

Modeling the effects of individual-tree size, distance, and species on understory vegetation based on neighborhood analysis

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Abstract: Quantifying how understory vegetation responds to individual neighboring trees is critical to understanding forest dynamics. To do so, we used a spatial neighborhood approach to quantify the competitive effect of individual trees on the density and height of dwarf bamboo (*Sasa senanensis* (Franch. et Savat.) Rehder) in a mixed conifer–broadleaf forest on the island of Hokkaido, northern Japan. Using hierarchical Bayesian models, we analyzed how the effect of neighboring trees varies with stem size, distance to the dwarf bamboo, and tree species. The effect of neighbors peaked when the tree reached a medium size (33.0–45.0 cm in diameter at breast height) 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. Our results provide evidence that neighborhood analysis is an effective approach for quantifying the effects of individual trees on understory vegetation and represents a critical step toward understanding how fine-scale interactions between understory vegetation and trees influence overall forest dynamics.

Résumé : Il est essentiel de quantifier la réaction de la végétation du sous-étage à chacun des arbres avoisinants pour comprendre la dynamique forestière. À cette fin, nous avons utilisé une approche spatiale de voisinage pour quantifier l'effet de compétition d'arbres individuels sur la densité et la hauteur du bambou nain (*Sasa senanensis* (Franch. & Savat.) Rehder) dans une forêt mixte sur l'île d'Hokkaido, dans le nord du Japon. À l'aide de modèles bayésiens hiérarchiques, nous avons analysé la façon dont l'effet des arbres voisins varie selon le diamètre de la tige, la distance du bambou nain et l'espèce d'arbre. L'effet des voisins culmine lorsqu'un arbre atteint une taille moyenne (33 à 45 cm de diamètre à hauteur de poitrine) et diminue lorsque les arbres sont plus gros. L'effet des voisins diminue avec l'augmentation de la distance du bambou nain. La pente de la diminution était plus faible pour les arbres plus gros. L'effet produit par les conifères était en moyenne 7,2 fois plus grand que celui des feuillus. Les espèces les plus tolérantes à l'ombre avaient plus d'effet. Les espèces qui débourraient tardivement et perdaient leur feuilles tôt avaient tendance à avoir moins d'effet. Nos résultats montrent que l'analyse de voisinage constitue une approche efficace pour quantifier les effets d'arbres individuels sur la végétation du sous-étage et représente une étape essentielle pour comprendre comment les interactions à petite échelle entre la végétation du sous-étage et les arbres influencent la dynamique forestière globale. [Traduit par la Rédaction]

Introduction

In many of the world's forest ecosystems, understory vegetation plays a crucial role in forest dynamics (Nakashizuka 1988; Abe et al. 2002; Royo and Carson 2006, 2008). The attributes of the understory vegetation (e.g., density, abundance, height, and species richness) are influenced by an array of factors, among which the characteristics of the overstory trees play a key role (Noguchi and Yoshida 2005; van Oijen et al. 2005; Wulf and Naaf 2009). Understory vegetation often expands to form clonal patches in tree fall gaps created by natural and anthropogenic disturbances (Abe et al. 2002; Royo and Carson 2006). In turn, changes in the forest-floor environment induced by the understory vegetation can significantly shift the rates and spatial patterns of tree regeneration (Nakashizuka 1988; Abe et al. 2002; Royo and Carson 2008). These shifts determine the density and distribution of future canopy trees, which in turn influence trees in lower parts of the canopy as well as understory vegetation. In forests where a large-scale disturbance has occurred, understory vegetation often forms persistent and nearly impenetrable layers (Royo and Carson

2006). These layers exclude tree regeneration for extended periods, and can shift succession of the system to grassland (Umeki 2003). Thus, quantifying the response of understory vegetation to overstory trees is critical to our understanding of forest dynamics.

The responses of understory vegetation to gap size, stand structure, and tree species composition have been widely studied (Anderson et al. 1969; Ehrenfeld 1980; Noguchi and Yoshida 2004; Barbier et al. 2008). However, previous studies were invariably conducted at a stand level (e.g., Wulf and Naaf 2009) or on a tree fall gap versus closed-canopy basis (e.g., Chavez and Macdonald 2010). To our knowledge, no research has focused on the characteristics of individual trees and on the associated changes in the understory environment. In stands as well as in gaps, the local understory environments vary significantly in response to changes in the number, stem size, and species of neighboring trees, as well as their distance from the focal point (Canham et al. 1999; Beaudet et al. 2011). Previous studies based on stand- and gap-level approaches could not distinguish such individual-level factors, and thus could not quantify the relative magnitudes of their effects on the attributes of the understory

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vegetation. An analysis that accounts for the characteristics of individual trees could, therefore, improve our understanding of the responses of understory vegetation to adjacent trees.

In this study, we used neighborhood analysis to account for these effects. This analytic approach assumes that plant communities are regulated by fine-scale spatial interactions among individuals (Canham and Uriarte 2006; Zhao et al. 2006). One of the most widely used methodologies in neighborhood analyses is the neighborhood competition index (NCI; Canham et al. 2004), which expresses the degree of competition among trees as a function of stem size, species, and the spatial configuration of the individuals. The index was developed and has been used for analyzing the effect of competition on tree growth and survival (e.g., Canham et al. 2004, Coates et al. 2009, Tatsumi et al. 2013) and has also been adapted for examining allelopathic interactions (Gómez-Aparicio and Canham 2008) and the structure of individual tree crowns (Thorpe et al. 2010a). Because of the mathematical simplicity and flexibility of NCI, we hypothesized that it could be further modified and applied to analyzing the responses of understory vegetation to individual trees.

In this study, we quantified the competitive effect of individual trees on attributes of the understory vegetation using NCI. Our study was conducted in a mixed conifer–broadleaf forest on the island of Hokkaido, northern Japan, where the forest floor is often covered by *Sasa senanensis* (Franch. et Savat.) Rehd., a type of dwarf bamboo. The forest consists of multiple tree species with a range of sizes and has a heterogeneous configuration of individual trees. Dwarf bamboo species are perennial, clonal, semi-woody plants that have a strong inhibitory effect on tree regeneration (Nakashizuka 1988; Abe et al. 2002; Noguchi and Yoshida 2004). Because the culm density and height of dwarf bamboo species depend strongly on the characteristics of the overstory trees (Noguchi and Yoshida 2005), they represent a good model system for our study. Our specific objectives were to quantify how individual trees affected the culm density and height of the dwarf bamboo (*S. senanensis*) as a function of the (i) stem size, (ii) distance to the dwarf bamboo, and (iii) species of the trees. Quantifying these variations represents a critical step toward understanding how the fine-scale responses of understory vegetation to individual trees will influence overall forest dynamics. This has important implications for current and future management practices.

