The potential role of an alien tree species in supporting forest restoration: Lessons from Shiretoko National Park, Japan

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A R T I C L E   I N F O

A B S T R A C T

Restoring forests has recently received considerable attention in the context of sequestering carbon and supporting biodiversity. Although considering alien species as a tool for natural forest restoration still remains controversial, harnessing alien species when they are already present in an ecosystem might result in overall benefits for nature and society. In this study we evaluated whether the presence of an alien tree species supports or hinders the establishment of naturally regenerating forests in Shiretoko National Park, Japan. In particular, we focused on *Larix kaempferi*, which is widely present yet non-native to the region, and examined how this alien species affects two factors influencing the success of restoration: wind disturbance and deer herbivory. We examined the following effects of *L. kaempferi* plantations on natural regeneration: (1) the windbreak function for protecting native tree growth and (2) the nursery function to promote the regeneration of native tree saplings and seedlings under high herbivory pressure. We assessed tree height and regeneration, using large-scale remotely sensed data and terrestrial inventory data in five major vegetation types. We found that *L. kaempferi* plantations can protect native species from predominant winds. Additionally, *L. kaempferi* canopy cover promoted abundance and species richness in understory saplings and seedlings compared to other vegetation types such as primary and secondary forests, even under excessive browsing pressure. No regenerating *L. kaempferi* individuals were observed during the field census, suggesting the species is likely not invasive in our study system. The positive relationship between alien tree species and the regeneration of native tree assemblages emphasizes that existing alien species have the potential to act as nurse plants. Our findings imply that the presence of alien species can contribute to natural forest restoration by improving the local environmental conditions for native species in the short-term. Given the multiple ecological and social needs in our changing world, careful consideration is required to evaluate the long-term consequences of alien species. Especially in ecosystems in which alien species have already established, using their positive functions rather than swiftly eradicating them from the landscape might be beneficial for long-term restoration goals. We conclude that managers need to be aware of the context-dependency of alien species to make restoration more effective.

1. Introduction

Restoring forests is of global importance for climate change mitigation and biodiversity protection. It is increasingly emphasized that naturally functioning forests have great potential for sequestering carbon (Lewis et al., 2019) and maintaining biodiversity (Gardner et al., 2019; Watson et al., 2018). To restore natural forests effectively in a rapidly changing world, potent management schemes are needed that harness the full breath of management options towards restoration objectives. Species assemblages that arise through deliberate or inadvertent introduction of alien species—sometimes called "novel ecosystems" (Hobbs et al., 2006)—have become increasingly common worldwide, as a result of unprecedented changes in abiotic and biotic conditions (Hobbs et al., 2006). Alien species—species clearly outside their natural range, although not necessarily in a different country (Richardson and Rejmánek, 2004)—can have negative impacts on species diversity and ecosystem services (Campagnaro et al., 2018; Gaertner et al., 2009; Okimura et al., 2016; Walsh et al., 2016). Thus, utilizing alien species in restoration, such as reforesting with fast-growing plantations of alien trees, is not generally an option for restoring naturally functioning forests (Seddon et al., 2020a). Although many ecological restoration programs have traditionally focused on historical ecosystems (Halme et al., 2013; Jackson and Hobbs, 2009), managing novel assemblages is gaining importance in restoration ecology (Hobbs et al., 2014).

At the local scale, alien species often play an important role in both society and restoration. Monocultures or mixed-species tree plantations including alien species often have commercial value in the context of wood and crop production (e.g., Brancalion et al., 2020; O'Hehir and Nambiar, 2010). Consequently, they provide local communities with direct economic benefits (Brancalion and Chazdon, 2017). Often alien species are promoted because of specific traits, such as rapid growth and resistance against harsh environments (D'Antonio and Meyerson, 2002). Previous studies show that alien trees as a commercial enterprise can become important allies of forest restoration (Amazonas et al., 2018; Brancalion et al., 2020). Moreover, some studies have shown that alien species can become an essential part of novel ecosystems (Ewel and Putz, 2004; Hobbs et al., 2009), providing other species with important habitat (Ramus et al., 2017) and serving as their food sources (Graves and Shapiro, 2003). Examples of alien tree species as nurse plants, i.e., plants supporting the establishment of native tree species, are also well documented (De Pietri, 1992; Svriz et al., 2013). As such, alien species can help to restore forest cover and species richness (Lugo, 2004).

