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Comparisons of recruitment, survival and growth in invasive and native saplings on a volcano

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Abstract

We monitored the recruitment, survival and growth of tree saplings on invasive (*Larix kaempferi*) vs native species (*Betula* and *Populus*) using 16 20 m × 20 m plots established along elevation gradient on the volcano Mount Koma, Japan, for seven years, because the sapling behaviors should determine forest structures. The crowding of overstory consisting mostly of *Larix* decreased with increasing elevation. *Larix* recruits were conspicuous, particularly at middle elevation where overstory crowding was intermediate, while *Betula* recruits were least. *Larix* overstory crowding inhibited the recruitment of all the taxa, although intermediate crowding promoted the recruitment of *Larix*. The restriction of sapling emergence was conspicuous at lower elevation where the overstory crowding was highest, probably because of shading, and/or competition with overstory trees. Sapling recruitment for all taxa was restricted at higher elevation, due to high stresses derived from direct solar radiation and strong wind without overstory. The survival percent of saplings was 96% for *Larix* and *Betula*, while it was ca 50% for *Populus*. *Larix* overstory decreased the survival and growth of all the taxa, except *Larix* survival and *Betula* growth. The results implied that *Larix* could establish by high survival once the recruits succeeded everywhere and native sapling regeneration was restricted by *Larix* overstory. Strong recruitment, survival, and growth of *Larix*, together with resistance to overstory crowding, enables it to dominate and persist in such disturbed areas regardless of the canopy closure.

1. Introduction

Forest regeneration is often modified by invasion of exotic species after disturbances (Levine et al. 2003; Wearne and Morgan 2004), and the clarification of dynamics on biological invasions is essential for understanding the mechanisms of forest regeneration (Levine et al. 2003). Invasive species exhibiting higher dominance than native species have high seed germination, seedling establishment, sapling growth, and reproduction (Rejmánek and Richardson 1996; Myers and Bazely 2003; Gómez-Aparico et al 2008). Since the sapling stage is decisive to determine forest dynamics, this stage should be a focus for study of forest ecosystem invasion (Clark et al. 1999; Rooney et al. 2000).

The recruitment, growth and survival of saplings are key determinants of sapling dynamics (Kobe 1999; Nathan and Ne'eman 2004). However, there have been few long-term studies on sapling recruitment, survival and growth for native vs. invasive plants (Yurkonis and Meiners 2004), although this is a prerequisite for clarifying mechanisms how biological invasions affect plant community dynamics (Clark et al. 1999; Rooney et al. 2000). Overstory trees suppress sapling regeneration via above- and below-ground competition (Levine et al. 2003; Yurkonis and Meiners 2004; Kueffer et al. 2007), and the suppression acts differently between species (Dullinger et al. 2005). Furthermore, low susceptibility of invasive saplings to suppressions by their parental overstories is a plausible mechanism to explain how invasive plants alter community composition (Reinhart et al. 2006a, b). Here, we evaluate the effects of overstory trees on the recruitment, growth and survival of both invasive and native saplings.

Three *Larix* species, *L. kaempferi*, *L. decidua* and *L. × manchlinsii* (synonym *L. decidua* × *kaempferi*), have naturalized in various regions of the world (Richardson and Rejmánek 2004), although there has been disagreements about mechanisms of invasion. On Mount Koma, northern Japan, biological invasion by *L. kaempferi* is conspicuous and has been modifying the landscape, but this species has not yet dominated the summit (Kondo and Tsuyuzaki 1999). Higher elevation restricts the growth and establishment of trees by decreasing air temperature, shortening growth period, increasing wind intensity (Šrutek and Lěps 1994).

Therefore, the elevational gradient is the best surrogate to investigate multiple changes in air temperature, growth period and wind intensity, so as to understand biological invasions in mountainous areas. Here, we evaluate differences in recruitment, survival and growth of saplings between invasive and native trees with reference to the influence of *Larix* overstory. We hypothesized that 1) the recruitment, survival and/or growth of invasive *L. kaempferi* saplings are higher than those of native tree saplings, in particular, under dense overstory, because competition between overstory and sampling and/or overstory shading influence the native species more than invasive species. 2) *L. kaempferi* saplings invade low-covered areas faster than native trees by utilizing its higher recruitment, survival and/or growth. 3) Consequently, *L. kaempferi* precludes native trees during sapling stage in bare grounds and areas covered with *L. kaempferi* overstory.