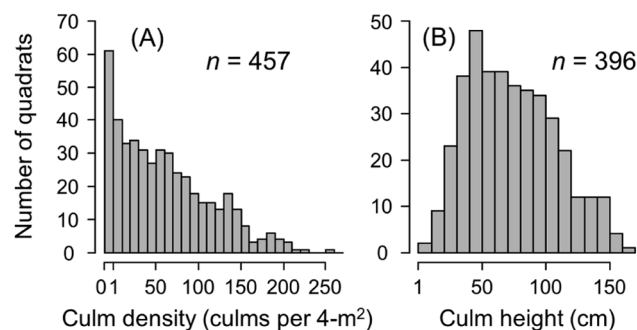
Materials and methods

Study sites

We conducted this study in the forest management unit 1 of the University of Tokyo Hokkaido Forest (43°10′–20′N, 142°18′–36′E, 190–850 m elevation, 12 234.5 ha). The forest is located between the cool-temperate and sub-boreal zones, where mean annual temperature and annual precipitation are 6.6 °C and 1577 mm, respectively (University of Tokyo Hokkaido Forest 2013). Mean monthly temperatures range from a minimum of –8.4 °C in January to a maximum of 21.2 °C in August (University of Tokyo Hokkaido Forest 2013). The forest floor is covered by snow from November to April, reaching a depth of approximately 1 m. The typical substrate and soil type are a welded tuff underlying a dark brown forest soil (Asahi 1963). The forest mainly consists of mixed conifer–broadleaf stands with evergreen conifers and deciduous broad-leaved species. The dominant canopy species are *Abies sachalinensis* (Fr. Schm.) Masters, *Tilia japonica* (Miq.) Simonkai, and *Acer mono* Maxim.

We collected data in 20 research plots that had been established throughout the study area. In two of the plots, the understory was dominated by ferns (e.g., *Dryopteris crassirhizoma* Nakai, *Osmunda cinnamomea* (L.) C. Presl, and *Arachniodes standishii* (T. Moore) Ohwi) rather than by dwarf bamboo. Because dwarf bamboo was the target species in this study, we excluded the data from these two

Fig. 1. Frequency distributions of (A) culm density and (B) culm height of dwarf bamboo in the data set.



plots from our analysis, and thus the remaining 18 plots were defined as our study plots. The distance between plots ranged from 0.2 to 15.0 km, with a mean of 7.3 km. The plots were rectangular, with the area and the length of their sides ranging from 0.24 to 0.48 ha and from 48.1 to 97.1 m, respectively. We could not use a constant plot size because the plots were established between 1968 and 1976, to meet different needs. The observed range of diameter at breast height (DBH) for all trees with DBH ≥ 5 cm was 5.0–96.9 cm (with a mean of 17.8 cm). The tree density and stand basal area (BA) ranged from 424.5 to 2153.5 trees·ha⁻¹ (with a mean of 978.1 trees·ha⁻¹) and from 22.5 to 57.5 m²·ha⁻¹ (with a mean of 34.9 m²·ha⁻¹), respectively. Most of the study plots had undergone at least one single-tree selection harvest (with a removal rate of approximately 16% of the stand volume). However, because the harvesting was conducted in winter, with snow cover on the forest floor, the dwarf bamboo experienced little damage, except right on the skid trails.

Data collection

In the study plots, the DBH and spatial position (x, y coordinates) had been measured from 2007 to 2012 by the staff of the University Forest for all trees with DBH ≥ 5 cm, with 0.1 cm and 0.1 m precision, respectively. The species had also been recorded, but species with similar morphological traits had been identified only to the genus level. In this study, we considered these species groups to represent a single species in our analysis.

In August and September 2012, we sampled the culm densities and heights in 2 m \times 2 m quadrats ($n = 16$ –37 quadrats per plot) set up at 8 m grid intervals in each of the study plots. All the quadrats were located at least 10 m from the nearest plot edge. We defined a culm that did not branch off from any other culm as an individual culm, but did not remove litter from the forest floor to confirm this (cf. Noguchi and Yoshida 2005). For culm height, we measured the dominant height within the quadrat to the nearest 5 cm, disregarding a few projecting culms (cf. Noguchi and Yoshida 2005). We excluded quadrats that were located on skid trails from our data. Our analysis included samples from a total of 457 quadrats, of which 61 quadrats had no dwarf bamboo. The observed range of culm density and height were 0–259 culms per 4 square metres quadrat (with a mean of 61.2 and SD of 54.0) and 10–170 cm (with a mean of 78.1 and SD of 34.6), respectively (Fig. 1). Note that we excluded the quadrats with no dwarf bamboo when calculating the culm height values because the absence of dwarf bamboo did not mean that the culm height was 0 cm.

Statistical modeling

We used hierarchical Bayesian models to analyze the competitive effect of neighbors on the culm density and height of the dwarf bamboo. We assumed that the observed culm density (D_i , culms per 4 square metres) in quadrat i followed a Poisson distribution because the variable took only integer values.

$$(1) \quad D_i \sim \text{Poisson}(D_i')$$

where D_i' is the expected culm density (culms per 4 square metres) in quadrat i .

Because culm height (H_i , cm) had continuous values (although we measured it at 5 cm intervals) and was non-negative, we assumed that the logarithm of H_i followed a normal distribution

$$(2) \quad \ln(H_i) \sim \text{Normal}(\ln[H_i'], \tau)$$

where H_i' is the expected culm height (cm) in quadrat i and τ is a variance parameter. Note that quadrats with no dwarf bamboo ($n = 61$) were included in the estimates of D_i (eq. (1)), because a density of 0 is a meaningful result, but were not included in H_i (eq. (2)), because a height of 0 was not meaningful.

