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Spatial pattern of post-fire forest succession in Central Kamchatka, Russia

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Fire is a natural component of vegetation dynamics in boreal forests. However, in Far East Russia, socio-economic changes following the dissolution of the Soviet Union have resulted in increased incidences of human-caused forest fires. Here, we compared the species composition and stand structure among three forest stands at various stages of recovery after fires in Central Kamchatka, to infer how intraspecific differences in regeneration strategies and subsequent patterns of survival affect post-fire forest succession. At 2 years after a fire, sprouted stems of *Populus tremula* and *Betula platyphylla* were clustered according to their modes of sprouting; root suckers at the 3-m scale, and stump sprouts at the 0.5-m scale, respectively. At 40 years after a fire, stems of *Larix cajanderi* originating from seeds were clustered at an 8-m scale. At 200 years after a fire, clumps of *B. platyphylla* and *L. cajanderi* were both randomly distributed and the clumps of *B. platyphylla* were maintained by sprouting. Bray-Curtis ordination analyses suggested that there may be multiple pathways of post-fire succession depending on the relative survival rates of *P. tremula* and *B. platyphylla*. If fire-return intervals become shorter in Central Kamchatka because of more frequent human-caused fires, the population size of *L. cajanderi* will decrease and early successional forests comprising *P. tremula* and *B. platyphylla* will dominate the landscape. On the other hand, if fires are suppressed, late-successional forests comprising *L. cajanderi* and *B. platyphylla* will dominate the landscape.

キーワード：森林火災，更新，空間解析，萌芽，植生動態

forest fire, regeneration, spatial analysis, sprouting, vegetation dynamics

ロシア，カムチャッカ中央部における 火災後の植生遷移の空間パターン

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北方林において森林火災は重要な自然かく乱であるが，極東ロシアにおいては，ソ連邦崩壊後の社会経済情勢に変化により，人為的な森林火災が増加している．本研究では，カムチャッカ半島中央部において火災後の植生回復年数が異なる 3 か所の林分で調査を行い，構成種による生存率と更新様式の違いが火災後の植生遷移にどのように影響するかを考察した．火災後 2 年目の林分では，*Populus tremula* と *Betula platyphylla* がそれぞれの更新様式（根萌芽および幹萌芽）に応じて，3 m および 0.5 m のスケールで集中分布していた．火災後 40 年目の林分では，種子由来の *Larix cajanderi* が 8 m のスケールで集中分布していた．火災後 200 年目の林分では，*B. platyphylla* の株と *L. cajanderi* がともにランダム分布しており，*B. platyphylla* の萌芽は個体群の更新・成長ではなく株の維持を担っていた．Bray-Curtis 法による解析の結果から，火災後の *P. tremula* および *B. platyphylla* の相対的な生存率の違いによって，二次遷移の方向性が異なる可能性が示唆された．今後，カムチャッカ半島において人為による火災頻度が高くなれば，*P. tremula* および *B. platyphylla* が優占する遷移初期の森林が拡大し，*L. cajanderi* の個体群は減少すると考えられる．一方，火災が抑制されれば，*L. cajanderi* および *B. platyphylla* が優占する遷移後期林が拡大するだろう．

1. Introduction

Forest fire is an important component of vegetation dynamics in boreal forests (Bradshaw et al., 2009; Drobyshev et al., 2014; Flannigan et al., 2009). In Far East Russia, socio-economic changes following the dissolution of the Soviet Union have resulted in increased incidences of human-caused forest fires (Mollicone et al., 2006). On the Kamchatka Peninsula, which is located in the eastern-most part of the Russian Federation, several hundred hectares of boreal forest burn every year. Although forest fires have likely been an inherent component of vegetation dynamics in Kamchatka (Eichhorn, 2010), the impact of human-caused fires on future vegetation dynamics is difficult to predict.

Vegetation recovery (secondary succession) following forest fire can vary depending on the intensity of the fire and the extent of the burned area (Kasischke and Stocks, 2000). These factors affect the survival and regeneration of tree species and determine the subsequent pattern of secondary succession. In Central Kamchatka, the driest region of the Peninsula, late-successional forests are dominated by *Picea ajanensis* and *Larix cajanderi*, while early-successional forests comprise *Betula platyphylla* and *Populus tremula* (Eichhorn, 2010; Kojima, 1994). The two coniferous species regenerate by seed, while the broad-leaved trees regenerate by both seed and sprouting. *B. platyphylla* regenerates from stump sprouts, while *P. tremula* regenerates from root suckers (Homma et al., 2003). Thus, we can expect the spatial distribution of species in a post-fire forest to reflect their respective regeneration strategies. In this study, to infer how species differences in regeneration strategies and subsequent patterns of survival affect post-fire forest succession, we compared species composition and stand structure among three

forest stands at different stages of recovery after fire in Central Kamchatka.