Natural forest restoration aims at fostering ecological processes such as natural regeneration of native species. In the case where residual forests composed of native species remain in a restoration area, the most cost-effective path toward restoring forests at the landscape scale can be through accelerating the process of natural regeneration (Lamb et al., 2005)—also known as secondary succession, forest regrowth or passive restoration (Chazdon et al., 2020). Natural regeneration of native species is, however, often limited by environmental factors such as changes in hydrology and soil chemistry in restoration areas. Novel assemblages including alien species are often better able to thrive under such altered environmental conditions (Cramer et al., 2008). This highlights the potential of alien species for overcoming abiotic barriers that prevent the recovery of degraded ecosystems. Reforestation with alien species could thus be a restoration alternative for degraded lands that are facing difficulties in the regeneration of native species (Guariguata et al., 2019). To achieve local socio-ecological goals, harnessing alien species when they are already present rather than eradicating them from the landscape might result in overall benefits for restoration (Ewel and Putz, 2004). However, for the goal of restoring native tree assemblages in the long term it is also important that alien species do not persist (D'Antonio and Meyerson, 2002). Therefore, it is necessary to evaluate whether novel species assemblages support or hinder the establishment of naturally regenerating forests, particularly considering the invasion success of alien species. In this context, further research on the mechanisms behind the effects of alien species on the local environment is needed (Kumschick et al., 2015).

The success of forest restoration programs is affected not only by alien species but also by disturbances from fire and herbivory (Stanturf et al., 2014). This is also true in Shiretoko National Park in northern Japan, where local communities have been committed to restoring natural forests since the 1970s. Numerous efforts—such as revegetation, establishment of fences as windbreaks and ungulate exclosures as well as watershed management—have been implemented there over the last 50 years. The evidence-based restoration efforts at Shiretoko National Park have been evaluated successfully in previous works (cf. Fujii et al., 2017; Mori et al., 2016). However, a knowledge gap exists regarding the role of Japanese larch (*Larix kaempferi* (Lamb.) Carrière) at Shiretoko, which was introduced to the region in the past and was widely planted because of its rapid growth and cold tolerance. In this study, we evaluated the roles of this alien species regarding the establishment and regeneration of native tree species. Specifically, we examined how *L. kaempferi* affects two important factors limiting the success of restoration at Shiretoko: wind disturbance and deer herbivory. Our objectives were to assess (1) the windbreak function of *L. kaempferi* for protecting native tree growth and (2) the nursery function of *L. kaempferi* plantations to promote the regeneration of native trees under high herbivory pressure. We used aerial light detecting and ranging (LiDAR) data to quantify tree height at a large scale, and vegetation inventory data to compare natural regeneration among different vegetation types. We hypothesized that spatial proximity to alien species stands forming wind breaks positively influences native tree height. We furthermore expected that canopy cover from an alien species can maintain higher diversity of native tree saplings and seedlings than other vegetation types, regardless of the presence of deer. Based on the investigation of these hypotheses, we discuss the potential role of alien species in natural forest restoration.