2. Study area and methods

2.1. Study area and materials

Mount Koma is an andesite stratovolcano located in southwest Hokkaido, Japan (42°02'N, 140°40'E). Complete deforestation occurred by its catastrophic 1929 eruption. A few eruptions subsequent eruptions did not damage the south slope (Akasaka and Tsuyuzaki 2005). A depressed treeline of *Betula ermanii* Cham. and *Alnus maximowiczii* (Call.) Hult. developed at 800-900 m elevation before the 1929 eruption, but a treeline is not yet well developed presently. Furthermore, over 56% of the surface area is still not covered by any vegetation at elevation above 505 m (Akasaka and Tsuyuzaki 2005). *Salix reinii* forms shrub patches less than 50 cm high with low cover, and patches formed by the other species are shorter than *S. reinii* patches (Uesaka and Tsuyuzaki 2004). Therefore, light competition between shrubs and trees should favour trees when the saplings overtop the shrub patches. Nutrients competition remains between shrub and trees but do not discuss this because total seedling biomass of *L. kaempferi* and *B. ermanii* seedlings less than 30 cm high did not differ between bare ground and *S. reinii* patches (Akasaka and Tsuyuzaki 2005). In the present study, therefore, the interactions between shrubs and trees are not examined to inspect the relationships between overstory trees and samplings (> 30 cm in height). At present a non-native deciduous conifer,

Larix kaempferi, has the highest relative dominance on the south slope. Its seeds have invaded from plantations at the foot of the mountain that were established after 1953 (Kondo and Tsuyuzaki 1999). The high seed germination and morphological plasticity of seedlings < 30 cm in height of *L. kaempferi* promote the invasion (Akasaka and Tsuyuzaki 2005). The original northern limit of *L. kaempferi* is 450 km south of Mount Koma. Common native tree species on this mountain are all in the members of two genera, *Betula* and *Populus*. There are three species of *Betula*, *B. platyphylla* Sukatchev var. *japonica* (Miq.) Hara, *B. ermanii* Cham., and *B. maximowicziana* Regel, and are two species in *Populus*, *P. sieboldii* Miq. and *P. maximowiczii* Henry (Tsuyuzaki et al. 2000). *Betula* and *Populus* were common in naturally-regenerated secondary forests at 300-505 m elevation (Nishi and Tsuyuzaki 2004). Nomenclature followed Ohwi (1975).

Climate is categorized as warm-cool temperate. From 2003 to 2005, mean annual temperature was 8.1°C with a maximum of 30.4°C in August and a minimum of -12.7°C in January (Mori Climatological Observatory, 10 m a.s.l., ca 9 km northwest from the summit). Annual precipitation is 1092 mm, and snow-free period is from May to October.

2.2. Plot survey

To quantify the characteristics of saplings between invasive and native taxa, 16 20 m × 20 m plots were established on the south slope between 546 m and 830 m elevation. The first census was conducted in the fall of 1997, after tagging all trees ≥ 0.3 m in height. We recorded species, height and diameter at breast height (DBH) if saplings were ≥ 1.3 m in height. The locations of all tagged stems were recorded on 1-m meshed lattice grids. The second and third censuses were made in the fall of 2000 and in the early spring of 2004, respectively. All the surveys were conducted when the trees had dropped their leaves. The same measurements with the first census were made on the second and third censuses, and the diameter at 10% of height on stems ≤ 1.3 m in height was additionally measured. When a stem that was more than 0.3 m in

height at the previous census became shorter than 0.3 m, we recorded if the tree was alive or dead. Basal areas at breast height on the stems of overstory trees were calculated from DBH.

Stems > 1.3 m in height were considered to be overstory trees, saplings had stems between 0.3 m and 1.3 m. All the stems < 0.3 m in height were treated as seedling. Age was evaluated for 90 *L. kaempferi* seedlings, confirming that they were ≤ 10 year old (Akasaka et al. 2007). Small saplings of *Betula* and *Populus* were not always identified to species at the first census. Thus we grouped species by genera, i.e., using three taxa, *Larix* (1 species), *Betula* (3), and *Populus* (2).

The canopy area of *L. kaempferi* is positively correlated with DBH (Kondo and Tsuyuzaki 1999), and thus basal area at breast height was used as a surrogate for crown area. To re-confirm this relationship for the evaluation of crowding effects on saplings, the long and short axes of crown and DBH of 112 *L. kaempferi* stems, that were more than 1.3 m high in the spring of 2004, were measured in the fall of 2004. The canopy area was calculated on the assumption of ellipse.

Latitude and longitude on each plot were marked by a differential GPS receiver (Trimble Pathfinder Pro XR, Sunnyvale). Elevations on the plots were calculated by the overlay of the plot locations on a digitized geographical map (scale: 1/5000) (Forest Agency of Japan, 1976), using ArcGIS (version 9.0, ESRI, Redlands).