2. Study Site and Methods

The study was conducted during 2000 to 2001 in a natural forest in the Central Kamchatka Depression (56°04'N, 160°01'E, 70 m a.s.l., Figure 1). This region is in the driest biogeoclimatic zone in the province (Krestov, 2003). See Homma et al. (2003) for details regarding the study site. We established three study plots in stands at various stages of recovery after fire. The youngest stand (plot size = 100 × 100 m) was burned 2 years before the study. The mid-seral stand (plot size = 50 × 100 m) was burned ca. 40 years before the study. The oldest stand (plot size = 50 × 100 m) was burned more than 200 years before the study. All plots had generally flat topography. The stand ages were estimated using increment cores.

We measured the diameter at breast height (DBH) of all aboveground stems taller than 1.3 m in height. In the 2-yr plot, we measured all standing dead trees. We mapped the position of the base of each stem within the plot using a surveying compass (S-25, Ushikata Co. Ltd., Yokohama, Japan). We also counted the number of saplings (seedlings and sprouts < 1.3 m height) of *P. tremula*, *B. platyphylla*, and *L. cajanderi* in each plot (Figure 2).

3. Data Analysis

The species composition and stand structure of the three plots were compared using a multi-variate Bray-Curtis ordination analysis (Beals, 1984), which allows a visual comparison of the relative position of each plot along a successional gradient. Both the abundance and basal area of the component species were used in the analysis. The horizontal spatial

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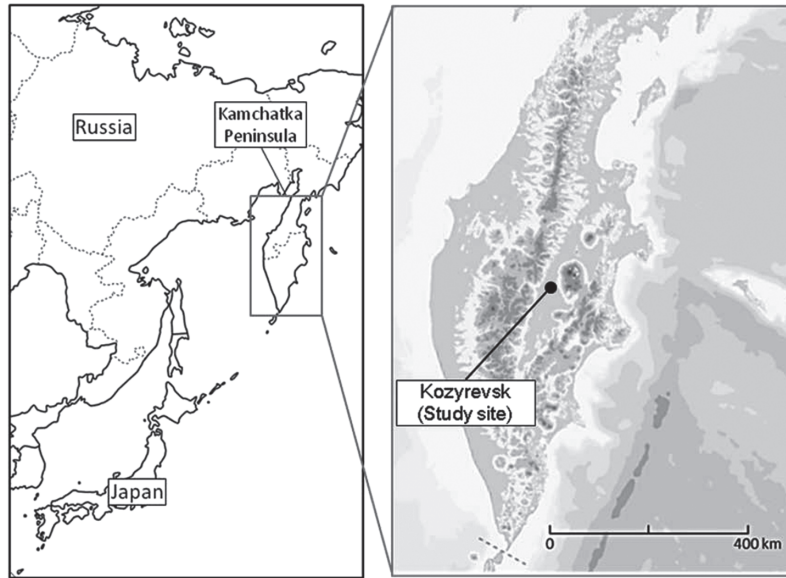


Figure 1 : Location of study site in Central Kamchatka, Russia. Map data were obtained from www.freemap.jp and Geospatial Information Authority of Japan website.