The effects of NCI on the culm density and height were examined using log-link functions. We used the log-link function because this is one of the most commonly used functions when dealing with response variables that have non-negative distributions (Clark 2007)

$$(3) \quad \ln(D_i') = \alpha_0 + \alpha_1 \text{NCI}_i + \ln(4)$$

$$(4) \quad \ln(H_i') = \beta_0 + \beta_1 \text{NCI}_i$$

where the term $\ln(4)$ is an offset term that transforms the units of D_i' from culms per 4 square metres to culms per square metre; α_0 , α_1 , β_0 , and β_1 are parameters; and NCI_i is the neighborhood competition index for quadrat i .

By modifying the functional form of NCI step by step, we tested five hypotheses for how the competitive effect of individual neighbors on dwarf bamboo is determined. As the basis of all NCI equations, we used the index developed by Canham et al. (2004), in which the total effect of neighbors on a target plant (in our case, on the dwarf bamboo at a given point) is expressed as the summation of the effects of individual neighbors

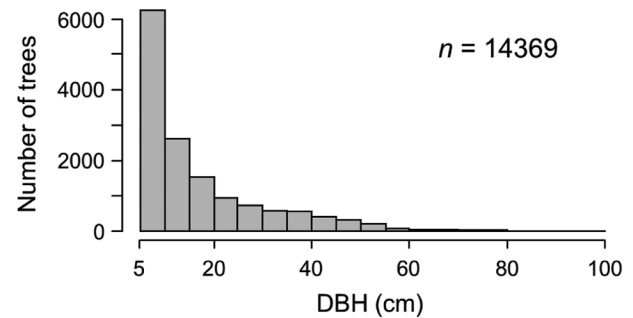
$$(5) \quad \text{NCI}_i = \sum_{j \in N_i} I_j$$

where N_i is the set of identification numbers for neighboring trees for quadrat i and I_j is the per capita effect of individual tree j .

The center of a quadrat was defined as the position of the quadrat and of the dwarf bamboo. Neighboring trees were defined as those individuals located within 10 m of each quadrat center. There were two reasons for selecting this neighborhood radius. First, defining a larger radius would have prevented us from obtaining a sufficient number of quadrats with completely mapped neighbors. Second, a previous study (Noguchi and Yoshida 2005) showed that the total BA of the neighboring trees within a 7.5 m radius was strongly correlated with both the culm density and the height of the dwarf bamboo. We extended the radius to 10 m to account for the effects of neighbors at greater distances and to increase the likelihood of robust estimations of the associated parameters. Each quadrat had an average of 31.4 neighbors within this radius. Note that it was possible for a given tree to be a neighboring tree for multiple quadrats. In total, we included 14 369 neighbors with DBH ranging from 5.0 to 96.9 cm (Fig. 2) and distances ranging from 0.1 to 10.0 m, with several species or species groups (four coniferous species and 32 broad-leaved species) in the analysis.

The simplest hypothesis assumed that the effect of individual neighbors varies monotonically with DBH and with distance to the dwarf bamboo and is equivalent among species

Fig. 2. Frequency distribution of the neighboring tree's DBH in the data set. The DBH ranged from 5.0 to 96.9 cm.



$$(6) \quad I_j = \exp(\gamma_1 \text{DB}_j + \gamma_2 \text{DI}_j)$$

where DB_j is the DBH (cm) of neighboring tree j , DI_j is the distance (m) from neighboring tree j to the quadrat, and γ_1 and γ_2 are parameters. Here, parameters γ_1 and γ_2 determine the slopes that define the effect of individual neighbors in terms of a rate of change with respect to changes in DBH and distance, respectively. Parameters γ_1 and γ_2 determine how the effects of individual neighbors vary, whereas α_1 (eq. (3)) and β_1 (eq. (4)) determine how much the total effect of the neighbors (i.e., NCI) influences culm density and height.

Previous NCI analyses, in which NCI was expressed similarly to eq. (6), have assumed that the effect of neighbors varies (increases) monotonically in response to DBH (e.g., Canham et al. 2004; Coates et al. 2009). As an alternative, we developed a second hypothesis to test whether the influence of a neighbor's DBH on its competitive effect followed a single-peaked pattern (i.e., had a maximum). This hypothesis was based on our belief that the characteristics of the understory vegetation were strongly affected by the sizes and vertical positions of the tree crowns. Generally, DBH is strongly correlated with crown size and position; that is, whereas a tree crown enlarges simultaneously with DBH growth, the crown also moves upward as a result of the self-pruning of lower branches (Thorpe et al. 2010a). We assumed that the tree density and stand BA of our study plots were high enough that the trees had begun to self-prune. It was thus likely that a tree with a very large DBH would have a large crown, but that the crown existed at a sufficient height that its shading effect might not strongly affect the forest floor. We hypothesized that when both the size and the position of a neighbor's crown were moderate, the competitive strength of the neighbor on the understory vegetation would be maximized.

$$(7) \quad I_j = \exp(\gamma_1 \text{DB}_j + \gamma_2 \text{DB}_j^2 + \gamma_3 \text{DI}_j)$$

In the third hypothesis, we tested whether the possible peak of the competitive effect as a function of the neighbor's DBH would shift to larger trees with increasing distance from the dwarf bamboo. This hypothesis was based on our belief that because larger trees have wider crowns, the extent to which they would exert their competitive effects would increase with increasing DBH; that is, the slope that describes the rate at which the effect of neighbors decreases with distance depended on DBH. Note that here we are focusing on the *spatial extent* of the effects, whereas the second hypothesis (eq. (7)) tests the *strength* of the effects. We tested this hypothesis by adding a term for the interaction between DBH and distance.

$$(8) \quad I_j = \exp(\gamma_1 \text{DB}_j + \gamma_2 \text{DB}_j^2 + \gamma_3 \text{DI}_j + \gamma_4 \text{DB}_j \text{DI}_j)$$

Table 1. Assumed patterns of the effects of predictor variables, values of the deviance information criterion (DIC), and differences in DIC (Δ DIC) from that of the selected model for the five models.

