

Hoshizaki, K., S. Takahashi, H. Tanaka, S. Oki, and M. Matsushita. Stochasticity of individual competition and local match-up inequality for saplings in a niche-structured forest. *Ecology*

## APPENDIX S1

### Descriptions of field sampling

#### SITE DESCRIPTIONS

The three study sites (Kanumazawa Riparian Research Forest, Oarasawa creek, and a forest road) were located in a temperate montane creek-scape, northern Japan (Fig. S1; totally 16.4 ha; 39°06' N, 140°51' E; altitude: 390-460 m). The climate is cool temperate, with an annual mean temperature of 8.6 °C. Annual precipitation is ca. 2100 mm, with heavy snowfall in winter (max. snow depth: ca. 2 m).

Kanumazawa forest has a closed canopy, comprising a mixture of mid- to late-successional tree species (Suzuki et al. 2002; 4.71 ha), and three small/intermediate-scale patches of boulder/gravel sedimentation created by fluvial transports (680, 615 and 144 m<sup>2</sup>; Figs. S1 and S2). In these fluvial deposits, abundant saplings of major component tree species are co-occurring (e.g. *Pterocarya rhoifolia*, *Ulmus laciniata*, *Aesculus turbinata*; hereafter, species are indicated only by genus names except for the two *Acer* species), and the partitioning of regeneration niches has been suggested (Masaki et al. 2007, 2008; Oki et al., 2013). The most influential events of fluvial transport occurred in 1988 and 2007 (see Oki et al. 2013 for descriptions of the disturbances).

At Oarasawa creek, we set up a 2.66-ha study plot in 2009. Here, frequent fluvial transports have resulted in a large, single patch of boulder sedimentation (6,066 m<sup>2</sup>) with sparsely remaining trees (mainly *Alnus*, *Salix* and *Cercidiphyllum*; Fig. S2). Here, recent major fluvial transport events occurred in 1998, 2002, and 2007. Saplings of diverse tree species, including

early-, mid-, and late-successional species, are colonizing on the sedimentation. Most of the *Alnus* and *Salix* saplings were sampled at this site.

The forest road connects the two creeks, was constructed in 1991-1992, and was abandoned in around 2004 (Fig. S2). Here, a few *Salix* and *Alnus* trees colonized in 1990s have started to join in seed dissemination. The surrounding canopy is mainly consisted of *Fagus*, *Quercus* and some other riparian elements (*Cercidiphyllum*, *Acer pictum*).

Light availabilities in these sites ranged from 1.0-12.2% for the sites in Kanumazawa and 9.5-45.5% for Oarasawa, The canopy openness on the forest road slope is intermediate (1.5-19.1%). The fluvial deposits consist of mainly boulders and woody debris, and soils are accumulating year by year. The soil conditions at Kanumazawa creek and the forest road slope are similar. The deposition site at Oarasawa creek is slightly dryer, but the survival and growth of the saplings are not limited by the soil moisture conditions because of the sufficient rainfall (approx. 600 mm during July-September).

#### SAPLING MEASUREMENT

At the Kanumazawa site, all saplings on the three fluvial deposit sites have been mapped and censused, as documented in our previous paper (Oki et al., 2013). In the present study, stems with 50-300 cm in height in 2011, excluding current year-seedlings, that were measured in 2007, were used and re-censused in 2011. At the Oarasawa site, in 2008 we placed two belt-transects (4×150 m and 4×100 m; 10-15 m distant from each other), covering the entire deposition area, and several seedlings and saplings were measured preliminarily. In 2009, all saplings in the 3-m slot of each transect were sampled (Fig. S1; total sampling area: 750 m<sup>2</sup>), and these saplings were measured again in 2011. At the forest road site, in 2009 we placed 5 sampling stations on the road slopes at intervals of approximately 50 m, and at each station two short belt-transects

(3×10 m each, n = 10) were established (Fig. S1).

At these survey areas, sapling banks had been formed after disturbances, and favorable conditions had been maintained. At all sites, saplings in the sampling area were mapped and have been measured repeatedly. The survey years were 2007 and 2011 for Kanumazawa and basically 2009 and 2011 for Oarasawa and the forest road sites. For the 50 additional samples for the analyses of matchup outcomes (described in the main text), measurement years were 2008 (or 2010 for samples using bud-scale scars) and 2012. In all years, the surveys were conducted at the end of September or in October.

We selected ten species for which samples were sufficient for comparison of height growth (Table 1). These species vary in a range of life history characteristics (Table 1). Individuals with severe damage and little association with inter-individual competition, i.e. those that recorded extraordinary reduction in height due to unnatural reasons such as measurement error and unintentional stem breakage at the measurement, were excluded from the analysis. A small portion of the saplings died during our observation, and they were also excluded in this study because their growth rate was not able to be determined and because the frequency of deaths was too small in late-successional species to obtain meaningful results.