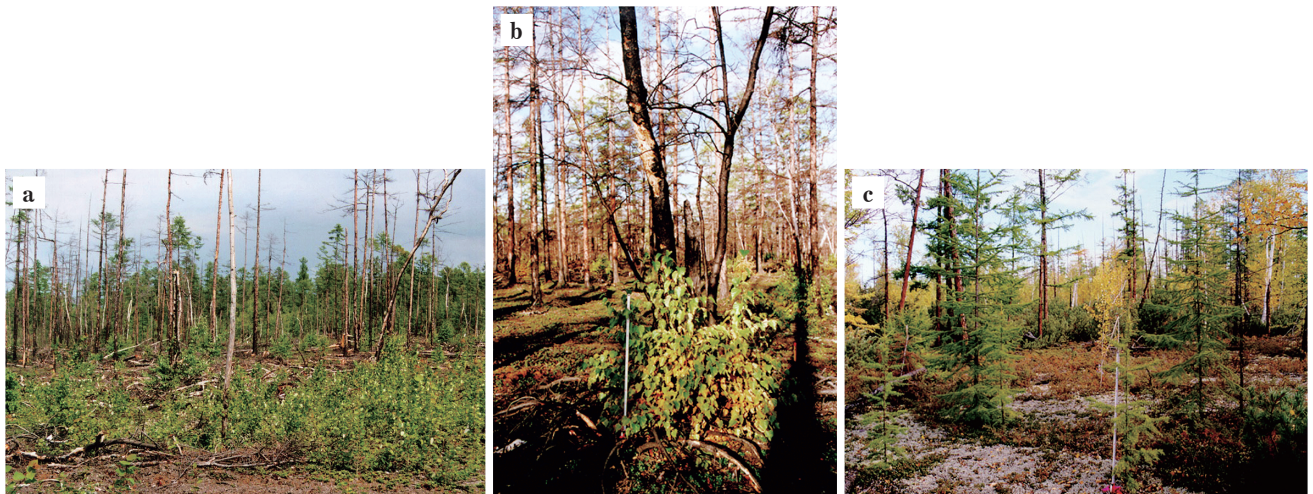


Figure 2 : Regeneration patterns of three study species in forest plots with different time intervals since last fire in Central Kamchatka: (a) mother tree and root suckers of *Populus tremula* 2 years after fire; (b) mother tree and stump sprouts of *Betula platyphylla* 2 years after fire; and (c) seedlings of *Larix cajanderi* 40 years after fire.

distribution of aboveground stems was analyzed using the L -function, which is a square-root transformation of Ripley's K -function (Freeman and Ford, 2002; Loosemore and Ford, 2006; Ripley, 1979).

$$L(r) = \sqrt{\frac{K(r)}{\pi}} - r. \quad (1)$$

where, r denotes distance between trees. $L(r)$ can be used to test whether an observed spatial point pattern is spatially random ($L(r) = 0$), clustered ($L(r) > 0$), or regular ($L(r) < 0$). In addition, $L(r)$ can be used to infer the spatial scale (e.g., cluster size) of the observed pattern. For *P. tremula*, adult trees and new sprouts (newly emerged in 2000) were analyzed separately. For *B. platyphylla*, stems and clumps (spatially clustered aboveground stems connected by a common root system) were analyzed separately. The

spatial analysis was conducted using the spatial statistics package in S-PLUS 2000 (MathSoft, Seattle, WA, USA). To calculate confidence intervals for $L(r)$, we generated 99 randomized realizations of the trunks in each plot.

4. Results and Discussion

In the 2-yr plot, 82% of the trees had died as a result of fire (Table 1). The mortality rates of *P. tremula* and *B. platyphylla* were high, while nearly half of the individuals of *L. cajanderi* had survived the fire. We expect that, before the fire, the stand structure of the 2-yr plot was similar to that of the 200-yr plot. The total stem density (live + dead trees) was much lower in the 2-yr plot than in the 200-yr plot, suggest-

Table 1 : Species composition of three study plots in the Central Depression, Kamchatka Peninsula, Russia.

Species	2 years since last fire		40 years since last fire		200 years since last fire	
	Density (ha ⁻¹)	Basal area (m ² ha ⁻¹)	Density (ha ⁻¹)	Basal area (m ² ha ⁻¹)	Density (ha ⁻¹)	Basal area (m ² ha ⁻¹)
<i>Populus tremula</i>	3 (28)	0.04 (0.09)	132	0.02	6	0.01
<i>Betula platyphylla</i>	29 (429)	0.16 (0.63)	690	2.11	241	1.08
<i>Larix cajanderi</i>	119 (235)	4.77 (5.41)	556	6.40	698	22.09
<i>Alnus fruticosa</i>			52	0.40	46	0.07
<i>Sorbus kamchatica</i>			8	0.004	5	0.010
<i>Salix bebbiana</i>			4	0.005	4	0.006
Total	151 (693)	4.97 (6.12)	1450	8.93	1296	23.27

Figures in parentheses indicate stems that had died as a result of fire.