Differences in number of recruits per plot between the two years (i.e., from 1997 to 2000, and from 2000 to 2004) and among the three taxa were examined by likelihood ratio test after Poisson regression (Fleiss et al. 2003). Differences in survival rates were compared between the two years and among the three taxa by likelihood ratio test after logistic regression.

2.3. Effects of overstory crowding

To quantify the effects of *Larix* overstory on the recruitment, survival and growth of saplings, the overstory crowding was quantified by neighborhood index (Stoll et al. 1994):

$$\text{Larix neighborhood index (LNI)} = \sum_{i=1}^N \{S_i \times (d_i + 1)^{-\alpha}\}, (\alpha \geq 1) \quad [\text{Eqn. 1}],$$

where N is the total number of overstory *Larix* stems, S_i is basal area (cm^2) of the i^{th} overstory stem within a given cutoff distance, and d_i is the distance (m) from each target sapling to i^{th} overstory stem. Alpha (α) is a parameter to qualify the distance decay of neighbor effects. We looked at α values of 0, 1, and 2. When α is 0, the equation is equivalent to $\sum_{i=1}^N (S_i)$, which means that there are no distance effects. When α is 1, the relationship declines proportionally with increasing distance. When α is 2, the relationship is inversely proportional to the square of distance. We looked at cutoff distances of 0, 1, 2, 3 and 4 m. The cutoff distance of 0 m means that the stems of *Larix* overstory established on the grid are used. We apply the LNI to express overstory crowding, because the index is made from the consideration of the effects of overstory stem sizes adjusted by distance between overstory stems and below-canopy saplings. To avoid plot-edge effects, we did not include stems from grids within 4 m from any edges of plots.

2.4. Procedures to extract significant factors on sapling establishment

We defined ‘recruit’ as stems becoming more than 0.3 m in height at the census time. The number of recruits was counted on every grid in each plot. Because the number of recruits was zero on many grids, recruitment patterns for the three taxa were examined by zero-inflated negative binomial regression analysis (Martin et al. 2005). Number of recruits is the dependent variable, and LNI, elevation, and year were independent variables for each taxon in the zero-inflated regression analysis. The final models that selected most explanatory determinants were decided by stepwise procedures with Akaike’s Information Criteria (AIC) for sapling recruitment, survival and growth (Burnham and Anderson 1998). The most explanatory radius and multiplier α on LNI in Equation 1 for each taxon was also determined by AIC.

Determinants of sapling survival for each taxon were extracted by logistic regression models. On the survival with respect to saplings between two censuses (dependent variable), four independent variables (LNI,

elevation, year and sapling height) were input into the models at the first step. Year was categorical, and survival, LNI and elevation were quantitative. Determinants of the growth rates of saplings between 2000 and 2004 for each taxon were investigated with multiple linear regression analyses, based on the stem volume that was calculated as circular cone. Relative growth rate was used as a dependent variable, and LNI and elevation were independent variables. Growth rate of each sapling was: obtained based on Schulze et al. (2005):

$$\text{Growth rate of each sapling} = [(\text{stem volume in 2004}) - (\text{stem volume in 2000})] / (\text{stem volume in 2000})$$

[Eqn. 2].

Negative growth rates were assigned as zero. The numbers of stems showing negative growth rates were 3, 21 and 18 for *Larix*, *Betula* and *Populus*, respectively. When saplings in 2000 became more than 1.3 m high in 2004, the diameter at 10% of height from the ground surface was used to calculate the growth rate for the saplings. The growth rate was log-transformed [$\log_{10}(\text{growth rate} + 0.01)$] prior to the multiple regression analyses. All statistical analyses were made with the statistical package R 2. 2.0 (R Development Core Team 2004).

3. Results

3.1. Spatio-temporal changes in tree composition

A total of 762 trees were marked in the 16 plots surveyed in 1997 (Table 1). *Larix*, *Betula* and *Populus* accounted for 28%, 24% and 39% of the total trees, respectively. The numbers of overstory stems increased annually for *Larix* but were relatively unchanged for *Betula* and *Populus*. *Larix*, *Betula* and *Populus* accounted for 64%, 22% and 11% of the stems in the overstory (Table 1). Other overstory trees recorded were *Salix bakko*, *Acer japonicum*, *Alnus maximowiczii*, *Pinus densiflora*, *Sorbus commixta*, *Cephalotaxus harringtonia*, and *Rhus trichocarpa*. *Larix* accounted for more than 90% basal area at breast height in all the plots, except one in low elevation plot, indicating that nearly all overstory crowding effects came from *Larix*.