To evaluate light conditions for the saplings, we took hemispherical photographs in early August 2011. The photographs were taken at 2-m intervals under an overcast sky during 11:00-15:00 (657 points, acquisition height: 2 m), according to the procedures described by Oki et al. (2013). Canopy openness was calculated using Canopon2 (Takenaka 2009; Oki et al. 2013).

#### **LITERATURE CITED**

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- Oki, S., Akiyoshi, T., Hoshino, D., Shibata, M., Matsushita, M. & Hoshizaki, K. (2013) Interactive effect of canopy and fluvial disturbances on sapling community structure and species diversity in a montane riparian forest. *Ecoscience* 20: 194-203
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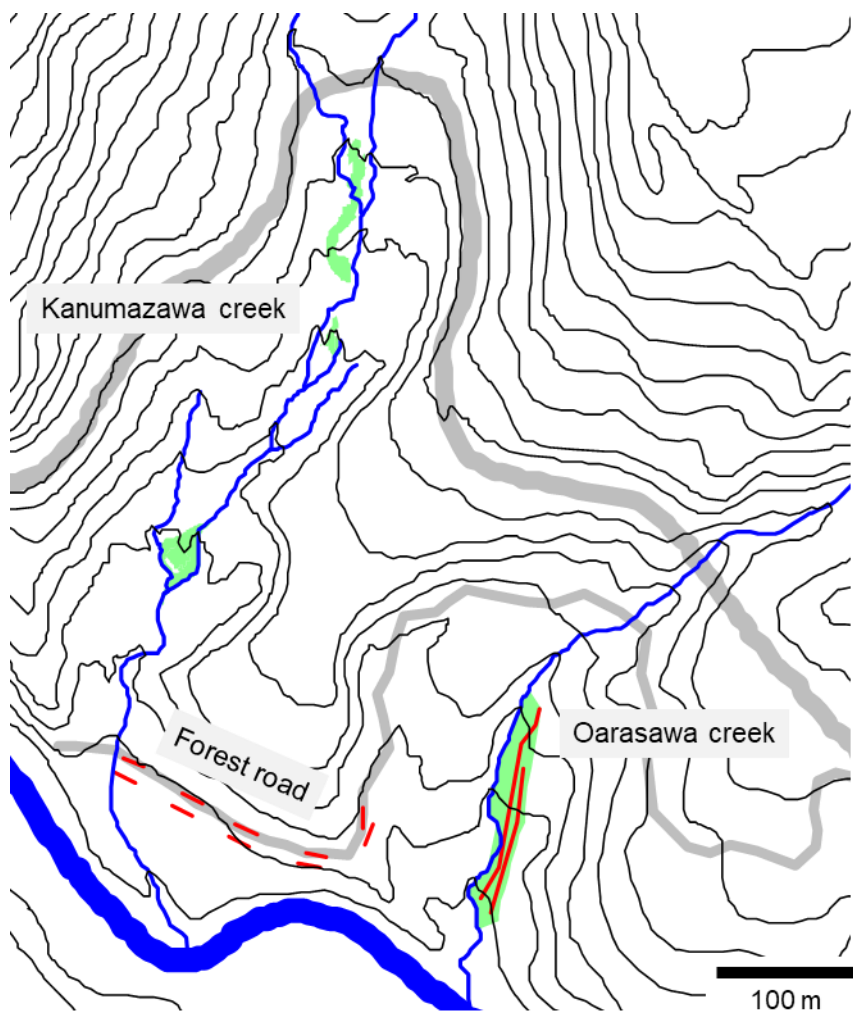


FIG. S1. Map showing fluvial sedimentation deposits (shown in green) and the sampling sites. In Kanumazawa, all saplings on the three fluvial deposits were sampled. In Oarasawa and the forest road sites, sampling was performed in line transects (shown in red). Contour lines are drawn at 10 m intervals. The gray thick and thin lines, respectively, represent Route 397 and the abandoned forest road.

a) A fluvial sedimentation site ( $615 \text{ m}^2$ ) at Kanumazawa creek



b) The large fluvial sedimentation site ( $6066 \text{ m}^2$ ) at Oarasawa creek



FIG. S2. Photographs showing the three sampling sites. Photo credit: K. Hoshizaki.



c) Abandoned forest road



FIG. S2. (continued)

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## APPENDIX S2

### **Verification of the use of sapling growth rates as the predictor of local matchups**

Here we explain the validity of our use of height growth rates as the predictor of win/loss in the local matchups, using a simple thought experiment and data testing. First, consider a local competition between an initially 50-cm-tall sapling with growth rate of  $0.2 \text{ yr}^{-1}$  vs. an opponent of initially 150 cm in height with 0.1 growth rate. This situation is quite common given that the actual height differences between saplings in local matchup ranged mostly from 0-100 cm (Fig. S1) and that these growth rates were observed at a wide range of light conditions in all species (Fig. 2: main text). This simple simulation indicates 13 years for the former to overtop the latter (Table S1). Next, consider another case of matchup with slightly different combination of initial heights, 50-cm-tall vs. 100-cm-tall saplings, but with the same growth rates as above (0.2 and  $0.1 \text{ yr}^{-1}$ ). Then it takes 8 years for the 50-cm sapling to overtake the 100-cm one (Table S1).