ing that many small trees had burned completely in the fire. Because we could not account for this, the mortality rates are likely to be much higher than those estimated here. The 40-yr plot was dominated by *B. platyphylla* and *L. cajanderi* in terms of basal area. Although there were many stems of *P. tremula*, its total basal area was relatively small. The 200-yr plot was dominated by *L. cajanderi*. The number of stems and basal area of *B. platyphylla* in the 200-yr plot were approximately half those in the 40-yr plot. There were only three individuals (> 1.3 m) of *P. tremula* in the 200-yr plot. The size-distributions of the three plots indicated that, before the fire, the stand structure of the 2-yr plot was similar to that of the 200-yr plot (Figure 3). In contrast, all three species showed positively skewed size distributions in the 40-yr plot, reflecting successful regeneration.

The number of saplings (seedlings and sprouts < 1.3 m height) of *P. tremula* and *B. platyphylla* was an order of magnitude greater in the 2-yr plot than in the other two plots (Figure 4). Saplings of *L. cajanderi* (all single-stemmed seedlings) were most abundant in the 40-yr plot. There was very little regeneration in the 200-yr plot, with the exception of stump sprouts of *B. platyphylla*. The number of *B. platyphylla* stems per clump, however, was higher in the 2-yr plot than in

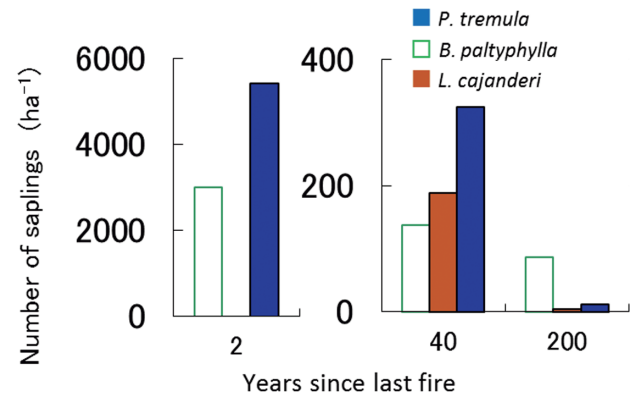


Figure 4 : Number of saplings (seedlings and sprouts < 1.3 m high) of three study species in forest plots with different time intervals since last fire in Central Kamchatka.

the 200-yr plot, indicating that clump growth had slowed and the clumps were maintained by sprouting (Figure 5).

The Bray-Curtis ordination analysis based on abundance (number of stems) indicated that the 40-yr plot did not fall in between the 2-yr and 200-yr plots (Figure 6). This suggests that there may be multiple pathways towards old-growth species composition, and that these pathways may depend on the intensity of the fire and the subsequent survival of the three study species. In this study, many individuals of *L. cajanderi* had survived the fire in the 2-yr plot,

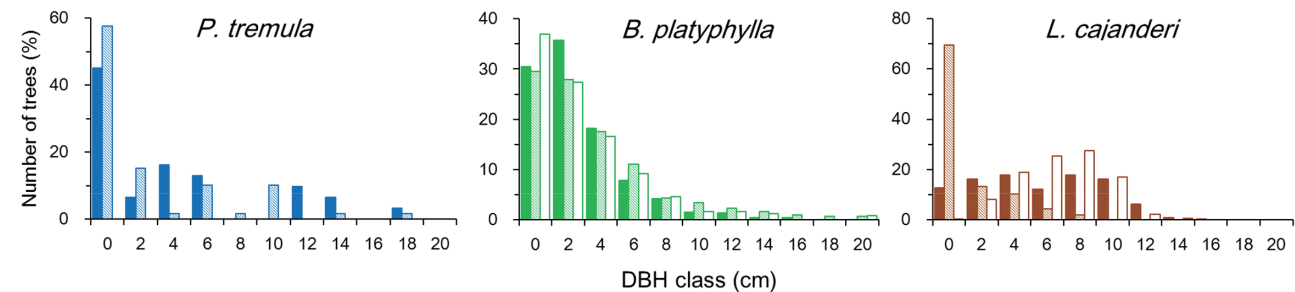


Figure 3 : Size structure (relative frequency distributions) of three study species in forest plots with different time intervals since last fire in Central Kamchatka. Note variations in axis ranges among species. Filled, hatched, and open bars show data from 2-, 40-, and 200-year plots, respectively. Number of trees in the 2-yr plot includes both live and dead trees.