2. Material and methods

2.1. Study area

The study was conducted within a restoration area in Shiretoko National Park in Hokkaido, the northernmost island of Japan. Mean annual temperature and mean annual precipitation between 1979 and 2018 were approximately 6.3 °C and 1191 mm (http://www.data.jma.go.jp/obd/stats/etrn/index.php). Shiretoko National Park is registered as a United Nations Educational, Scientific and Cultural Organization (UNESCO) World Natural Heritage Site because of its high biodiversity. Approximately 90% of the terrestrial area in the park is covered with pristine natural vegetation, which is mostly mixed conifer–hardwood forests. The remaining land areas were used for agriculture in the early 20th century, but were abandoned by settlers in the late 1960s. Since the 1970s, numerous natural forest restoration projects aiming at revegetation with native species have been conducted. Restoration measures included the establishment of fences (as windbreaks and ungulate exclosures) to address problems such as tree growth inhibition by wind and overgrazing by large herbivores. The area is exposed strong southeasterly winds blowing down from the main mountain range of the peninsula to the sea throughout the year (Fig. 1a; Supplementary Fig. 1). Consequently, wind is a major factor limiting tree growth e.g., through desiccation. Furthermore, the overabundance of sika deer (*Cervus nippon yesoensis*) has resulted in strong overgrazing of forest understory vegetation since the late 1980s. Various types of plantations were created by settlers or restoration activists from the 1950s to the 1990s, planting Sakhalin fir (*Abies sachalinensis* (F. Schmidt) Mast.), Japanese larch (*L. kaempferi*), Sakhalin spruce (*Picea glehnii* (F. Schmidt) Mast.), Japanese white birch (*Betula platyphylla* Sukaczev var. japonica (Miq.) H. Hara) and Japanese oak (*Quercus crispula* Blume). Of these species, *L. kaempferi* is the only species that has been introduced to Hokkaido for the main purpose of silviculture. This species was originally from high-elevation areas on the main islands of Japan. However, in Shiretoko
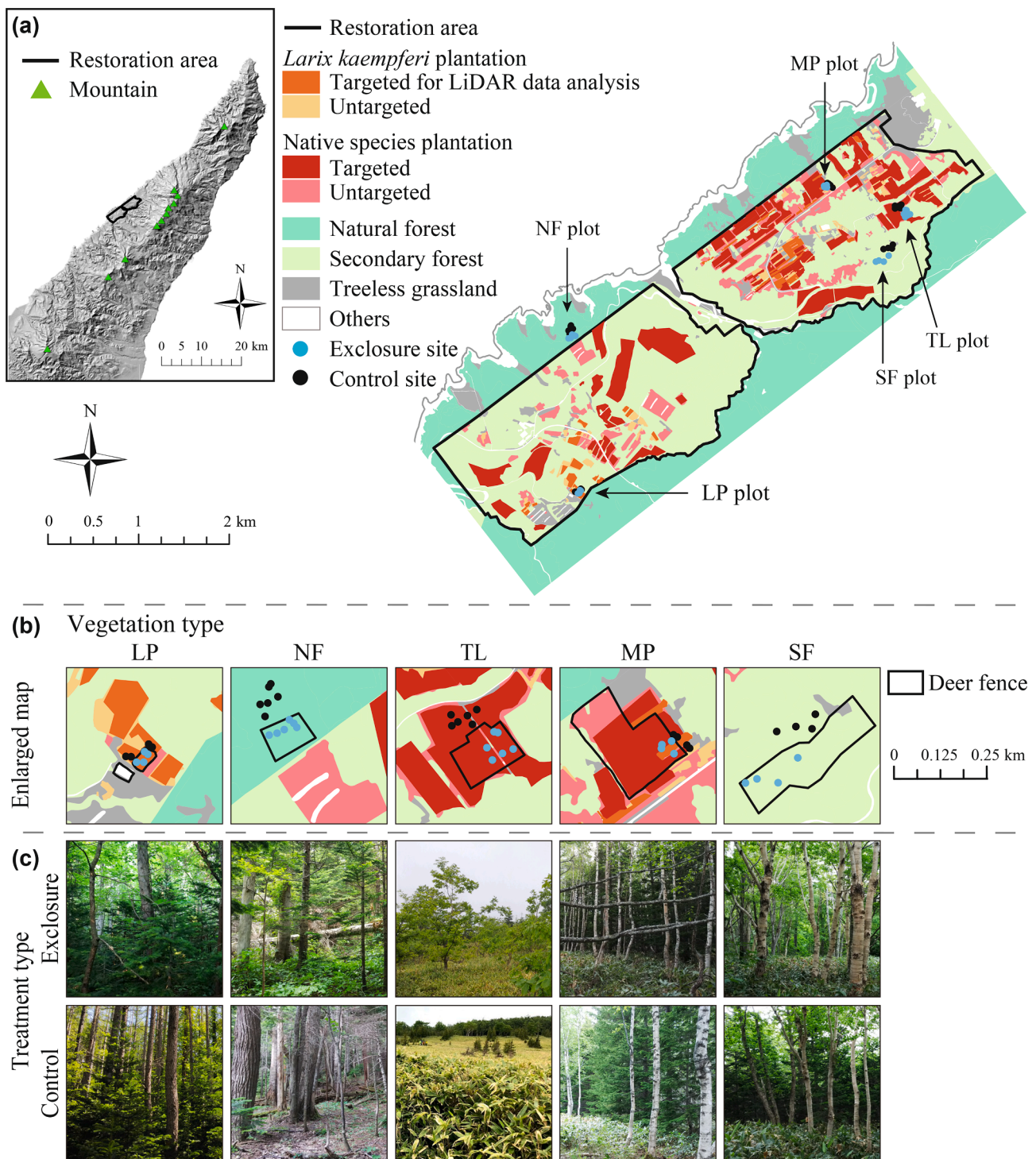
Fig. 1. (a) Map of the Shiretoko Peninsula on Hokkaido Island, northern Japan. The restoration area (black solid line) and main mountains (green triangle) are indicated. This area is exposed to strong wind blowing down from the mountains to the sea. Vegetation classifications are based on a vegetation map presented by the Shiretoko Nature Foundation. Targeted plantations for LiDAR data analysis are displayed (41 *L. kaempferi* stands and 83 stands of native trees). Vegetation data were collected in 48 10 m × 10 m plots inside (exclosure sites; blue point) and outside fences (control sites; black point), in five vegetation types (*LP L. kaempferi* plantation, *NF* natural forest, *TL* treeless land, *MP* mixed plantation, and *SF* secondary forest). The map of the Shiretoko Peninsula was downloaded from the Geospatial Information Authority of Japan website. **(b)** Map of the enlarged plots for each vegetation type. These plots were partitioned into eight plots each in LP, MP, and SF, and 12 plots each in NF and TL. Half of the plots were located inside and outside fences. LP, MP, and TL plots were located within the targeted forest stands for LiDAR data analysis as follows: LP plot within a *L. kaempferi* plantation created in 1967; MP plot within a mixed plantation of *B. platyphylla* and *P. glehnii* created in 1978; and TL plot within treeless land which used to be an *A. sachalinensis* plantation created in 1992 (right stand) and a mixed plantation of *A. sachalinensis* and *P. glehnii* created in 1993 (left stand). **(c)** Views of the plots for each management type (vegetation type × treatment type). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