Model No.	Assumed pattern of the effects of predictor variables			DIC	Δ DIC
	DBH	Distance	Species		
1 (eq. (6))	Monotonic	DBH independent	Equivalent	18446.3	6173.0
2 (eq. (7))	Single peaked	DBH independent	Equivalent	17997.1	5723.8
3 (eq. (8))	Single peaked	DBH dependent	Equivalent	17940.4	5667.1
4 (eq. (9))	Single peaked	DBH dependent	Conifers versus broad-leaved trees	13196.7	923.4
5 (eq. (10))	Single peaked	DBH dependent	36 species	12273.3	0

Previous stand-level studies have found distinct differences between conifers and broad-leaved trees in terms of their competitive effects on dwarf bamboo (Ishibashi 1998; Noguchi and Yoshida 2004). To determine whether such a difference occurs on an individual level, our fourth hypothesis tested a form of NCI (I_j) that includes an individual-level multiplier, λ (Canham et al. 2004)

$$(9) \quad I_j = \exp(\lambda_{CB_j} + \gamma_1 DB_j + \gamma_2 DB_j^2 + \gamma_3 DI_j + \gamma_4 DB_j DI_j)$$

where CB_j is the variable (identification number) that defines whether the neighboring tree j is a conifer or a broad-leaved tree (where $CB_j = 1$ and $CB_j = 2$ correspond to conifers and broad-leaved trees, respectively). Here, the per capita effect of each individual neighbor is multiplied by $\exp(\lambda)$. The value of λ_1 was fixed at 1, whereas the value of λ_2 was estimated. By calculating the estimated ratio of $\exp(\lambda_1)$ to $\exp(\lambda_2)$ (i.e., $y = \exp(\lambda_1)/\exp(\lambda_2)$), the relative difference in the per capita effect between conifers and broad-leaved trees can be estimated.

Finally, our fifth hypothesis tested whether the difference in competitive effect extended to the species level. To conduct this test, we further modified the parameter λ to have a hierarchical structure in which its value was determined first based on whether the neighbor was coniferous or broadleaved and, subsequently, was determined based on its species

$$(10) \quad \begin{aligned} I_j &= \exp(\lambda'_{SP_j} + \gamma_1 DB_j + \gamma_2 DB_j^2 + \gamma_3 DI_j + \gamma_4 DB_j DI_j) \\ \lambda'_S | (S \in C) &\sim \text{Normal}(\lambda_1, \sigma) \\ \lambda'_S | (S \in B) &\sim \text{Normal}(\lambda_2, \sigma) \end{aligned}$$

where SP_j is the identification number for the species of neighboring tree j , C is the set of identification numbers for coniferous species ($n = 4$), B is the set of identification numbers for broad-leaved species ($n = 32$), and σ is a variance parameter. Here, the species-specific parameters λ'_S are assumed to share a common mean value, either λ_1 or λ_2 , which correspond to conifers and broad-leaved trees, respectively. Parameter σ represents the variance of the interspecific difference within the two groups (conifers and broad-leaved trees). In a hierarchical modeling context, σ is referred to as a hyperparameter and is estimated simultaneously with the other parameters. As in eq. (9), the value of λ_1 was fixed at 1, whereas the values of λ_2 and λ'_S were estimated. The relative difference in per capita effect between species x and species y can be estimated by calculating the ratio of $\exp(\lambda'_x)$ to $\exp(\lambda'_y)$.

Noninformative normal distributions with a mean of 0 and a variance of 10 000 were specified for the prior distributions of parameters α , β , γ , and λ_2 . For the prior of the variance parameter τ , we specified a noninformative gamma distribution, $\text{Gamma}(1, 0.001)$, for $1/\tau$. We chose a gamma distribution as the prior of $1/\tau$ because

the inverse-gamma distribution is the conjugate prior for variance (Clark 2007). Note that the gamma distribution is parameterized such that for $\text{Gamma}(a, b)$, its mean and variance are a/b and a/b^2 , respectively. For hyperparameter σ , we specified a subjective prior, $\text{Gamma}(1562.5, 12.5)$, for $1/\sigma$. These parameters of the prior gamma distribution ($a = 1562.5$ and $b = 12.5$) were determined by reference to the results of a previous analysis of tree competition at our study site (Tatsumi et al. 2013). This analysis showed that the mean value and 95% credible interval of hyperparameter σ were 0.003 and 0.001–0.007, respectively. We assumed that the interspecific difference in the competitive effect on dwarf bamboo would be somewhat larger than the differences among trees and, thus, that the value would be approximately 0.008.

Parameter estimation

We fitted the five models to the data by using the Markov Chain Monte Carlo (MCMC) method implemented by the WinBUGS 1.4.3 software (Lunn et al. 2000) via the R2WinBUGS package (Sturtz et al. 2005) in the R 2.15.0 software (R Development Core Team 2012). For each model, we obtained posterior samples using three independent MCMC samplings, in each of which 2000 values were sampled with a 350 step interval after a burn-in period of 50 000 MCMC steps. We confirmed the convergence of the MCMC calculations by using the Gelman and Rubin \hat{R} parameter (Gelman et al. 2004). We used the deviance information criterion (DIC; Spiegelhalter et al. 2002) for model selection. The model with the lowest DIC was considered the best model; the distance between a given model and the model with the lowest DIC is expressed as Δ DIC, so that Δ DIC = 0 for the model with the lowest DIC. Although there is no consensus on model selection for high-dimensional Bayesian models (Spiegelhalter et al. 2002), DIC is generally considered to be a reliable measure in ecological data analysis (McCarthy 2007).

The original data and the WinBUGS code are available as Supplementary data.¹ The materials include (i) the original spatial data for the trees within the 18 plots (x,y coordinates, DBH, and species of each tree), (ii) the original spatial data for each quadrat within the 18 plots (x,y coordinates and the culm density and height of dwarf bamboo), and (iii) the WinBUGS code for model 5.