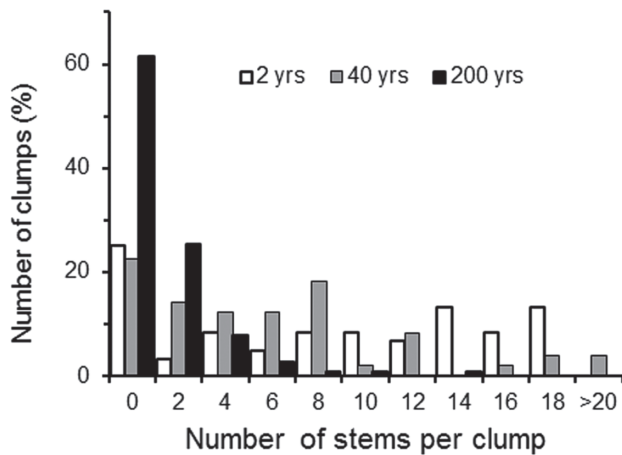


Figure 5 : Relative frequency distribution of number of stems per clump of *Betula platyphylla* in forest plots with different time intervals since last fire in Central Kamchatka.

although seedlings were not yet present. In contrast, seedlings of *L. cajanderi* were abundant in the 40-yr plot, suggesting that surviving trees act as seed sources and contribute to regeneration of *L. cajanderi* some years after fire. Several individuals of *B. platyphylla* also survived the fire and regenerated by stump sprouting in both the 2-yr and 40-yr plots. After a more intense fire, the mortality rates of *B. platyphylla* and *L. cajanderi* may be higher and the subsequent regeneration rate of *B. platyphylla* by stump sprouting may be lower. Below-ground roots of *P. tremula*, on the other hand, are likely to survive intense fires and the post-fire stand may be dominated by *P. tremula* root suckers. The basal-area based analysis indicated a uni-directional change from the 2-yr toward the 200-yr plot via the 40-yr plot. This was likely driven by the continuous increase in the relative basal area of *L. cajanderi* with increasing stand age.

In the 2-yr plot, surviving trees of *P. tremula* were clustered at a 7-m scale, reflecting the patchy pattern of survival after fire (Figure 7). The newly sprouted stems of *P. tremula* were clustered at a 3-m scale,

reflecting the spatial spread of the root system of the mother trees. In the 40-yr plot, the adult trees and sprouts of *P. tremula* were clustered at 3-m and 2-m scales, respectively. These results suggest that while some self-thinning occurs, sprouting of *P. tremula* continues into mid-seral stages at a relatively constant spatial scale. In all three plots, stems of *B. platyphylla* were tightly clustered at 0.5-m to 1-m scales, indicating that they originated as stump sprouts from a single mother tree. The clumps of *B. platyphylla*, however, were randomly distributed in all three plots, suggesting that there had been random mortality or additional recruitment by seed following fire. *L. cajanderi* was clustered at a 12-m scale in the 2-yr plot, reflecting the patchy spatial pattern of survival after fire. In the 40-yr plot, *L. cajanderi* was clustered at an 8-m scale, suggesting that there had been clump mortality and additional recruitment by seed. In the 200-yr plot, however, there was a random spatial distribution of *L. cajanderi*, although we expected a regular distribution as a result of self-thinning. This may have resulted from the long-term survival of *B. platyphylla* clumps, which were randomly distributed and maintained by continuous sprouting.

Our results suggest that, although *P. tremula* and *B. platyphylla* are both able to regenerate quickly after fire by sprouting, their relative survival rates could result in multiple pathways of post-fire succession. The species composition and size structure of the 40- and 200-yr plots suggested that if fire intervals exceed 40 years, the abundance of *P. tremula* will decrease markedly. In contrast, *B. platyphylla* is able to survive for more than 200 years by sprouting continuously. Because it takes some years for *L. cajanderi* to establish by seed, if the intervals between fires become shorter in Central Kamchatka due to the frequent occurrence of human-caused fires, the population size of *L. cajanderi* will decrease and early