Although this thought experiment might be more or less oversimplified, these results are realistic in shade tolerant species because our site conditions are not too dark, with  $>5\%$  of canopy openness experienced by most of the saplings (Fig. S2, see also Table 1 in the main text and photos in Appendix S1). Second, suppression by larger, nearby sapling(s) is not so severe; as presented in Results in the main text, the number of opponents per sapling was on average 3.5. Furthermore, in our sites saplings of shade-tolerant species can persist for 10 or more years; most of the samples in Kanumazawa sedimentation patches are those we have monitoring since 1996



(Oki et al. 2013).

As the second way of the verification, we examined how smaller, faster-growing sapling caught up or overtook the larger, slower-growing opponent in each matchup, using our actual data. We examined the change in the height difference between locally competing saplings during our observation, i.e. the difference between the heights for the competing samplings in 2011 (endpoint of our height measurements) against the difference between their initial heights (for 2007 in Kanumazawa site, for 2009 in other two sites). As demonstrated in the scatter plot (Fig. S3), during just two or four years of our census interval there were many matchups in which the losers lost initial height advantage (points on areas of  $x > 0$ , near  $y = 0$ ) or were overtaken (points in the fourth quadrant of the scatterplot), and vice versa (sapling growing better offset the initial height disadvantage or overtook the initially-larger one). Based on these results, extension of the interval years would make the height overtakes by the saplings with greater growth rates more pervasive. Thus, using growth rates is verified in determining the “winning/losing” of local competition among the saplings.

#### **LITERATURE CITED**

Oki, S., Akiyoshi, T., Hoshino, D., Shibata, M., Matsushita, M. & Hoshizaki, K. (2013)

Interactive effect of canopy and fluvial disturbances on sapling community structure and species diversity in a montane riparian forest. *Ecoscience* 20: 194-203

Table S1. A thought experiment for the hypothetical matchup between saplings. The years when the smaller but faster-growing focal sapling overtakes the larger, slower-growing opponents were shown in boldface.

	Focal	Opponent 1	Opponent 2
Growth rate ( $\text{yr}^{-1}$ )	0.2	0.1	0.1
$n$	Height (cm) after $n$ years		
Initial	50	150	100
1	60	165	110
2	72	182	121
...			
7	179	292	195
<b>8</b>	<b>215</b>	322	<b>214</b>
...			
12	446	471	314
<b>13</b>	<b>535</b>	<b>518</b>	345

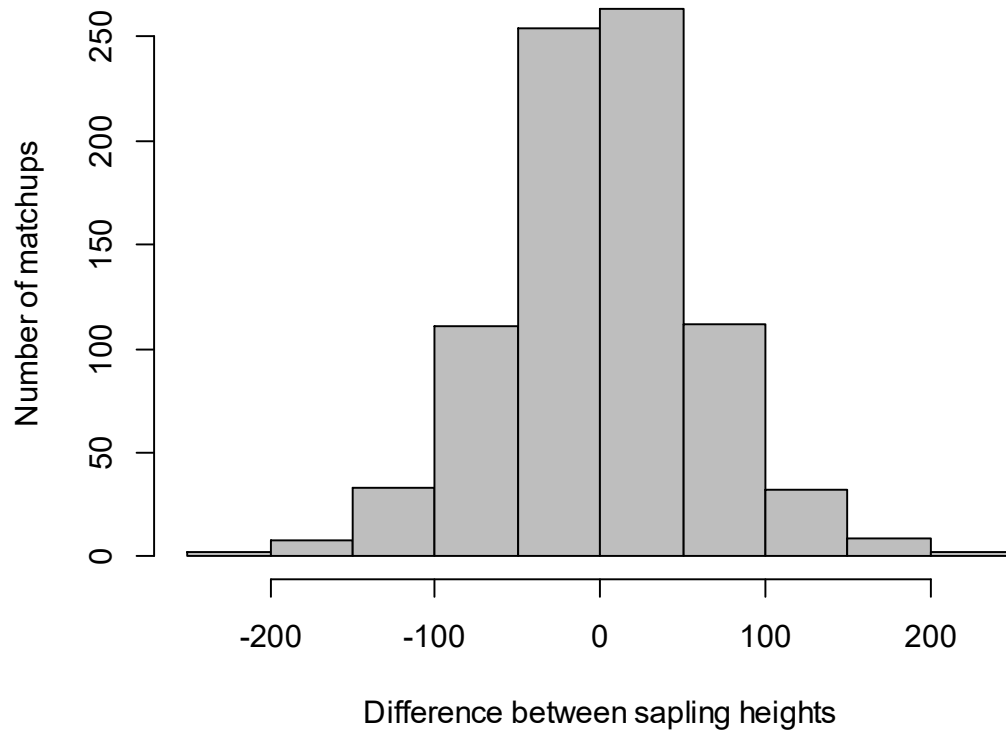


FIG. S1. Histogram of height differences between two saplings engaged in local matchpup.