Results

Model selection and goodness of fit

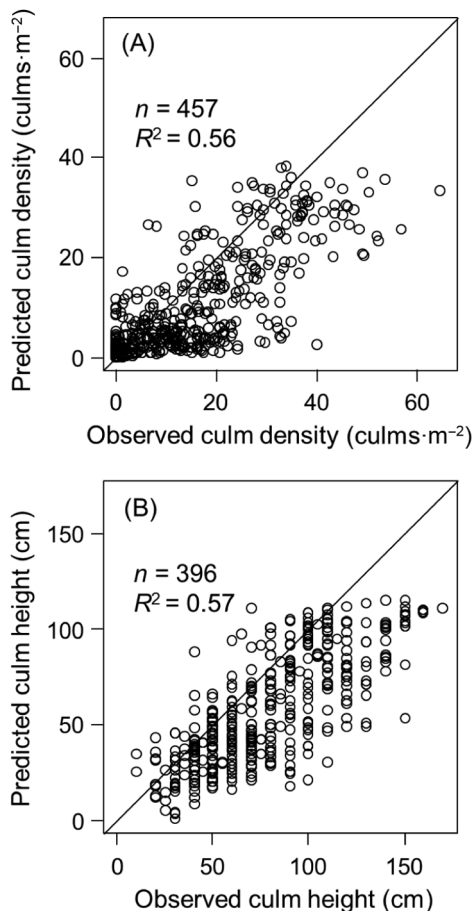
DIC decreased from model 1 to model 5, so the model corresponding to the fifth hypothesis was the best model (Table 1; DIC = 12 273.3). All of the associated parameters of the five models converged adequately ($\hat{R} < 1.1$; Gelman et al. 2004). The selected model and its parameter estimates (Table 2) provided a good fit to the observed culm density and height, with $R^2 = 0.56$ and 0.57 , respectively (Fig. 3, using the mean values of the posterior distributions for each parameter for prediction). Parameter estimates for models 1–5 are provided in Supplementary data Table S1.¹

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2013-0111>.

Table 2. Summary of the posterior distribution of the parameters for the best selected model (model 5, Table 1; the posterior distributions of the parameters l and λ' are shown in Fig. 5).

Parameter	Mean	Credible interval of the posterior sample	
		2.5%	97.5%
a_0	3.7261	3.6430	3.7710
α_1	-0.0781	-0.0972	-0.0612
β_0	4.7889	4.7150	4.8560
β_1	-0.0374	-0.0472	-0.0288
γ_1	0.0702	0.0572	0.0863
γ_2	-0.0011	-0.0014	-0.0009
γ_3	-0.3068	-0.3476	-0.2648
γ_4	0.0030	0.0013	0.0046
σ	0.0092	0.0085	0.0100
τ	0.1152	0.1006	0.1334

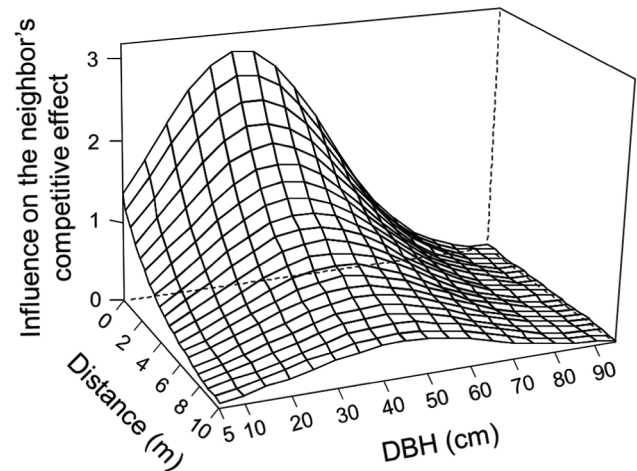
Fig. 3. Relationships between observed and predicted values of (A) culm density and (B) culm height. The best selected model (model 5, Table 1) and mean values of each parameter estimate (Table 2 and Fig. 5) were used for the prediction. The culm densities, which were sampled in 4 m² quadrats, were divided by four to present the results on a per square metre basis. The line represents $y = x$.



Influence of the neighbor's DBH, distance, and species on competitive effects

The selected model and its parameter estimates showed that the effect of an individual tree on the dwarf bamboo (I_j) depended significantly on DBH, distance, and species. Figure 4 shows the

Fig. 4. The influence of the neighboring tree's DBH and distance to the dwarf bamboo on the neighbor's competitive effect. The best selected model (model 5, Table 1) and mean values of each parameter estimate (Table 2) were used for the prediction.



effects of DBH and distance on I_j . There was a clear peak of I_j as a function of DBH. The I_j value decreased with increasing distance. The peak shifted to a larger DBH with increasing distance. For example, the I_j of trees located 1, 5, and 10 m from the dwarf bamboo peaked when they reached a DBH of 33.0, 38.3, and 45.0 cm, respectively, and decreased thereafter. A tree with a 33.0 cm DBH located 1 m from the dwarf bamboo had 2.4, 2.3, and 37.8 times the I_j of a tree with a DBH of 5, 60, and 90 cm, respectively, located at the same distance.

Figure 5 shows the posterior distributions of $\exp(\lambda)$ and $\exp(\lambda')$, the multipliers that determine the difference between conifers and broad-leaved trees and the interspecific differences in the per capita effect of neighbors. Conifers had an average of 7.2 times the I_j of broad-leaved trees (i.e., $\exp(\lambda_1)/\exp(\lambda_2) = 7.2$). For the coniferous species, *Taxus cuspidata* Sieb. et Zucc. and *Picea jezoensis* (Sieb. et Zucc.) Carr. had the largest and smallest I_j , respectively. For the broad-leaved species, *Styrax obassia* Sieb. et Zucc. and *Fraxinus lanuginosa* Koidz. had the largest and second largest I_j , respectively, whereas *Magnolia obovata* Thunb. and *Betula* spp. (*Betula maximowicziana* Regel and *Betula platyphylla* var. *japonica* (Miq.) Hara) had the smallest and second smallest I_j , respectively. As for the three most dominant species based on the number of individuals, *A. sachalinensis* had the third-largest I_j among the four coniferous species, and *Tilia* spp. (*T. japonica* and *Tilia maximowicziana* Shiras.) and *Acer mono* had respectively the 9th and 28th largest I_j among the 32 broad-leaved species. The I_j values of minor broad-leaved species, such as *Picrasma quassioides* (D. Don) Benn., *Syringa reticulata* (Blume) H. Hara, and *Carpinus cordata* Blume, were relatively close to the mean I_j value of the broad-leaved trees. However, the fact that minor species had average levels of I_j could be attributed, in part, to their small sample sizes; that is, the values may have been drawn toward the average as a result of "Bayesian shrinkage" (Link and Sauer 1996).