National Park, *L. kaempferi* has been regarded as an alien tree whose non-persistence is perceived to be desirable by managers in the long term. Today, the restoration areas are a mosaic of different vegetation types, including plantations, remnants of natural forests, secondary forests developing naturally in abandoned areas, and treeless windswept grasslands dominated by dwarf bamboo (mainly *Sasa spiculosa* (F. Schmidt) Makino) (Fig. 1a). In our study area where LiDAR data and vegetation data were collected, there was no human intervention except for tree planting and the establishment of deer fences.

2.2. Windbreak analysis using LiDAR data

2.2.1. Data collection for LiDAR data

We focused our analysis only on plantations for which information on tree species and year of plantation was available from spatially explicit management records of the Shiretoko Nature Foundation. We identified 41 *L. kaempferi* stands and 83 stands of native trees that were planted between 1954 and 1997, and we delineated them using aerial photographs taken in 2004 and manual image interpretation done in ArcGIS (v 10.3.1; ESRI, Redlands, CA, US) (Fig. 1a; Supplementary Table 1). We defined a forest stand as a cluster of trees planted in the same year and composed of the same species, and we created stand boundaries using the polygon feature in ArcGIS. Two 2.5 m spatial resolution raster datasets (the year of plantation and planted tree species) were converted from forest stand polygons, using the ArcGIS Conversion toolbox.

LiDAR data were collected by Kokusai Kogyo Co., Ltd. using an ALS50 system, from an average altitude of 2850 m above ground in June 2004. Data were captured with a scan rate of 27.22 Hz and a scan angle of ±12.5°. The average density of first-return points was 0.5 points per m². From the point clouds, we derived a 2.5 m spatial resolution canopy height model (CHM) and digital terrain model (DTM). We omitted pixels with a tree height <3 m in order to exclude dwarf bamboo from the analysis. For each forest stand, stand height was calculated as maximum canopy height value of all 2.5 m CHM pixels within the stand. From the DTM, terrain slope angle (in degrees) and slope direction (in degrees) were calculated for each 2.5 m pixel using ArcGIS. We also estimated the distance of each 2.5 m pixel from the edge of the nearest stand in the prevailing wind direction (southeasterly) as an indicator of spatial arrangement. We used R software 3.5.0 (R Core Team, 2018), specifically employing the 'lidR' (Roussel and Auty, 2018), 'rgdal' (Bivand et al., 2018), and 'sf' (Pebesma, 2018) libraries.

2.2.2. Statistical analysis of LiDAR data

To test whether *L. kaempferi* stands act as windbreaks we first developed a linear model (LM) predicting stand height from two forest stand metrics (years since planting on the date of LiDAR acquisition in 2004 and planted tree species) and two topographic metrics (slope angle and slope direction), since stand height was normally distributed according to the Shapiro-Wilk test. We focused on forest stand height as a proxy for the windbreak effect (Brandle et al., 2004). Planted tree species (*L. kaempferi*, *A. sachalinensis*, *B. platyphylla*, *P. glehnii*, and *Q. crispula*) were included as binary dummy variables. Slope direction values were sin- and cos-transformed, representing the degree of north-south alignment (hereafter NS) and of east-west alignment (EW), respectively. Those variables ranged from −1 to +1, indicating that the slope direction was closer to either the south or north and the west or east. Years since planting and slope angle were standardized to z scores. We fitted models for all 512 possible combinations of predictors and selected the most parsimonious model based on Akaike's Information Criteria (AIC).

To test whether tree height (2.5 m pixel) in leeward stands was related to the spatial arrangement of windward *L. kaempferi* stands, we used a linear mixed-effects model (LMM). We focused only on pixels whose distance from windbreaks was within ten times the height of the windbreak (i.e., if a windbreak was 10 m tall, the windbreak effect was

tested for a horizontal distance from the windbreak of up to 100 m) (Tamang et al., 2009). In total, 7,313 2.5 m pixels (15 stands) of native tree species in a leeward position of 10 *L. kaempferi* stands were considered to test for a possible windbreak effect (Supplementary Fig. 2). Tree height per 2.5 m pixel was used as the response variable. The explanatory variables were the distance from windbreaks as a fixed effect and stand as a random effect. We used R software 3.5.0 (R Core Team, 2018) with the 'nlme' library (Pinheiro et al., 2018) for the analysis.