The total number of tree stems more than 1.3 m in height and the basal area declined with increasing elevation (Fig. 1). Only A few stems of all the taxa established above 750 m elevation. Therefore, the overstory crowding effects should decline with increasing elevation, although the crowding did not decline linearly along an elevational gradient (Fig. 1). The total basal area of *Larix* increased annually at every elevation while the area of *Betula* and *Populus* fluctuated little. Mean canopy radius of *L. kaempferi* that was taller than 1.3 m in the spring of 2004 was 1.6 ± 0.7 m (mean $\pm$ SD, $n = 115$) and ranged 1.4 - 5.5 m in the fall of the year. The relationship between basal area at breast height (x) and canopy radius (y) was positively correlated ($\log y = 0.25 \log x + 3.02$, $p < 0.001$), indicating that LNI could be used as surrogate of the overstory effects.

The number of *Larix* saplings increased annually, especially from 2000 to 2004 (Table 1). In contrast, the number of *Betula* and *Populus* saplings was static. *Betula* showed the lowest number of recruits throughout the surveyed periods, while sapling mortality was $< 4\%$. The number of dead *Populus* saplings was approximately equivalent to the number of recruits. The numbers of saplings for the three taxa decreased gradually with increasing elevation in 1997 (Fig. 2). After 1997, *Larix* saplings numbers increased between 550m to 700 m in elevation, while *Populus* sapling numbers decreased in 12 plots and 8 plots of the 16 plots in 2000 and 2004, respectively. *Betula* numbers did not change greatly between years. Increase in the number of stems was mostly due to *Larix* stems, which had the highest recruitment and survival of the three taxa (Table 1). The survival rate of *Larix* was more than 98% for both intervals. The survival of *Betula* was more than 96% between each interval, while the recruitment was the lowest, i.e., ≤ 1 stems/plot. *Populus* recruited ca 4 stems/plot in the two years, and the survival was the lowest of the three taxa.

3.2. Characteristics of recruitment patterns

The best-fitting models for recruitment, survival and growth for the three taxa, had coefficient α in

equation 1 was 0 (zero) in each case (Table 2), i.e., there was no effect of distance within the cutoff distance. Because the elevation and year were constant in the regression models, the best models were selected on the basis of the LNI at different radii. The values of LNI of all three taxa were negative, demonstrating that the overstory *Larix* negatively affected the recruitment for all the taxa. Furthermore, recruitment for *Larix* and *Populus* were less frequent at lower elevation where overstory *Larix* developed well (Fig. 2). The recruitment of *Betula* was less than that of the other two dominant taxa in all the plots (Table 1). Radii adopted by the best models varied between the taxa i.e., 2 m, 4 m and 1 m for *Larix*, *Betula* and *Populus*, respectively.

The number of *Larix* and *Populus* recruits decreased with increasing elevation (Table 2). In particular, *Larix* recruited well between 640 m and 710 m in elevation, but the number of recruits decreased suddenly at 750 m and above (Fig. 2). The effect of elevation was separated from those of overstory crowding on the selected models (Table 2). Elevation did not affect the recruitment of *Betula*. The numbers of recruits of *Larix* and *Populus* differed significantly between the two intervals. The coefficient of year on number of *Larix* recruits was positive, while the coefficient on presence/absence of *Larix* recruits on grids was negative. This implied that the number of grids with recruits decreased with time, but the number of recruits increased within the grids, i.e., the recruitment of *Larix* occurred contagiously.

3.3. Sapling survival and growth

The best models did not use elevation and year to explain sapling survival for each taxon (Table 3), showing that these two factors were not of prime importance for sapling survival. Because of the high sapling survival rate varied little between plots, i.e., more than 96% in any plots of *Larix*, the survival was not explained by all the three independent variables, elevation, crowding or stem height. Survival rates of the two native taxa were affected negatively by the index of neighborhood crowding. These indicated that *Larix* overstory restricted sapling survival on native trees but did not influence *Larix* saplings. Distances between

saplings and neighborhood overstory trees affecting sapling survival differed between the two native taxa, i.e., the radius of *Populus* was 2 m and that of *Betula* was nil. Since elevation did not affect the survival rate of *Populus*, the high mortality rates were determined mostly by overstory crowding. *Populus* was suppressed with longer distance by overstory than *Betula*. For *Betula* and *Populus*, stem height at the later monitoring was positively related to the survival, indicating that larger stems survived more.

