of damage to residual trees after single-tree selection harvesting in northern Japanese mixedwood stands”) に掲載済みであり、インターネット公表に対する承諾が得られていない。

第六章（chapter 6, pp. 63–75）の内容は学術誌 Ecological Applications に投稿予定のため、インターネットに公表できない。

Chapter 7

Conclusions

1. Summary of results

In this study, I developed a spatially explicit, individual-based model and explored forest dynamics under a variety of single-tree selection harvesting scenarios in Hokkaido. Through its development, I conducted Bayesian modeling of *Sasa* and trees' recruitment, growth, and mortality. The key findings in each chapter were as follows:

Chapter 2: Understory vegetation submodel

I used a spatial neighborhood approach based on Bayesian modeling to quantify the competitive effect of individual trees on the density and height of *Sasa*. We analyzed how the effect of neighboring trees varies with stem size, distance to *Sasa*, and tree species. The effect of neighbors peaked when the tree reached a medium size (33.0 to 45.0 cm in DBH) and decreased for larger trees. The effect of neighbors decreased with increasing distance to *Sasa*. The slope of the decrease was gentler for larger trees. Conifers exerted an average of 7.2 times the effect of broadleaved trees. Species with higher shade tolerance exerted larger effects. Species with late leaf-flush and early defoliation tended to exert smaller effects.

Chapter 3: Recruitment submodel

We used the modeling approach similar to chapter 2 to quantify the interactions among three biotic components: adult trees, *Sasa*, and tree recruitment. The direct negative effect of adult trees on tree recruitment peaked when the adult tree reached a DBH of 73.2 cm and decreased thereafter. Adult conifers had 8.7 times the larger competitive effect of adult broad-leaved trees. *Sasa* had direct negative effect on tree recruitment. Tree species with larger capacity to sprout was less affected by dwarf bamboos. Overall, the indirect positive effect of adult trees on recruitment mediated by dwarf bamboo overwhelmed the direct negative effect, thereby the net effect to be positive. Adult conifers had remarkably larger facilitative effect than adult broad-leaved trees. Mid-sized trees had larger facilitative effect. Thus, it was indicated that to maintain the density of mid-sized conifers is the key for ensuring continuous tree recruitment in Hokkaido.

Chapter 4: Growth submodel

I used a spatial neighborhood approach based on Bayesian modeling to explore the interspecific difference among trees' competitive ability. I analyzed how the effect of neighboring trees on target tree's diameter growth varies with stem size, distance between the trees, and species identity. The competitive effect of neighbors increased with its DBH and decreased with increasing distance to target trees. Among three alternate models, a model that represented the interspecific variability as a random effect was selected the best model (based on model selection using the deviance information criterion), followed by a model that represented it as a fixed effect. The estimated interspecific variability was smaller than previously reported; only three species out of 39 species were considered to have significant difference with other species. Results showed that although there is a clear evidence for interspecific variability, the species-specific effects are not independent to each other, but rather have somewhat of similarity.

Chapter 5: Mortality submodel

I used hierarchical Bayesian model to quantify individual-level effects (tree size, tree species, and the distance from residual trees to felled trees and skid trails) on residual tree mortality. Among the 4,961 trees that we studied, 373 (7.5%) were damaged, and 148 of these trees (3.0%) died during logging. The risk of damage to residual trees increased with increasing size of the felled trees and with increasing proximity to felled trees and skid trails. Smaller residual trees had the greatest risk of damage. Species differed in their susceptibility to damage; *Abies sachalinensis* and *Picea jezoensis* were the most susceptible species in our sample plots. The damaged trees had higher risks of postharvest mortality than the undamaged trees.

Chapter 6: Forest dynamics simulation

I developed a spatially explicit, individual-based model by integrating the Bayesian models and explored forest dynamics under a variety of single-tree selection harvesting scenarios. I first evaluated the goodness of fit of the model. The model reconstructed the dynamics of target forest quite well; predicted changes in stand structures (stand BA, diameter-class distribution, and species composition) were comparable to observed values. Next, I simulated the change in stand structures and the expansion of *Sasa* for the next 200 years in two plots: control plot and pre-harvested plot (in the past 40 years, no harvesting had been conducted in the control plot whereas single-tree selection harvesting had been repeatedly conducted in the pre-harvested plot). Without harvesting, stand structures were predicted to be maintained at the same state in the control plot; in contrast, the tree density decreased and *Sasa* expanded in the pre-harvested plot. In both plots, dwarf bamboo expanded under the current harvesting regime (10-years harvesting interval, 15% removal in terms of stand BA, conifers accounted for 90% of the harvested tree, and no harvesting of small-sized broadleaved trees). To explore an alternative regime, I conducted an exhaustive simulation in which all possible combinations of harvesting parameters were examined. The results showed that the stand structure can be maintained under a harvesting regime in which harvesting interval was 30-years, removal was 35%, conifers accounted for 60% of the harvested tree, and small-sized broadleaved trees were harvested.