2.3. Regeneration analysis using vegetation inventory data

2.3.1. Vegetation data collection

In May 2013, we established 48 10 m × 10 m study plots in five major vegetation types. The five vegetation types were (1) monoculture plantations of *L. kaempferi* (hereafter, LP); (2) mixed plantations of *B. platyphylla* and *P. glehnii* (MP); (3) mixed natural forests of coniferous and broad-leaved species, which are considered primary forests and are dominated mainly by *A. sachalinensis*, *Kalopanax septemlobus* (Thunb.) Koidz., *Acer* spp. (*A. japonicum* Thunb. and *A. pictum* Thunb. subsp. mayrii (Schwer.) H. Ohashi) and *Q. crispula* (NF); (4) secondary forests dominated by mainly *Betula* spp. (*B. erimani* Charm. and *B. platyphylla*), *A. sachalinensis*, *Alnus hirsuta* (Spach) Turcz. ex Rupr. var. hirsute and *Q. crispula* (SF); and (5) treeless lands dominated by a dwarf bamboo (mainly *S. spiculosa*) (TL) (Fig. 1b; c; Supplementary Table 2). Eight plots were located in LP, MP and SF, and 12 plots in NF and TL vegetation types. These plots were designed to minimize the influence of environmental heterogeneity within the same vegetation type. We placed half of the plots in ungulate exclosures protecting vegetation from deer herbivory (exclosure sites), and the other half in areas located outside fences (control sites). In each plot, we randomly established a 5 m × 5 m subplot and five 1 m × 1 m quadrats (48 subplots and 240 quadrats in total). In the summer of 2013 and 2018, we conducted vegetation surveys in all plots. Plant communities were separated into four development stages: canopy trees ≥ 1.3 m in height and ≥ 5 cm in diameter at breast height (DBH) in each plot, tree saplings ≥ 1.3 m in height and < 5 cm in DBH in each plot, tree seedings ≥ 0.5 m and < 1.3 m in height in each subplot, and forest floor plants < 0.5 m in height in each quadrat. All species were identified taxonomically and the number of individuals was counted for each species. Although shrub species are an important component in natural forests, restoring the species composition of canopy trees in natural forests is the main goal of restoration activities at Shiretoko National Park. We thus focused only on the species reaching the forest canopy to estimate the total number of individuals (abundance), species richness and similarity index in the sapling and seedling stages (the regeneration stage).

In each plot, we measured species richness of canopy trees as an indicator of seed supply. In each quadrat, forest floor plants were divided into three groups: tree species, dwarf bamboo species (*Sasa kurilensis* (Rupr.) Makino et Shibata and *S. spiculosa*), and others including woody shrubs, vines and herbaceous species. We calculated the total vegetation cover (%) on the forest floor as an indicator of local crowdedness, and derived the relative cover of each species group. We also measured two indicators of light conditions: relative photosynthetic photon flux density (rPPFD) 0.5 m above the ground with a quantum sensor (LI-190SZ; LI-COR Inc., Lincoln, NB, USA), and canopy openness (%) based on hemispherical photographs using CanopOn2 software (A. Takenaka, available at http://takenaka-akio.org/etc/canopon2/). rPPFD and canopy openness were measured at the center of each quadrat in the summers of 2013 and 2018, respectively.

2.3.2. Statistical analysis of vegetation data

To detect which plot is suitable for saplings and seedlings to regenerate, we compared differences in abundance and species richness (Supplementary Table 3) among vegetation types (LP/NF/TL/MP/SF) and among treatment types (exclosure/control), separately for each

survey year (2013/2018) using two-way analysis of variance (ANOVA). According to the result of this analysis, interaction effects between vegetation type and treatment type were significant for species richness of the regeneration stage in both survey years, except for that of seedlings in 2018 (Supplementary Table 4). Thus, we compared differences in abundance and species richness of the regeneration stage among vegetation types using Tukey's HSD test, and among treatment types using *t*-test. We also compared species richness of seedlings in 2018 among management types (vegetation types × treatment types) using Tukey's HSD test.

To investigate the similarity in species composition between canopy trees in natural forests and the regeneration stage in each vegetation type, we calculated Sørensen's similarity index based on species presence/absence data, separately for each survey year and treatment type. In light of the restoration target described above, we used species composition of canopy trees in NF as a reference. The similarity values range from 0 to 1, indicating that two species compositions share few and many species, respectively. We made a pair of plots by considering exclosure/control categories and survey year (e.g., saplings in the LP exclosure plots in 2013 (4 plots) were compared with canopy trees in the NF exclosure plots in 2013 (6 plots), yielding 24 combinations). Differences in the similarity index were compared among vegetation types, for saplings and seedlings using Tukey's HSD test.