For the growth rate of *Larix* saplings, the best model selected a LNI of 4-m radius with negative effect but elevation was not included (Table 3). The distance of overstory crowding affecting *Larix* sapling growth was longer than that affecting recruitment and survival, although the crowding effect was weak, i.e., the coefficient on LNI was -0.007. On *Populus* saplings, the radius that affected growth was 2 m and LNI was negatively related to growth, independent of elevation. Therefore, the growth of *Larix* saplings was less inhibited by *Larix* overstory than that of *Populus* saplings. The growth rate of *Betula* sapling was not affected by LNI but was affected positively by elevation.

4. Discussion

4.1. Effects of overstory crowding on sapling regeneration

Overstory crowding, here expressed by LNI, often inhibits the establishment of seedlings and saplings in coniferous forests (He and Duncan 2000; Mori and Takeda 2003). LNI indicates that the extending overstory influences ≤ 2 m to *Larix* and *Populus* saplings. Since the overstory *Larix* developed horizontal stems at least 1.4 m, the sapling recruitment of *Larix* and *Populus* should be negatively affected directly by the overstory branches. While, the recruitment of *Betula* was reduced by the overstory crowding up to 4 m wide, suggesting that the mechanisms of overstory effects on the recruitment of *Betula* were not only direct interferences, but also shading and/or indirect factors. Shading did not significantly reduce growth of the sapling stage of *Larix*, because the coefficient of LNI was low ($= 0.007$). However, most seedlings under *Larix* overstory grew poorly (Akasaka and Tsuyuzaki 2005), and died within a 5-year monitoring period from

1998 to 2003 (Tsuyuzaki, unpublished data). Therefore, the effects of overstory should differ between seedling and sapling stages on *Larix*.

Plant communities maintain higher diversity in habitats under *Larix* overstories than in open habitats at high elevation on Mount Koma (Titus and Tsuyuzaki 2003). *Larix* overstory traps seeds, but inhibits growth and reduces survival of seedlings, probably by severe shading. This suggests that the effects of overstory on saplings differ from those on seedlings. *Larix*, *Betula* and *Populus* shade-intolerant (Landhausser and Lieffers 2001; Dolezal et al. 2004). The low survival and recruitment of *Populus* under *Larix* overstory suggest that *Populus* is the most sensitive of those three taxa. *Larix* can exhibit survival rate and better recruitment on moderate overstory crowding compared to any other species. Likewise, seedlings of an invasive tree *Acer platanoides* were suppressed less and were even facilitated by their parental canopies, compared with native seedlings (Reinhart et al. 2005). This difference in susceptibility was derived from higher morphological plasticity on *Acer* seedlings (Reinhart et al. 2006). For *L. kaempferi* seedlings adaptively changed their allocation pattern toward inhabited condition more than natives (Akasaka and Tsuyuzaki 2005), higher morphological plasticity may partly support higher survival rate on the sapling stage. *Larix* regenerates and persists there, even though the growth is restricted. Consequently, the modification of native plant community structure by *Larix* should intensify over time.

4.2. Sapling regeneration patterns along elevational gradient

Elevation negatively affected the recruitment of *Larix* and *Populus*. and the sapling growth of *Betula* was positively affected. The survival of all taxa was not influenced by elevation. Elevation and factors correlated to it differently affect recruitment, survival and growth of different taxa (Clark et al. 1999; Callaway et al. 2002). The plantation of *Larix* and natural forest including *Betula* and *Populus*, both of which are distributed on the foot of the Mount Koma, supply a large amount of seeds to mountain slopes. Therefore, the revegetation is faster in areas closer to the foot of the mountain. However, the number of *Larix* saplings

did not decrease with increasing elevation and was faster than any other native tree species. These results suggest that seed limitation is not the prime determinant on sapling regeneration on the three taxa on the slopes of this mountain. The positive effects of elevation on *Betula* sapling growth could be related to increasing solar radiation, probably because the growth of *Betula* is most susceptible to shading among the three taxa (Kobe and Coates 1997; Niinemets and Kull 1999; Dolezal et al. 2004), although open habitats increasing with increasing elevation became more stressed by wind, drought, and low temperature in air and soil (Šrutek and Lěps 1994; Nishi and Tsuyuzaki 2004). In contrast, the recruitment of *Betula* appears to be limited primarily by overstory crowding. The effect of overstory crowding on the recruitment of *Betula* extends the farthest of the three taxa, i.e., overstory *Larix* affects recruitment of *Betula* at large distances (4 m) which often exceeds the length of lateral branches of overstory *Larix*. Therefore, shading is considered to be the first determinant of *Betula* recruitment. In this sense, elevation affected the sapling recruitment and growth in opposite ways for *Betula* relative to *Populus* and exotic *Larix*.