2. Limitations and further development of the models

By using neighborhood approach based on Bayesian modeling, I successfully estimated and predicted the major structural attributes (e.g. stand BA, diameter-class distribution, and density of *Sasa*) of a forest in Hokkaido. However, my models have clearly a potential for improvement from both basic and applied ecology point of view. Perhaps one of the most important factors that I did not consider in my study is the influence of typhoons. Typhoon is a major type of natural disturbance in Hokkaido and has important effects on forest dynamics (Ishikawa and Ito 1989). I did not incorporate the influences of typhoon in the model because of the limitation in my data and because I have put focus on anthropogenic disturbance (i.e. harvesting) in this study. However, incorporating them into the current model could further improve its accuracy and help to explore the combined effects of natural and anthropogenic disturbances on forest dynamics.

There are many management options that I did not examine in this study. For example, we did not explore how supplementary planting could influence forest dynamics. Also, the range of harvesting methods explored in this study was fairly limited, especially in terms of spatial arrangement and size of harvested trees (where trees were harvested in descending order of its DBH). Employing a more complex harvesting algorithm (e.g. Arii et al. 2008) could permit investigation of a broader range of harvesting scenarios, including widely applied methods such as shelterwood and group-selection.

3. Management implications

My results showed that mid-sized conifers strongly suppress *Sasa* (Chapter 2). Furthermore, because the direct negative effect (of adult trees on recruitment) overwhelms the indirect positive effect (of adult trees on recruitment mediated by *Sasa*), the mid-sized conifers was deemed the key component to suppress dwarf bamboos and to ensure continuous tree recruitment (Chapter 3). These results imply the existence of a positive feedback loop in which the decrease in adult confers density decreases conifer recruitment via the expansion of *Sasa*, which will in turn decrease the adult confers' density (Fig. 7.1).

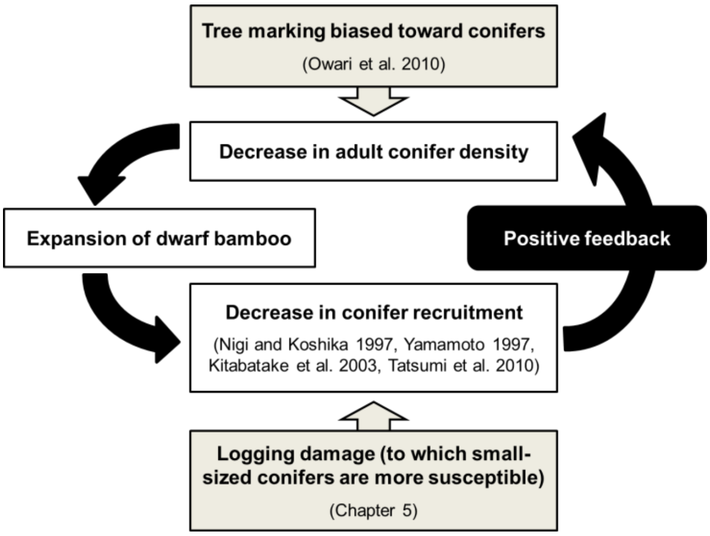

Fig. 7.1. Feedback mechanism that could lead to an irreversible transition of stand structure in the study site. White boxed and grey boxed show the component of forest dynamics and possible causes of transition, respectively.

Indeed, such decrease in conifer recruitment has been observed in many selection-managed stands in Hokkaido (Yamamoto 1995, Nigi and Koshika 1997, Kitabatake et al. 2003, Tatsumi et al. 2010). This may be largely attributed to the tendency in tree marking and to logging damage during selection harvest. A case study on tree marking by Owari et al. (2010) showed that *Abies sachalinensis*, the most dominant conifer species in Hokkaido, was disproportionately selected in a tree marking process. This tendency likely stemmed from the fact that this species frequently defoliates after reaching a certain size (ca. 60–70 cm), and thus tree markers prefer to select them before they lose their timber values. As for logging damage, my results showed that major conifer species (*Abies sachalinensis* and *Picea jezoensis*) were the most susceptible species (i.e. they had highest risks to be dead by logging damage) (Chapter 5). Under the current single-tree selection regime in which tree marking is biased to conifers and harvesting is frequently conducted (10-years interval), *Sasa* will likely expand and consequently tree density will decrease in the future (Fig. 7.1). My simulation results indicated that, to obviate such shift in stand structure in our study site, proportion of conifers among harvested trees should be kept at relatively low level (60%) and harvesting interval should be set longer (30 years) so as to reduce logging damage (Chapter 6).

My model predicted that under the alternative harvesting regime, single-tree selection can be continuously conducted without causing shifts in stand structure in mixed conifer–broadleaf forests of Hokkaido. I must note that, however, my model has many limitations and is based on multiple assumptions that have to be validated in the future. Nevertheless, I believe that further modification of the current model, together with the accumulation of data and knowledge in the field, would lead to the development of a single-tree selection system that is grounded on scientific evidence.

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