To evaluate the effects of environmental conditions on the regeneration stage in each vegetation type, we used a classification tree approach. In this model, the data are partitioned into two groups based on the value of the explanatory variable at each split (De'ath and Fabricius, 2000). The response variable was vegetation type (LP/NF/TL/MP/SF) and the explanatory variables were treatment type (exclosure/control), light conditions (rPPFD in 2013, canopy openness in 2018), seed source index (species richness of canopy trees) and forest floor indices regarding competition (the relative cover of each species group to the total vegetation ground cover). Given the close relationships between the total vegetation ground cover and the coverage of dwarf bamboo species (Supplementary Fig. 3), we excluded the total vegetation ground cover from the explanatory variables. The tree-based models were constructed separately for each survey year, following the strategy recommended in De'ath and Fabricius (2000). First, we carried out 50 sets of ten-fold cross-validation, and then selected the optimal tree size from each cross-validation based on the 1-SE rule, with the best result being the smallest tree with an estimated error rate within one standard error of the minimum cross-validated error (De'ath and Fabricius, 2000). Second, we estimated the most frequent tree size in 50 selected tree sizes (Supplementary Fig. 4). The resulting complexity parameter associated with the optimal size of each tree model was 0.042 in 2013 and 0.029 in 2018. Finally, according to those parameters, we pruned the full tree to its optimal size and produced two classification tree models. In the control settings to fit 'rpart' models, 20 was set as the minimum number of observations in a node before attempting a split. We used R software 3.5.0 (R Core Team, 2018), with the 'vegan' (Oksanen et al., 2018) and 'rpart' (Therneau and Atkinson, 2018) libraries for data analysis.

3. Results

3.1. Tree height

We first examined the relationships between stand height and both forest stand metrics and topographic metrics. The best combination of variables to explain stand height were planted species *L. kaempferi*, *A. sachalinensis*, *B. platyphylla*, and *P. glehnii*, slope angle, and EW (LM, adjusted $R^2 = 0.6675$, $P < 0.01$; Table 1). The coefficient for *L. kaempferi* was 4.63 ± 1.01, showing that whether the stand is composed by *L. kaempferi* strongly affects stand height. Indeed, *L. kaempferi* stand height was the highest of the five planted tree species (Supplementary Table 1). Given a positive relationship between windbreak effects and

Table 1
Coefficients and standard errors (SE) of the most parsimonious model applied to stand height ($n = 124$). Significance levels: *$P < 0.05$. NS: not significant.

Variable		Coefficient	SE
Planted species	*L. kaempferi*	4.63*	1.01
	A. sachalinensis	−1.10[NS]	0.73
	B. platyphylla	1.62*	0.62
	P. glehnii	−2.99*	0.87
Geographical factors	Slope angle	1.52*	0.29
	Slope direction (EW)	1.66*	0.52
Intercept		15.66*	0.90
AIC		588.85	
Adjusted R^2		0.6675	

stand height (Brandle et al., 2004), *L. kaempferi* stands were expected to have a higher windbreak function than other plantations.

We next assessed the effect of spatial arrangement of windbreaks on tree height (2.5 m pixel), considering *L. kaempferi* stands as windbreaks based on the abovementioned results. Mean *L. kaempferi* stand height was about 20 m (19.94 m, n = 41; Supplementary Table 1), so we analyzed 7,313 2.5 m pixels of 15 leeward stands, considering a maximum windbreak effect of 200 m (Supplementary Fig. 2). Time since planting of the leeward stands ranged from 10 to 26 years, indicating that these stands were at a comparatively early stage of stand development. Native tree species height significantly decreased with distance from windbreaks (LMM, conditional $R^2 = 0.544$, $P < 0.01$; Fig. 2), indicating that the spatial proximity to the alien species *L. kaempferi* positively affected the initial height growth of native species.

3.2. Tree regeneration

We analyzed vegetation data and environmental data in both 2013 and 2018, but similar trends were observed. Here, we mainly showed the results of 2013, and we provide those of 2018 in the Supplementary
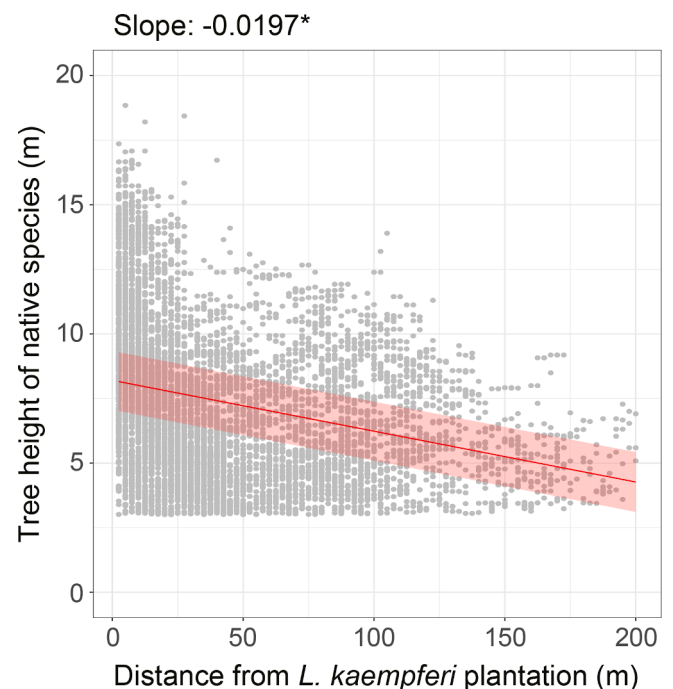