4.3. Changes in species composition with landscape level

The high rates of survival and recruitment by *Larix* are likely to maintain the dominance of this invasive species on the mountain, while the saplings of all the taxa are suppressed by *Larix* overstory in various ways. In *L. kaempferi* forests and plantations in central Honshu, Japan, where *L. kaempferi* occurs naturally, the regeneration of *L. kaempferi* is often limited by the lack of saplings (Nakamura 1985; Nagaike 2002). *Larix* is one of the common invasive conifers in the world (Peterken 2001; Richardson and Rejmánek 2004). Invasiveness of *Larix* could be explained in part by that the life history traits of non-native species are unique and help promoting invasive success. For example, invasive species grows more in the invaded habitats than in the native habitats (Hierro et al 2006). Biological invasion of *L. kaempferi* is promoted by its ability to produce saplings even under a closed *Larix* canopy. Overstory trees thin the saplings of certain species in the understory, and determine understory plant community structures (Clark et al. 1996; Chen et al. 2004).

Larix overstory does not influence the its own sapling regeneration, but restricts sapling regeneration of native species. This asymmetric suppression of *Larix* overstory also alleviates the interspecific competition on *Larix* from other species of saplings, and may accelerate *Larix* invasion. Native sapling regeneration was inhibited by *L. kaempferi* overstory probably because of shading. *L. kaempferi* may exhibit high dominance because of its abilities in sapling regeneration, despite the moderate overstory crowding at the invaded disturbed mountain.

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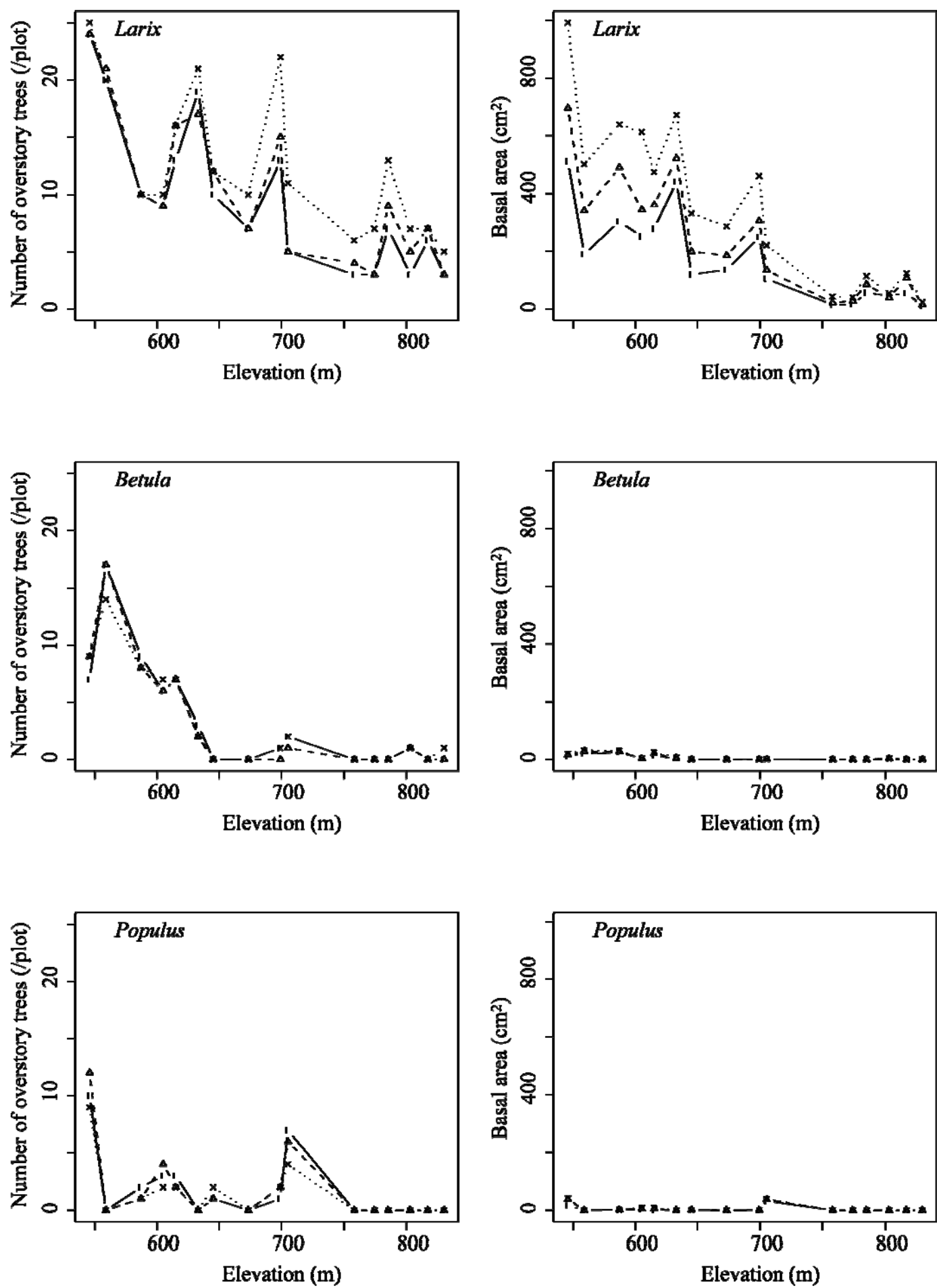
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Figure captions