Competitive effects of neighbors on dwarf bamboo

Figure 6 shows the per capita effect of neighbors (I_j) as a function of DBH and distance for three species: *Taxus cuspidata* (the species with the largest λ' estimate; Fig. 6A), *A. sachalinensis* (the most dominant species based on the number of individuals; Fig. 6B), and *M. obovata* (the species with the smallest λ' estimate; Fig. 6C). The I_j value varied widely as a function of DBH and distance for *Taxus cuspidata* and *A. sachalinensis*, whereas the value remained remarkably small irrespective of DBH and distance for *M. obovata*. Neighboring trees that reached a very large size

Fig. 5. Sample size for each species and the influence of the neighboring tree's species on the magnitude of its competitive effect. The λ value for conifers was fixed at 1. (a) *Tilia japonica* and *Tilia maximowicziana*. (b) *Euonymus oxyphyllus*, *Euonymus macropterus*, *Euonymus planipes*, and *Euonymus tricarpus*. (c) *Salix bakko* and *Salix sachalinensis*. (d) *Acer japonicum* and *Acer palmatum* var. *amoenum*. (e) *Betula maximowicziana* and *Betula platyphylla* var. *japonica*.

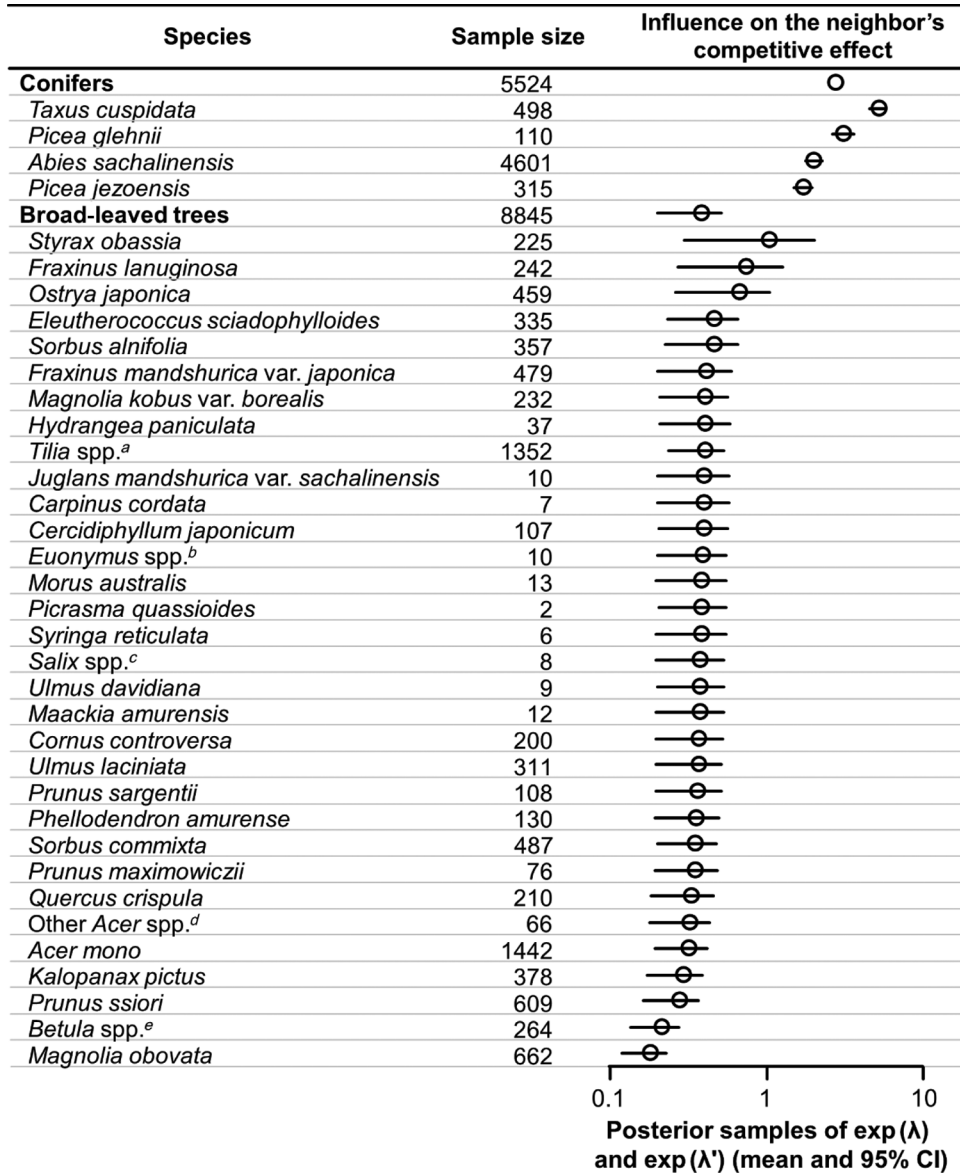


Fig. 6. Predicted competitive effect of individual (A) *Taxus cuspidata*, (B) *Abies sachalinensis*, and (C) *Magnolia obovata* with varying DBH as a function of the distance to the dwarf bamboo.

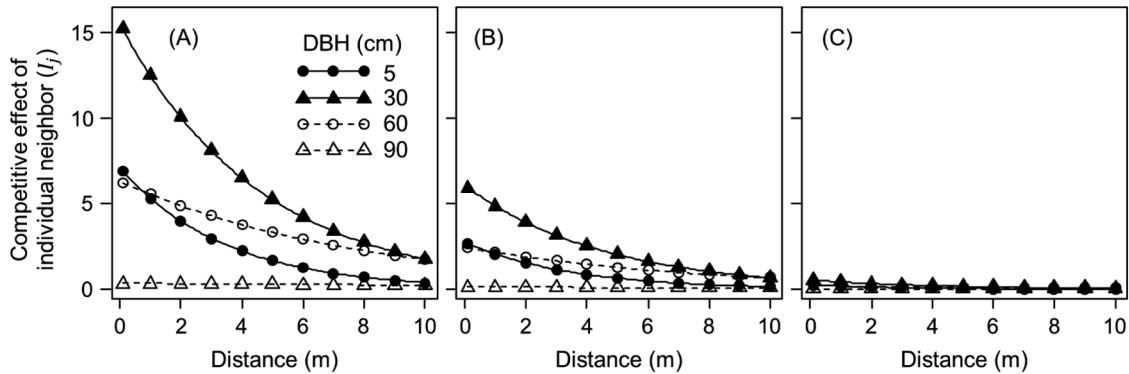
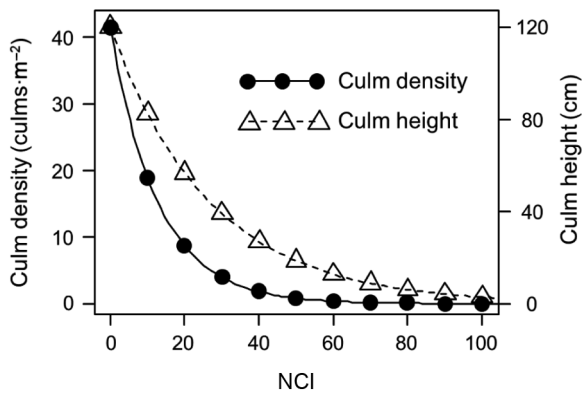


Fig. 7. Predicted culm density and height as a function of the neighborhood competition index (NCI).