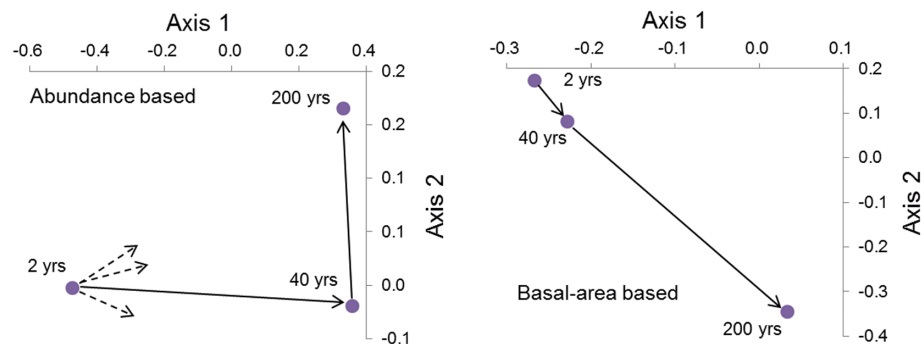


Figure 6 : Bray-Curtis ordination based on abundance and basal area of tree species in forest plots with different time intervals since last fire in Central Kamchatka. Broken arrows indicate multiple pathways of succession after fire.

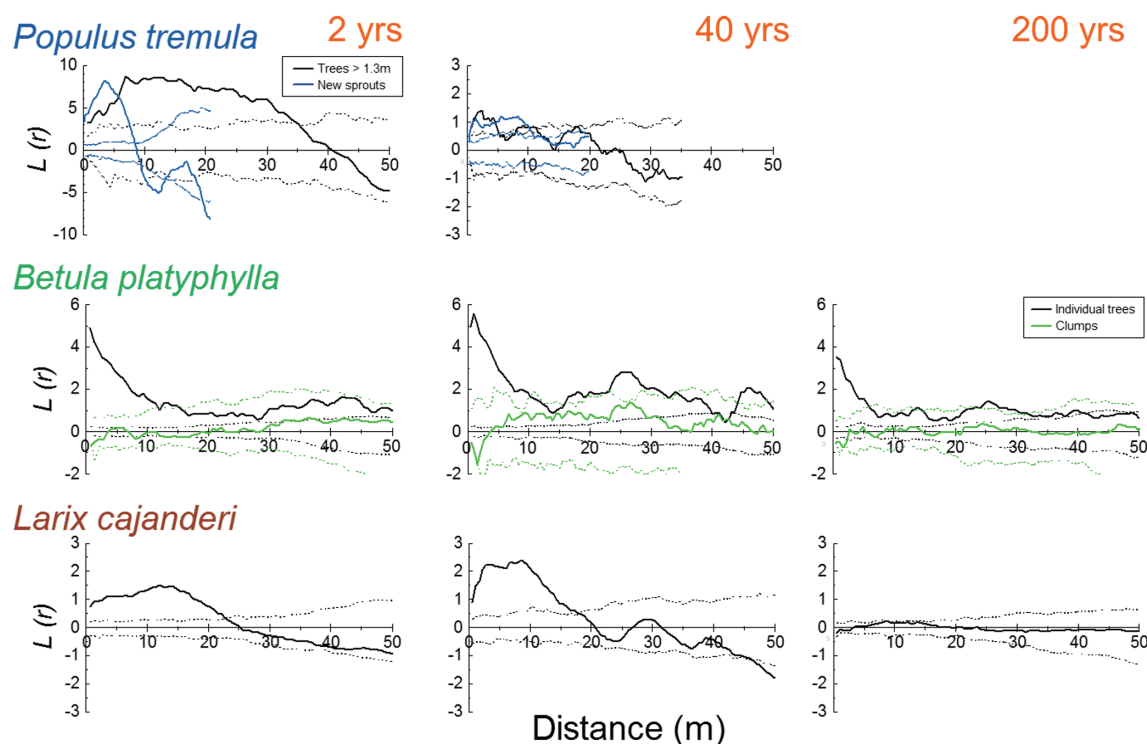


Figure 7 : Results of spatial distribution analysis of three study species in forest plots with different time intervals since last fire in Central Kamchatka. Broken lines indicate 99% confidence envelope for $L(r)$. Distance (r) where observed distribution goes above or beyond confidence envelope indicates scale of clustering and inhibition, respectively.

successional forests comprising *P. tremula* and *B. platyphylla* will dominate the landscape. On the other hand, if fires are suppressed, late-successional forests comprising *L. cajanderi* and *B. platyphylla* will dominate the landscape.

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