Figure 1. Spatio-temporal changes in overstory trees (> 1.3 m in height). Number of tree stems and total basal area at breast height per plot are shown on three dominant taxa. Open circles with solid lines indicate values measured in 1997, open triangles with dashed lines are those in 2000, and crosses with dotted lines are those in 2004.

Figure 2. Spatio-temporal changes in numbers of saplings per plot for three dominant taxa. Symbols, refer to Fig. 1.



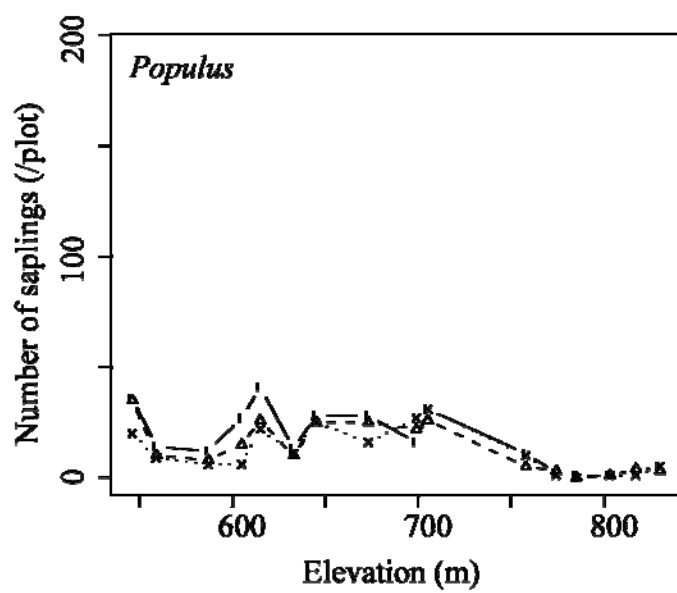
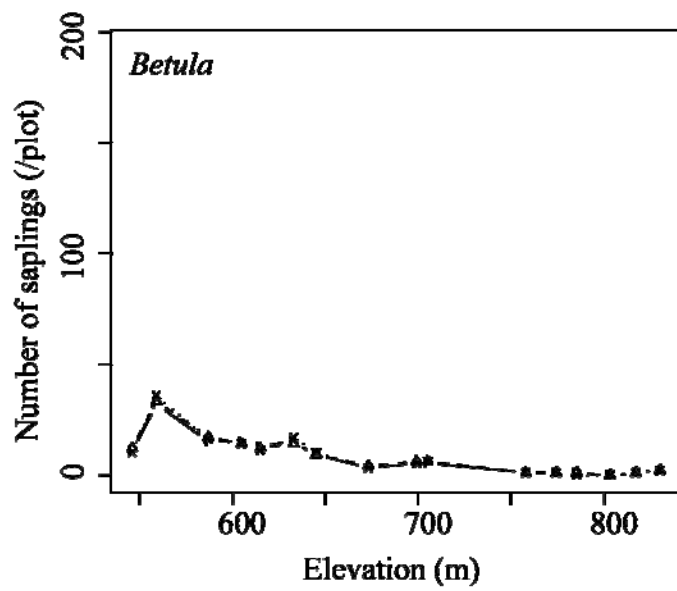
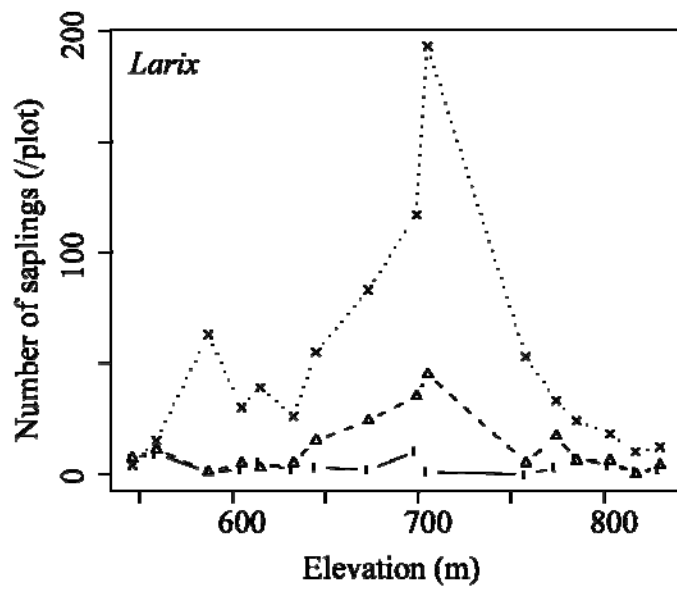