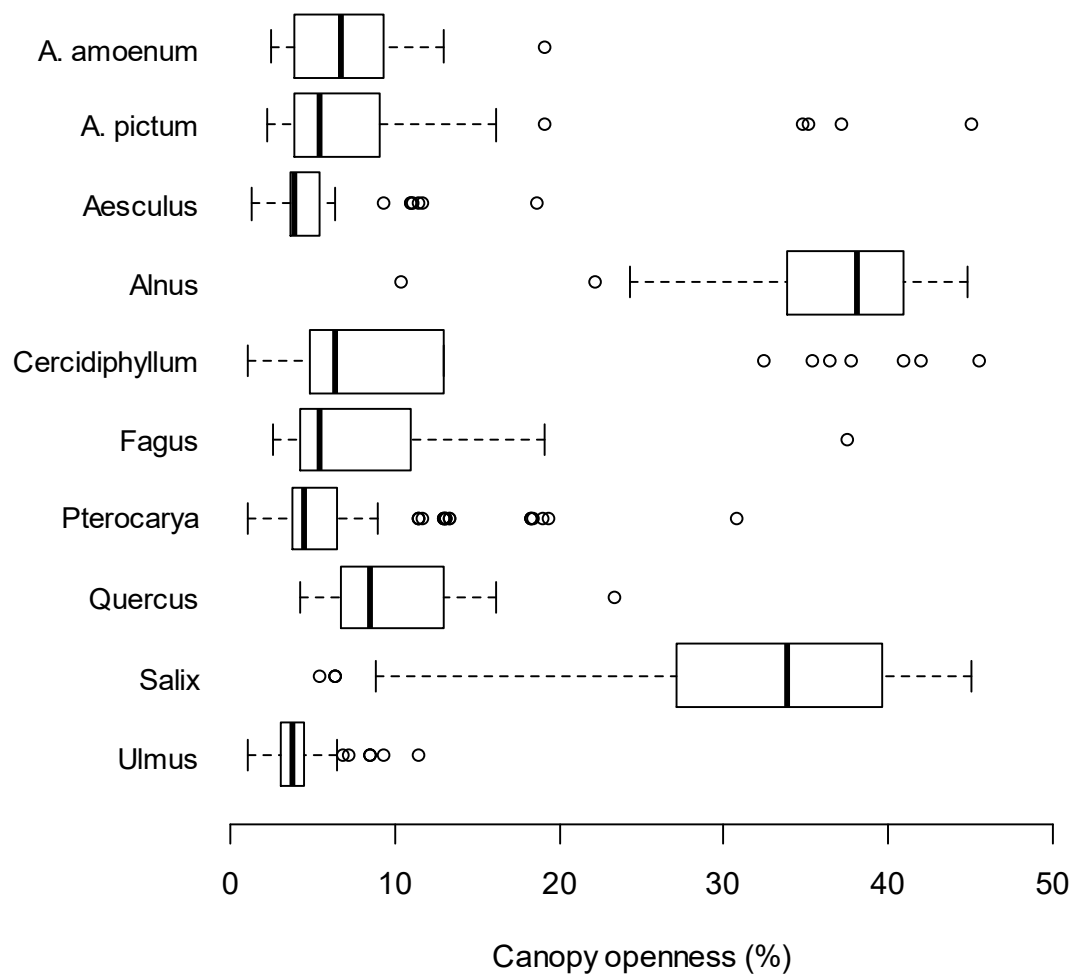


FIG. S2. Light availabilities of saplings by species.

