論 文 の 内 容 の 要 旨

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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）

Prediction of forest dynamics has been one of the primary focuses of forestry since the inception of the discipline. 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 model allows for a wide range of conditions within single stands and thus offers the most viable approach for modelling uneven-aged stands. Many spatially explicit, individual-based models have been developed, but some common challenges remain to be solved. One of the major challenges is that they typically lack to take into account the presence of understory vegetation, an important factor that affects tree recruitment. Also, despite many researchers have documented the importance of tree mortality caused by logging practices, the models that explicitly incorporate these impacts are still scarce.

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 competitive interactions among plants by expressing them as functions of plant biomass, species identities, and the spatial configuration of individuals. Bayesian approach provides a flexible modeling framework in which individual-based factors can be efficiently analyzed. By integrating the estimated Bayesian models and associate parameters, I developed a spatially explicit, individual-based model.

The objectives of this study were to develop a spatially explicit, individual-based model and to explore the dynamics of uneven-aged forests under a variety of 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 mortality, I investigated the influence of logging on residual tree's mortality in a spatially explicit manner. I conducted this study 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. As for silvicultural practices, single-tree selection has been widely conducted throughout Hokkaido for more than a century. Thus, forest in Hokkaido represents a good model system of which the basic and applied ecological background corresponds to my study objectives. Results of this study offer novel methodologies for modeling forest dynamics using individual-based approach and provide new insights into single-tree selection management in Hokkaido. The summary of results is as follows.

*Recruitment*

I used a spatial neighborhood approach based on Bayesian modeling to quantify the competitive interactions among three biotic components: adult trees, dwarf bamboos, and tree recruitment. First, I analyzed how the effect of individual adult trees on dwarf bamboo varies with stem size, distance to the dwarf bamboo, 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 the dwarf bamboo. 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. Next, I investigated the negative effects of dwarf bamboo on tree recruitment. I found that tree species with larger capacity to sprout were less affected by dwarf bamboos. Finally, I analyzed the direct negative effect of adult trees on tree recruitment. The effect of neighbors peaked when the 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. 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.

*Growth*

By using a similar modeling approach described above, I explored the interspecific difference among trees' competitive ability. I analyzed how the effect of neighboring trees on the diameter growth of target tree (*Abies sachalinensis*, the most dominant species in my study site) 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, 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. Also, while previous studies estimated that the effect of some species had dozens of times larger the competitive effect of other species, in my study, the species with largest effect had only 6.6 times larger the effect of species with smallest effect. 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.

*Mortality*

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 I 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 my study site. The damaged trees had higher risks of postharvest mortality than the undamaged trees.

*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. 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. I simulated the change in stand structures and the expansion of dwarf bamboo 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 dwarf bamboo expanded in the pre-harvested plot. In both plots, dwarf bamboo expanded under the current harvesting regime (in which harvesting interval was 10-years, removal rate in terms of stand BA was 15%, conifers accounted for 90% of the harvested tree, and small-sized broadleaved trees were not harvested). To explore an alternative regime, I conducted simulations in which all possible combinations of harvesting parameters were examined. The results showed that, in the pre-harvested plot, the stand structure can be maintained under a harvesting regime in which harvesting interval was 30-years, removal rate was 35%, conifers accounted for 60% of the harvested tree, and small-sized broadleaved trees were harvested.

*Conclusions*

Bringing together field-based empirical studies, neighborhood analysis, Bayesian modeling, and individual-based simulation, I demonstrated a new methodology for modeling forest dynamics and evaluated single-tree selection harvesting in Hokkaido. Results showed that mid-sized conifers strongly suppress dwarf bamboos. Furthermore, the indirect positive effect (of adult trees on recruitment mediated by dwarf bamboos) overwhelmed the direct negative effect (of adult trees on recruitment). These results indicate that mid-sized conifers are the key component to suppress dwarf bamboos and to ensure continuous tree recruitment. They also imply the existence of a positive feedback loop in which the decrease in adult confers' density enhances the decrease in conifer recruitment via the expansion of dwarf bamboos, which will in turn decrease the adult confers' density (Fig. 1).

Indeed, such decrease in conifer recruitment has been observed in many selection-managed stands in Hokkaido. This may be largely attributed to the tendency in tree marking and to logging damage during selection harvest. A previous case study on tree marking 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 decays after reaching a certain size (ca. 40–50 cm), and thus tree markers prefer to select them before losing 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). Under the current single-tree selection regime in which tree marking is biased towards conifers and harvesting is frequently conducted (10-years interval), dwarf bamboo will likely expand and, consequently, tree density will decrease in the future. My simulation results indicat that, to obviate such change in stand structure in my 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.

My spatially explicit, individual-based model predicted that under the alternative harvesting regime, single-tree selection can be continuously conducted without causing changes in stand structure in a mixed conifer–broadleaf forest of Hokkaido. Note that, however, my model has many limitations and is based on multiple assumptions that have to be validated in the future. Still, 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.

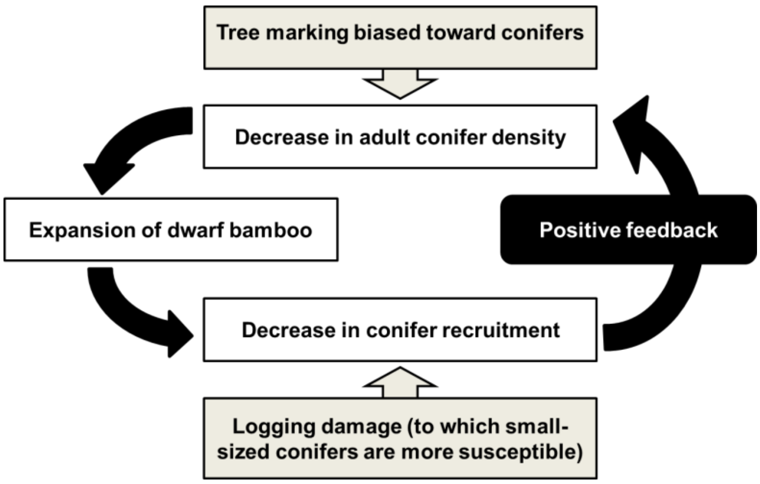


Fig. 1. Feedback mechanism that may cause changes in stand structure in the study site. White boxes and grey boxes show the component of forest dynamics and possible causes of the changes, respectively.