Figure 2

Table 1. Numbers of tree stems in 1997, 2000 and 2004, and the numbers of recruited and dead or lost saplings from the later census on three dominant taxa. Numbers of stems > 1.3 m in height are shown in parentheses. Numbers of recruited and survived saplings are significantly different between years and among three taxa (likelihood ratio test, $p < 0.01$).

Year	<i>Larix</i>	<i>Betula</i> *	<i>Populus</i> *	Others**	Total
Number of stems					
1997	214 (155)	182 (53)	296 (27)	70 (8)	762 (243)
2000	356 (167)	184 (51)	246 (28)	86 (5)	872 (251)
2004	977 (202)	185 (52)	213 (22)	103 (12)	1478 (288)
Number of recruits					
2000	144	14	61	28	247
2004	630	10	64	33	737
Number of dead or lost saplings perished					
2000	1	4	76	2	83
2004	2	5	62	16	71

* In 2004, the most stems were identified at species level. Of the identified stems in 2004, the leading species of *Betula* was *B. platyphylla* var. *japonica* explaining ca 72% of total *Betula* stems. The leading species of *Populus* was *P. sieboldii* accounting for 53% *Populus* stems.

** Others recorded in 1997: *Salix bakko* Kimura (62 stems), *Acer japonicum* Thunb. (1), *Alnus maximowiczii* Callier (3), *Pinus densiflora* Sieb. et Zucc. (2), *Sorbus commixta* Hedl. (1), *Cephalotaxus harringtonia* K.Koch (1), and *Rhus trichocarpa* Miq. (1). Additionally, *Fraxinus lanuginosa* Koidz. (1) was recorded in 2004.

Table 2. The best zero-inflated negative binomial models that explain the numbers of recruits in 2000 and 2004 (dependent variable) by independent variables (neighborhood index, elevation and census period) evaluated by AICs. Probability and density of recruitment were calculated simultaneously. -: variables are not adopted in the models.

Taxa	LNI	Elevation (m)	Census period	Intercept	Radius (m)
Probability of recruitment occurred in grids					
<i>Larix</i>	-0.132	-0.074	-2.478	47.664	2
<i>Betula</i>	-3.558	-	-37.798	35.061	4
<i>Populus</i>	-0.381	-0.033	-	22.441	1
Density of recruits					
<i>Larix</i>	-0.081	-0.010	1.034	3.714	2
<i>Betula</i>	-0.002	-	-2.047	-4.929	4
<i>Populus</i>	-0.103	-0.020	-	10.402	1

Table 3. Coefficients of the best multiple regression models to explain sapling survival (dependent variable) by four independent variables (LNI, sapling stem height, elevation, and census period), and growth rate (dependent variable) by two independent variables (LNI and elevation) evaluated by AICs. Stem height was not considered in growth rate models because the rate was standardized with the height. Census period was not considered in the growth rate models because datum were available on one census period. Elevation and census period were not adopted on the best models in any cases for sapling survival. -: variables are not adopted into the models.

Taxa	LNI	Stem height (cm)	Elevation (m)	Intercept	Radius (m)
<i>Sapling survival</i>					
<i>Larix</i>	-	-	-	26.566	-*
<i>Betula</i>	-0.129	0.041	-	3.057	0
<i>Populus</i>	-0.008	0.010	-	0.166	2
<i>Sapling growth rate</i>					
<i>Larix</i>	-0.007		-	-0.277	4
<i>Betula</i>	-		0.012	-11.030	-*
<i>Populus</i>	-0.036		-	-2.767	2

* Radius is not determined, since neighborhood index was not adopted.