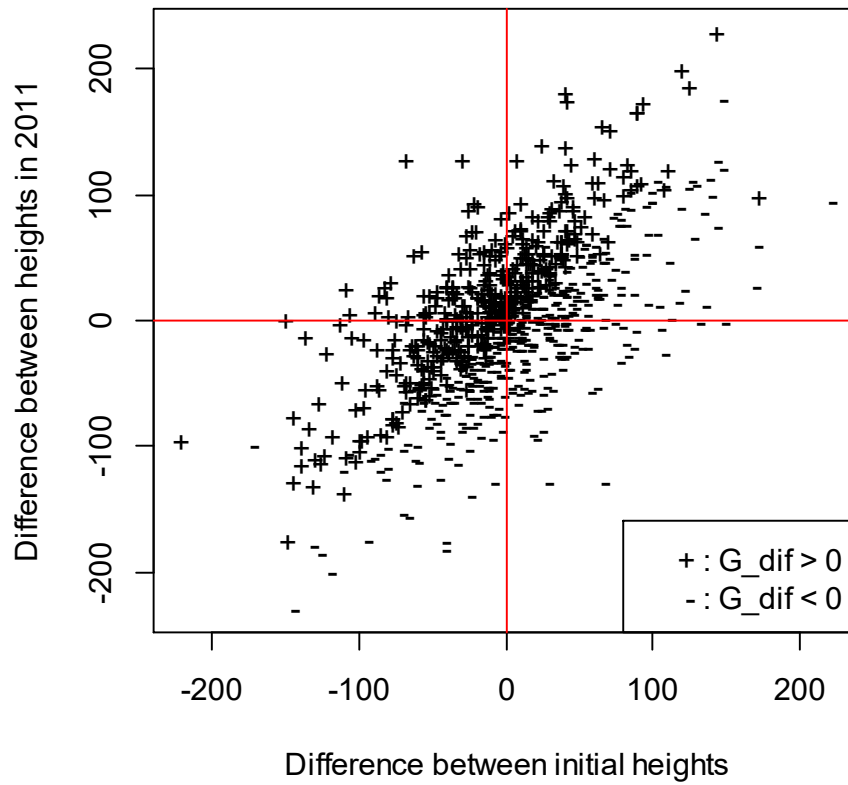


FIG. S3. Scatterplot representing the relationship between the difference between sapling initial heights (in 2007 or 2009) and the difference between the heights in 2011 (endpoint of our observation) for each matchup, as plotted by positive/negative difference the growth rates,  $G\_dif$ , between the two saplings. Points represented by “+” symbol refer to “winners” (growing faster than the opponent) and those with “-” to “losers” (growing slower).

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## APPENDIX S3

### Detailed descriptions for the results of individual matchups in inter-species competition

#### *Species-level growth and occurrence of individuals*

The height growth rate for each species varied as a function of light (Fig. S1 and Table S1; for comparison of species' mean responses, see Fig. 2 in the main text), and showed several well-known major patterns, such as a slow increase in the growth rate with an increase in light availability (e.g., *Acer pictum*), and a growth rate not severely decreasing in the dark (e.g., *Fagus* and *Aesculus*), and markedly increasing growth rate under higher light availability but lower occurrence under lower light (e.g., *Salix*) (Fig. 2).

In the primary samples collected in 2011, there was a total of 1,722 local matchups from the 10 species, and 917 of them were interspecies matchups. Five species, *Ulmus*, *Pterocarya*, *Acer pictum*, *A. amoenum* and *Cercidiphyllum*, recorded >50 interspecies matchups. In contrast, *Alnus* and *Salix* had fewer interspecies matchups (<15 matchups), with a high ratio of isolated individuals for *Alnus* (55% in isolation, Table 2). As stated in the main text, each sapling (n=263) experienced interspecies matchups with a mean of 1.9 (SD: 0.9) species, ranging from 1.0 (*Alnus*) to 2.7 (*Quercus*), and the number of species with which each sapling competed differed significantly between species. The number of heterospecies individuals each sapling encountered also differed significantly among species, with 5 species pairs showing a significant imbalance in matchup frequencies (Table S3). Based on the post-hoc analysis of pairwise contrast (Tukey



HSD), examined using *multcomp*, *Acer amoenum* experienced a significantly larger number of matchups against other late successional species (*Aesculus*, *Fagus Pterocarya* and *Ulmus*; Table S3)

#### *Outcomes of individual matchups*

Among the wide variations in winning percentages for specific species-pairs being matched-up (Table S4), a small number of species pairs, i.e. 7.5% (5 pairs) of the overall pairs, showed a significantly biased winning percentage (good/bad compatibility, based on binomial test; Table S4). This bias was often confirmed in slow-growing, late- and moderately-late successional species, suggesting the importance of determinism in their competitiveness. Among those, *Acer pictum* was highly distinct; it showed significantly good compatibilities in matchups against *Cercidiphyllum* and *Pterocarya*, whereas significantly bad against *Fagus* and *Acer amoenum* (Table S4). Among the matchups between slow-growers, *Ulmus* had significantly bad compatibility against *Fagus*. These biased compatibilities were in accordance with the species rankings (Table S4).

As stated in the main text, the outcomes (winning or losing) of individual matchups were basically predictable based both on the species-level rankings at the light level under which the matchup was occurring and on the heights of the two individuals in competition (Table S5). Standardized coefficients of the GLMM indicated that the species-level advantage/disadvantage (i.e. difference between potential growth rates of saplings being matched-up) had a significant influence on the matchup outcomes to a similar extent to the effect of the height difference. Nevertheless, we also found that unexpected outcomes of the matchup, namely, results divergent from expectation based on the ranks given by the species means, accounted for 37.8% (n = 387) of all the matchups. Furthermore, 234 of these (22.9% of all, 60.5% of the unexpected outcomes)

were unexpected despite large differences in the potential growth rates, based on the species-mean growth, being outside the first and third quartiles (i.e., the species-level advantage/disadvantage was evident).