Fig. 2. Linear mixed-effects model fit for the effect of distance from *L. kaempferi* plantation on native tree height ($n = 7313$). Red line and shaded area indicate the mixed model fit and the 95% confidence interval, respectively. Slope values are shown with significance levels: *$P < 0.01$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Material for additional confirmation based on data collected in 2018 (cf. Supplementary Fig. 6–9).

3.2.1. Species diversity and species composition

In areas located outside deer fences (control sites) in LP, NF and SF vegetation types, only *A. sachalinensis* was observed in both sapling and seedling stages (the regeneration stage). Among all plots, *L. kaempferi* was not observed in the regeneration stage, but four individuals were found in the forest floor stage in 2013 (one in LP and three in MP). Between the two observation years, no new recruits into the canopy tree stage were observed for *L. kaempferi*.

The abundance of trees in the regeneration stage was significantly higher in LP compared to other vegetation types (Fig. 3). Species richness in the regeneration stage was significantly higher inside fences (exclosure sites) in LP compared to other management types (vegetation types × treatment types) (Fig. 4). In LP and TL, there were significant differences in species richness of the regeneration stage between the exclosure and control sites. Moreover, excluding deer significantly affected the abundance and species richness of trees in the regeneration stage (Supplementary Table 4), while there were no significant differences in abundance and species richness between treatment types, except for the abundance of seedlings in 2013 and the species richness of seedlings in 2018 (Supplementary Fig. 5c; e).

In the exclosure sites, there were significant differences in similarity index of the regeneration stage between LP and TL, and that of seedlings between NF and TL (Fig. 5a; c). Mean similarity values in the exclosure sites in LP tended to be higher than those in other vegetation types, indicating that species composition of the regeneration stage in LP was more similar to that of the overstory in NF. In the control sites, the species compositions in the regeneration stage was similar between LP, NF and SF (Fig. 5b; d). Note that mean similarity values in the control sites tended to be high, but only *A. sachalinensis* regenerated in LP, NF, and SF.

3.2.2. Environmental conditions of understory vegetation

The optimal model in 2013 retained four environmental variables: the species richness of the overstory; the relative cover of tree species, dwarf bamboo species, and other species of vegetation ground cover. The optimal number of branches in the tree-based model was five (Fig. 6; Group 1–5).

Vegetation type category was best reflected by the species richness of the overstory. All TL quadrats (60 quadrats) were classified as Group 5. Of the remaining quadrats (richness of overstory ≥ 1), 180 quadrats were classified into two groups, according to whether the relative cover of dwarf bamboo species to the total vegetation ground cover was low (106 quadrats) or high (74 quadrats). Almost half of the quadrats in LP (Group 1, 17 quadrats) were separated from most quadrats in NF (Group

2, 58 quadrats), indicating differences in the relative cover of tree species to the total vegetation ground cover between LP and NF. Indeed, the coverage of tree species tended to increase with the total vegetation ground cover in LP, whereas that of others including woody shrubs, vines and herbaceous species tended to increase in NF, in each year (Supplementary Fig. 3).

4. Discussion

Here, we provide evidence for the positive effects of an alien tree species on naturally regenerating forests at the local scale. The contributions of the alien species in focus here are two-folds: alleviation of wind-induced growth inhibition and provision of suitable regeneration habitat. Specifically, *L. kaempferi*, a domestic alien species which was initially not planted with the intention to restore natural forests, acts as a nurse plant for native tree species. This nursery function facilitated native tree growth in early stages of stand development on the leeward side of non-native plantations, and facilitated native sapling and seedling establishment under non-native trees. Generally, nurse plants can be useful tools to improve restoration projects because they enhance survival and growth of native species (Padilla and Pugnaire, 2006), even if they are non-native (Schlaepfer et al., 2011). Our findings suggest that the utilization of alien species as nurse plants could be an effective restoration tool at early stages of ecosystem recovery, with aliens mitigating environmental barriers for native species recovery.