(DBH > 90 cm) exerted hardly any competitive effect, regardless of distance and species.

The estimates of NCI_i , expressed as the sum of I_j within a 10 m radius of the center of quadrat i (eq. (5)), ranged from 1.1 to 193.9. Both the culm density and culm height decreased steeply with increasing NCI (Fig. 7). For example, mean culm density at $NCI = 2, 50,$ and 100 were estimated to be 35.5, 0.7, 0.01 culms·m⁻², respectively, versus corresponding values for culm height of 111.5, 18.5, and 2.9 cm.

Discussion

To our knowledge, this is the first study that quantified the effect of individual trees on understory vegetation. Previous studies have used regression analyses (e.g., generalized linear models; Noguchi and Yoshida 2004) or multivariate analyses (e.g., canonical correspondence analysis or redundancy analysis; van Oijen et al. 2005; Chavez and Macdonald 2010) to examine the effects of overstory trees on understory vegetation. However, such analytical methods only accept explanatory variables expressed at a stand level (e.g., stand BA and dominant species) or on a tree fall gap versus closed-canopy basis (e.g., gap size), and, thus, cannot be applied for individual-level analysis. In contrast, our approach based on neighborhood analysis successfully quantified the effect of individual trees on the understory vegetation under varying conditions of DBH, distance, and species (Fig. 6).

Influence of the neighbor tree's DBH, distance, and species on competitive effects

The model selection results supported our hypothesis that the influence of a neighbor tree's DBH on its competitive effect (I_j) follows a single-peak pattern (model 5, Table 1). The I_j value of trees located 1 m from dwarf bamboo peaked at a 33.0 cm DBH and decreased thereafter (Fig. 4). An analysis of allometric equations for the major tree species at our study site (Tatsumi et al. 2012) showed that DBH was strongly correlated with crown size and crown position (the height of the lowest live branch) and that for most species, the crown position moves higher even after the DBH reaches 33.0 cm. As we originally hypothesized, this increase in the distance between the tree crown and the forest floor might decrease the effect of large trees. Although previous studies have used stand BA to examine the effects of stand structure on dwarf bamboo (Ishibashi 1998; Noguchi and Yoshida 2004), our results indicate that the use of such measures, which increase monotonically with the size of the component trees, could be misleading in some cases.

Based on the results for neighbor tree DBH, we hypothesize that dwarf bamboo is affected more strongly by aboveground competition than by belowground competition. If belowground competition were the dominant factor, the competitive effect of neighbors would have increased monotonically with increasing

DBH, because DBH is generally strongly correlated with root biomass (Drexhage and Colin 2001). There are two possible reasons why aboveground competition exerted the dominant control. One is that our study site is relatively rich in precipitation and soil nutrients, suggesting that neither would be limiting for plant growth. Another is related to the physiological traits of dwarf bamboo as a clonal species; that is, each culm is physiologically integrated with many other culms, and water and nutrients can be translocated from one culm to another through their rhizomes (Saitoh et al. 2002). We observed patches with dense and tall culms even in environments where belowground competition is likely to be high (i.e., near trees with a very large DBH), possibly because these culms were supported by translocation of belowground-derived resources from more favorably located patches.

The effect of individual trees decreased with increasing distance to the dwarf bamboo (Fig. 4). However, compared with the decrease in the competitive effects among trees ($\gamma_3 = -0.373$; Tatsumi et al. 2013), the decrease found in the present study was gentler ($\gamma_3 = -0.307$; Table 2), irrespective of the tree's DBH. This finding likely reflects the fact that the average distance between the tree crown and the forest floor is greater than the distance among tree crowns, and, thus, the effect of individuals would have a larger spatial extent. On the other hand, the peak of I_j shifted to larger DBH with increasing distance (Fig. 4). This result supports our original hypothesis that because trees with larger DBH generally have wider crowns, they are capable of exerting their effects over a broader area and, therefore, the relative influence of larger trees increases with increasing distance.

Our results showed that the difference in the competitive effect between conifers and broad-leaved trees, which was found in previous stand-level studies (Ishibashi 1998; Noguchi and Yoshida 2005), was also evident at an individual-tree level (Fig. 5). Conifers exerted an average of 7.2 times the I_j of broad-leaved trees. Because dwarf bamboo maintains photosynthetic activity from early spring to late autumn, the species is capable of significant carbon uptake during the period when deciduous broad-leaved trees are leafless (Lei and Koike 1998). Evergreen conifers probably exerted greater competitive effects because they shade dwarf bamboo throughout the year (Noguchi and Yoshida 2004, 2005). The difference between evergreen conifers and deciduous broad-leaved trees might also have resulted from the fact that the conifers generally have a larger leaf area ratio, defined as the total leaf area per unit leaf mass (Cannell 1989), and, thus, cast deeper shade. Another possible reason is that evergreen conifers have smaller throughfall rates in winter (i.e., they intercept more snow) than deciduous broad-leaved trees (Noguchi and Nishizono 2010). Snow cover protects dwarf bamboos, which are perennial evergreen species, from low temperatures in winter (Usui 1961). The fact that individual conifers have a shallower snow depth under their canopies might have contributed indirectly to their high competitive strength.