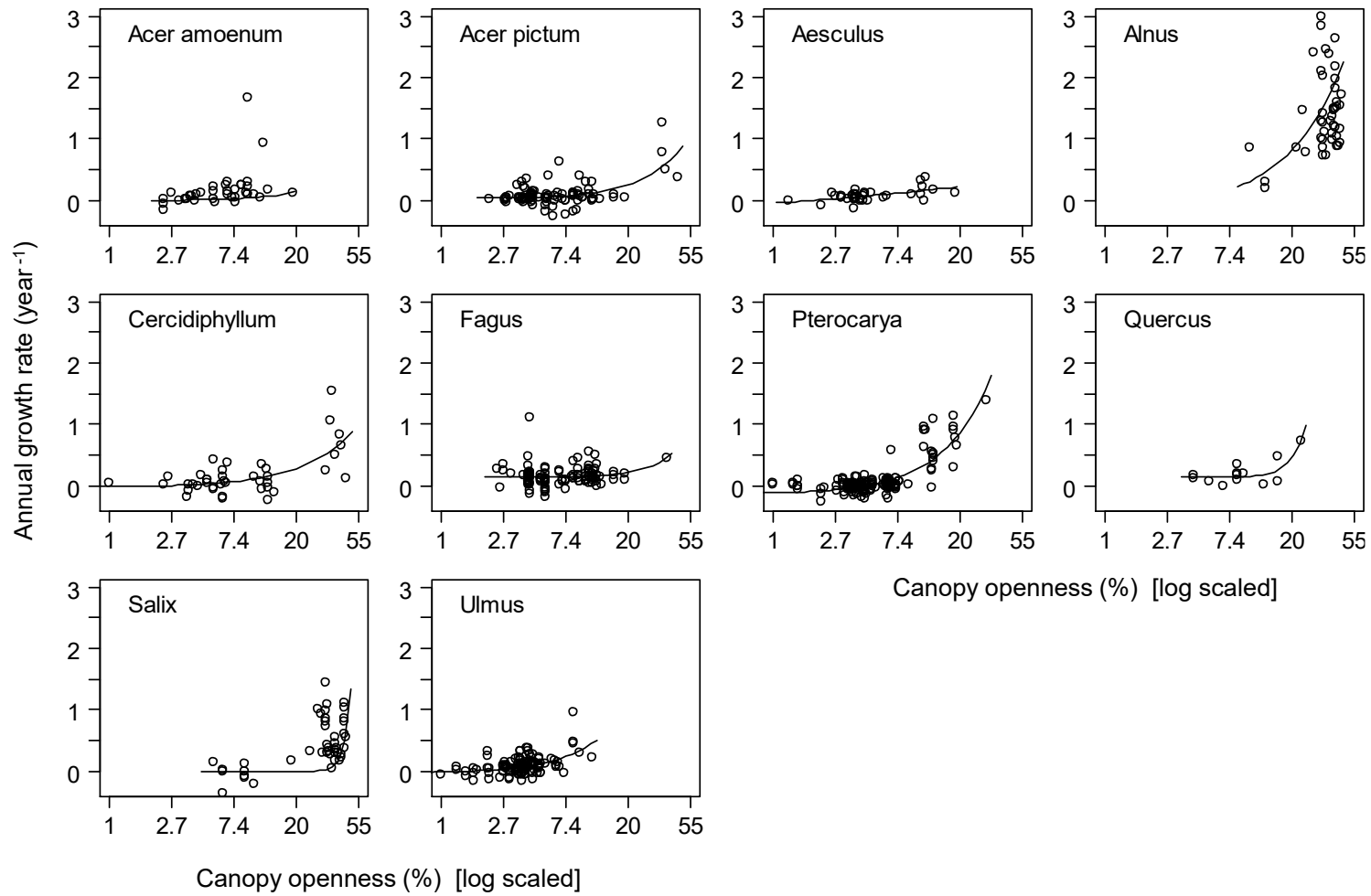


FIG.S1. Light dependence of sapling height growth rate. Curves were fitted via non-linear regression (fitted parameters shown in Table S1). Note that the horizontal axis is natural log-scaled.

TABLE S1. Regression parameters for the light dependence of sapling growth rates. Parameters  $a$ ,  $b$ , and  $c$  were obtained via non-linear regression:  $G = a + \exp(b L + c)$ , where  $G$  and  $L$  denote, respectively, annual growth rate in sapling height and canopy openness (log).

Species	$a$	$b$	$c$
<i>Acer amoenum</i>	-0.01	1.62	-6.80
<i>Acer pictum</i>	0.02	1.52	-6.05
<i>Aesculus turbinata</i>	-0.44	0.18	-0.95
<i>Alnus hirsuta</i>	-0.16	1.10	-3.34
<i>Cercidiphyllum japonicum</i>	-0.03	1.21	-4.83
<i>Fagus crenata</i>	0.13	2.21	-9.16
<i>Pterocarya rhoifolia</i>	-0.14	1.31	-3.91
<i>Quercus crispula</i>	0.13	4.27	-13.96
<i>Salix</i> spp.	0.00	10.01	-38.59
<i>Ulmus laciniata</i>	-0.04	1.35	-3.99

TABLE S2. Results of post-hoc multiple contrasts for the number of opponent species in the individual matchups. Significance level was determined based on adjusted P-values with the single-step method in the function *glht()*.

Contrast	Estimate	S.E.	P
Acer amoenum - Acer pictum	0.17	0.14	0.95
Acer amoenum - Aesculus	0.45	0.18	0.27
Acer amoenum - Alnus	0.83	0.39	0.44
Acer amoenum - Cercidiphyllum	0.17	0.17	0.99
Acer amoenum - Fagus	0.02	0.17	1.00
Acer amoenum - Pterocarya	0.15	0.12	0.96
Acer amoenum - Quercus	-0.15	0.20	1.00
Acer amoenum - Ulmus	0.29	0.13	0.36
Acer pictum - Fagus	-0.16	0.14	0.98
Aesculus - Acer pictum	-0.27	0.16	0.78
Aesculus - Cercidiphyllum	-0.28	0.19	0.89
Aesculus - Fagus	-0.43	0.19	0.37
Aesculus - Pterocarya	-0.30	0.15	0.60
Aesculus - Quercus	-0.60	0.22	0.12
Aesculus - Ulmus	-0.16	0.16	0.99
Alnus - Acer pictum	-0.65	0.38	0.73
Alnus - Aesculus	-0.38	0.40	0.99
Alnus - Cercidiphyllum	-0.66	0.39	0.76
Alnus - Fagus	-0.81	0.39	0.48
Alnus - Pterocarya	-0.68	0.37	0.68
Alnus - Quercus	-0.98	0.40	0.26
Alnus - Ulmus	-0.54	0.37	0.89

Cercidiphyllum - Acer pictum	0.00	0.14	1.00
Cercidiphyllum - Fagus	-0.15	0.17	1.00
Pterocarya - Acer pictum	0.02	0.09	1.00
Pterocarya - Cercidiphyllum	0.02	0.13	1.00
Pterocarya - Fagus	-0.13	0.13	0.99
Pterocarya - Quercus	-0.30	0.17	0.67
Pterocarya - Ulmus	0.14	0.08	0.68
Quercus - Acer pictum	0.33	0.18	0.65
Quercus - Cercidiphyllum	0.32	0.20	0.81
Quercus - Fagus	0.17	0.20	1.00
Salix - Acer amoenum	-0.32	0.31	0.99
Salix - Acer pictum	-0.14	0.30	1.00
Salix - Aesculus	0.13	0.32	1.00
Salix - Alnus	0.51	0.47	0.98
Salix - Cercidiphyllum	-0.15	0.31	1.00
Salix - Fagus	-0.30	0.31	0.99
Salix - Pterocarya	-0.17	0.29	1.00
Salix - Quercus	-0.47	0.33	0.89
Salix - Ulmus	-0.03	0.29	1.00
Ulmus - Acer pictum	-0.11	0.09	0.96
Ulmus - Cercidiphyllum	-0.12	0.14	1.00
Ulmus - Fagus	-0.27	0.14	0.55
Ulmus - Quercus	-0.44	0.17	0.18

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TABLE S3. Results of post-hoc multiple contrasts for the matchup frequencies which each sapling experienced by species pairs. Use of adjusted P-values is the same as in Table S2.

Significantly more or fewer species-pairs are shown in boldface.

Contrast	Estimate	S.E.	P
Acer amoenum - Acer pictum	0.37	0.14	0.15
<b>Acer amoenum - Aesculus</b>	<b>0.74</b>	<b>0.20</b>	<b>&lt;0.01</b>
Acer amoenum - Alnus	1.47	0.51	0.09
Acer amoenum - Cercidiphyllum	0.28	0.17	0.77
<b>Acer amoenum - Fagus</b>	<b>0.66</b>	<b>0.20</b>	<b>0.03</b>
<b>Acer amoenum - Pterocarya</b>	<b>0.71</b>	<b>0.13</b>	<b>&lt;0.01</b>
Acer amoenum - Quercus	0.29	0.23	0.94
<b>Acer amoenum - Ulmus</b>	<b>0.47</b>	<b>0.13</b>	<b>&lt;0.01</b>
Acer pictum - Fagus	0.29	0.19	0.84
Aesculus - Acer pictum	-0.37	0.19	0.55
Aesculus - Cercidiphyllum	-0.45	0.21	0.43
Aesculus - Fagus	-0.08	0.24	1.00
Aesculus - Pterocarya	-0.03	0.18	1.00
Aesculus - Quercus	-0.45	0.26	0.73
Aesculus - Ulmus	-0.27	0.18	0.86
Alnus - Acer pictum	-1.10	0.51	0.42
Alnus - Aesculus	-0.73	0.53	0.91
Alnus - Cercidiphyllum	-1.18	0.52	0.34
Alnus - Fagus	-0.81	0.53	0.85
Alnus - Pterocarya	-0.76	0.50	0.86
Alnus - Quercus	-1.18	0.54	0.40