Our results showed that the difference in competitive effect extended to the species level (Fig. 5). The interspecific difference likely resulted from a species' shade tolerance and phenological traits. In terms of shade tolerance, *Taxus cuspidata*, which exerted the largest competitive effect, is the most shade-tolerant species in our study area (N. Kimura, University of Tokyo Hokkaido Forest, personal communication (2013)); in contrast, *M. obovata* and *Betula* spp., which exerted the smallest and second smallest effects, respectively, were the two least shade-tolerant species (Tatsumi et al. 2012). This trend is consistent with previous findings in northeastern North America, where species with higher shade tolerance tend to have a lower level of crown openness and, thus, create deeper shade (Canham et al. 1994; Beaudet et al. 2002). In terms of phenological traits, *M. obovata* and *Kalopanax pictus* (Thunb.) Nakai, which exerted the smallest and fourth smallest effects, respectively, have a relatively late leaf-flush season (Kimura et al. 1995), and *Prunus ssiroi* Fr. Schm., which exerted the third smallest

effect, has a relatively early defoliation season (N. Oikawa, University of Tokyo Hokkaido Forest, personal communication (2013)). We hypothesize that the small competitive effects of these broad-leaved species derived at least in part from their lack of shade for dwarf bamboo in the early spring and late autumn.

The three most dominant species (*A. sachalinensis*, *Tilia* spp., and *Acer mono*) exerted average levels of competition within the conifers and the broad-leaved trees (Fig. 5). On the other hand, subdominant species such as *Taxus cuspidata*, *P. jezoensis*, *S. obassia*, and *M. obovata* exerted remarkably different levels of competition from the other conifers and broad-leaved trees. Previous studies typically focused only on the effect of dominant species on understory vegetation (van Oijen et al. 2005; Barbier et al. 2008; Chavez and Macdonald 2010). However, our results indicate that accounting for both the dominant species and the subdominant species would offer deeper insights into the effect of species composition on understory vegetation.

Effect of individual trees on dwarf bamboo and recruitment

The per capita effect of individual trees (I_j) varied widely in response to changes in DBH, distance, and species (Fig. 6). The culm density and culm height of dwarf bamboo both decreased steeply in response to increasing NCI (Fig. 7), which is the sum of the I_j values. Iwamoto and Sano (1998) examined the relationship between tree seedling density and what they called the “dwarf bamboo mass index”, which equaled the culm density (culms·m⁻²) multiplied by the culm height (cm), and found significantly fewer seedlings in quadrats with a mass index > 3000. The mass index of 3000 approximately corresponds to an estimated NCI of 4.4 in this study ($\exp(\alpha_0 + 4.4\alpha_1) \times \exp(\beta_0 + 4.4\beta_1) = 3001.8$, see eqs. (3) and (4)). Because trees with a very large DBH and broad-leaved trees had remarkably small I_j values (Fig. 6), the aggregate of such trees would likely be unable to meet the NCI = 4.4 condition within a limited spatial extent. We, thus, hypothesize that small- to mid-sized conifers may be the key components for ensuring continual tree recruitment at our study site. However, this hypothesis requires careful examination because overstory trees with an NCI > 4.4 can suppress not only dwarf bamboo but also tree recruitment. To comprehensively understand the interactions among overstory trees, dwarf bamboo, and tree recruitment, further study that separately quantifies the impacts of the following mechanisms will be needed: (i) the direct negative effects of overstory trees on tree recruitment and (ii) the indirect positive effects (i.e., indirect facilitation; Callaway 2007) of overstory trees on tree recruitment via the suppression of dwarf bamboo.

Further model development

The selected model provided a good fit to the culm density and height data (Fig. 3). However, the predicted values were somewhat underestimated, especially at high density and at high height levels, which indicates that there is potential for improvement. Most importantly, we did not include topographic factors in the model even though topography is an important predictor of dwarf bamboo attributes (Ishibashi 1998; Noguchi and Yoshida 2005). In addition, we did not account for temporal variation in the attributes of the dwarf bamboo or the trees, even though this variation is especially pronounced in dwarf bamboo species, which also exhibit a phenomenon in which they wither synchronously once in a period of several decades (Nakashizuka 1988; Abe et al. 2002). The effects of topography and temporal variation were not included in the model because we focused on the effects of individual trees in this study. However, incorporating these variables into the current model would likely expand its spatial range of applicability and improve its prediction accuracy. Also, because of limitations in our data, we could use only DBH as an explanatory variable to express the difference in stem size. However, because attributes such as tree height can also affect shading, such data

should be collected during future research and incorporated into our model.

Conclusion

Our results confirmed that NCI enables explicit modeling and flexible hypothesis testing for the effects of individual trees on understory vegetation. Although our study was conducted in a single area, using a single understory species (*S. senanensis*), and predicted limited attributes of the species (density and height), we believe that our analytical approach can be readily adapted to other individual-level studies. For example, a previous stand-level study indicated that pruning intensity indirectly affected understory vegetation by altering the relationship between DBH and crown size (Chen 2008); such a hypothesis could be tested at an individual-tree level by adding a term for the interaction of pruning intensity with DBH. Further modifications of NCI may help to reveal the underlying mechanisms specific to certain forest types, understory species, and management regimes.

Our analytical approach follows a recent trend in forest dynamics modeling in which a spatially explicit individual-based approach is becoming commonplace (Pacala et al. 1996; Kubo and Ida 1998; Thorpe et al. 2010b; Yasuda et al. 2012). Such forest dynamics models, however, have typically failed to incorporate the presence of understory vegetation (Royo and Carson 2006). Even when a model incorporated this vegetation, the density and height of the understory vegetation were assumed not to change in response to changes in the characteristics of the overstory trees (Kubo and Ida 1998; Yasuda et al. 2013). Such inaccuracies will likely result in biased prediction of the germination rates and growth and survival of seedlings (Royo and Carson 2006). We expect that incorporating the results of the present study into a spatially explicit individual-based forest dynamics model would improve the model's accuracy and our understanding of the effect of understory vegetation on overall forest dynamics.

The effects of individual trees on understory vegetation that were revealed by our study have particular relevance for forest management. For example, in mixed conifer–broadleaf forests on Hokkaido, single-tree selection has been widely conducted since the early 20th century (Noguchi and Yoshida 2004). The removal rates at each harvesting entry have been determined on a stand-by-stand basis (Tatsumi et al. 2012). However, our results indicate that even if the removal rate is homogeneous throughout the stand, the response of dwarf bamboo (and thus of tree regeneration) to harvesting would vary dramatically depending on the sizes, species, and spatial configuration of the harvested trees. Accounting for the characteristics of individual trees would likely lead to improvements of the management systems that are used in forests where the understory vegetation plays an important role in stand dynamics.

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