Alnus - Ulmus	-1.00	0.50	0.55
Cercidiphyllum - Acer pictum	0.09	0.15	1.00
Cercidiphyllum - Fagus	0.37	0.21	0.70
<b>Pterocarya - Acer pictum</b>	<b>-0.34</b>	<b>0.10</b>	<b>0.03</b>
Pterocarya - Cercidiphyllum	-0.42	0.14	0.07
Pterocarya - Fagus	-0.05	0.18	1.00
Pterocarya - Quercus	-0.42	0.21	0.52
Pterocarya - Ulmus	-0.24	0.09	0.14
Quercus - Acer pictum	0.08	0.21	1.00
Quercus - Cercidiphyllum	-0.01	0.23	1.00
Quercus - Fagus	0.37	0.26	0.90
Salix - Acer amoenum	-0.55	0.34	0.79
Salix - Acer pictum	-0.18	0.33	1.00
Salix - Aesculus	0.19	0.36	1.00
Salix - Alnus	0.92	0.59	0.84
Salix - Cercidiphyllum	-0.27	0.34	1.00
Salix - Fagus	0.11	0.36	1.00
Salix - Pterocarya	0.15	0.32	1.00
Salix - Quercus	-0.26	0.37	1.00
Salix - Ulmus	-0.08	0.32	1.00
Ulmus - Acer pictum	-0.10	0.10	0.99
Ulmus - Cercidiphyllum	-0.18	0.14	0.94
Ulmus - Fagus	0.19	0.18	0.98
Ulmus - Quercus	-0.18	0.21	1.00

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TABLE S4. Wins and losses for individual-based heterospecific matchups, by species combination using both primary and additional samples. Number of matchups is denoted as wins/losses for each combination. Species are shown in decreasing order of overall winning percentage (the same as in Table 1 of the main text), and initialized for opponents. Boldface and asterisks indicate, respectively, significant ( $P < 0.05$ ) and marginally significant ( $P < 0.1$ ) departure from the overall winning percentage of the species (binomial test).

Species of focal sapling	Species of opponent individual										Total outcomes with heterospecifics	% wins
	AH	FC	UL	AA	AP	QC	AT	PR	CJ	<i>Salix</i>		
<i>A. hirsuta</i>		.	.	.	.	.	.	1/0	4/0	34/2	39/2	95.1
<i>F. crenata</i>	.		7/0	3/3	12/0	5/3	4/0	.	2/3	3/2	36/11	76.6
<i>U. laciniata</i>	.	<b>0/7</b>		14/11	39/25	2/0	9/2	89/46	6/4	.	159/95	62.6
<i>A. amoenum</i>	.	5/2	13/15		9/1	3/1	2/1	17/11	1/0	.	50/31	61.7
<i>A. pictum</i>	.	<b>0/7</b>	25/43	<b>1/10</b>		1/1	1/5	<b>34/17</b>	<b>7/0</b>	.	69/83	45.4
<i>Q. crispula</i>	.	8/7	0/3	1/5	9/3		1/0	0/2	0/2	0/2	19/24	44.2
<i>A. turbinata</i>	.	1/5	2/4	1/3	3/3	0/1		7/8	2/2	0/1	16/27	37.2
<i>P. rhoifolia</i>	.	.	45/88	11/17	17/35	.	6/7		13/18	.	92/165	35.8
<i>C. japonicum</i>	0/4	0/1	4/6	0/2	0/7	0/1	0/4	17/13*		0/1	21/40	34.4
<i>Salix</i> spp.	1/30	3/5	.	.	0/1	1/0	.	.	3/0		8/36	18.2

Note: Since saplings located in the 1-m margin of each sampling area were not counted as focal individuals but were counted as opponents of the matchups, the numbers are not always consistent between species pairs at the upper site and the lower site on the diagonal line of the table.

TABLE S5. Summary of the generalized linear mixed model examining the effects of species-level advantage in potential growth and size advantage between the two individuals in the matchup (fixed effects) and species:individual (random effect) on the outcome of individual competition.

Parameter	Standardized coefficient	Standard error	P value
$\alpha$ (intercept)	0.09	0.29	0.77
$\beta$ (fixed effect)			
Difference in species-mean growth rates	1.23	0.27	<0.001
Difference in sapling heights	1.15	0.16	<0.001
Random effect for intercept	Variance	Standard deviation	<0.001
Within species	3.27	1.81	
Among species	0.46	0.68	