Our results show that *L. kaempferi* plantations could protect native tree species from predominant winds (Table 1), as it is well adapted to harsh conditions, and has rapid growth and high cold tolerance (Gower and Richards, 1990; Isebrands and Hunt, 1975). These traits make it an efficient mechanical barrier to wind damage (Salem, 1989). Consequently, larch species have been widely used as windbreaks historically, even outside of their natural range, such as Europe (Mitchell, 1972) and Japan (Tsuji et al., 2005). In particular, we here focused on the distance to *L. kaempferi* stands as an indicator of its windbreak function (Fig. 2). Distance from windbreak negatively correlated with tree height on the leeward side, resulting from the negative effects of distance on wind-speed reduction (Brandle et al., 2004). Most native tree plantations were not located on the windward side, where a windbreak function was expected (Supplementary Fig. 2). Although it is not fully certain why *L. kaempferi* was planted in our study area, the spatial pattern of *L. kaempferi* plantations (linear features and distributed across open lands) implies that this alien tree has been predominately planted to break strong winds. In addition to distance, windbreak porosity, which is considered the ratio of the open portion of the windbreak to its total volume, possibly affects windbreak effects (Tamang et al., 2009). *L. kaempferi* stands allow some wind to penetrate because of their high porosity during winter (deciduous species), resulting in lower turbulence on the leeward side of windbreaks. Additionally, snow damage, which is another important limitation of tree regeneration (Mori and Hasegawa, 2007; Mori et al., 2008), is expected to be mitigated by *L. kaempferi*, although we here did not measure the spatial redistribution of snow around windbreaks (Schmidt, 1982). In general, windbreaks have been used for centuries mainly to protect agricultural crops and railway lines from wind damage and erosion (Salem, 1989). Our finding highlights that we could have not only a social benefit but also an ecological benefit from the introduced species, even if it was not intentionally established as windbreak and shelterbelt for native tree establishment.

We found that *L. kaempferi* plantations positively affected tree assemblages at the regeneration stage (Fig. 3), even under excessive browsing pressure (Fig. 4). Similarity of species composition did not show significant difference between *L. kaempferi* plantations and other vegetation types (Fig. 5), suggesting that the recovery of species composition tends to be slower than that of species richness (Chazdon et al., 2009; Matos et al., 2020). While deer fencing has certain effects on local vegetation recovery in various regions worldwide (Côté et al.,
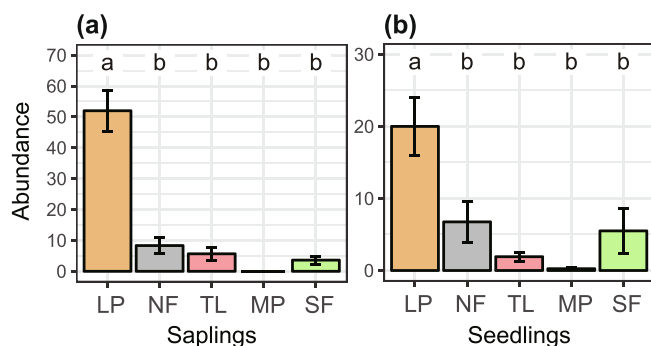

Fig. 3. Abundance of saplings and seedlings. Results are based on a survey in 2013 (see Supplementary Fig. 6 for results from the 2018 survey). Different lower-case letters indicate significant differences between vegetation types in each regeneration stage ($P < 0.05$). Means are shown with standard error. For abbreviations of vegetation types, see Fig. 1.
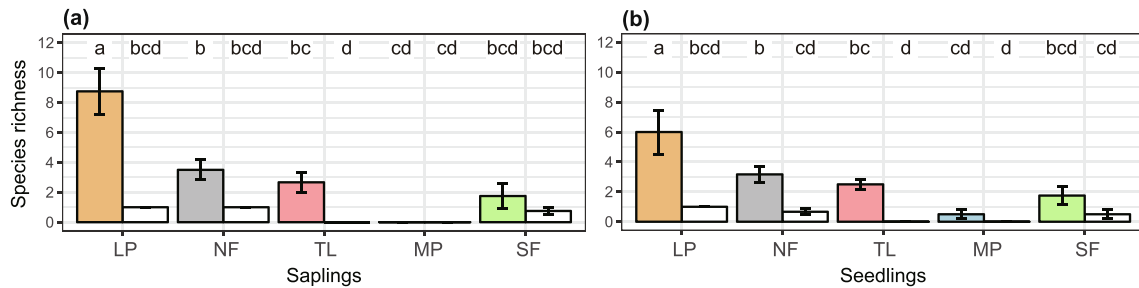
Fig. 4. Species richness of saplings and seedlings. Results are based on a survey in 2013 (see Supplementary Fig. 7 for results from the 2018 survey). Different lower-case letters indicate significant differences between management types (vegetation type × treatment type) in each regeneration stage (*P* < 0.05). Colored bars and white bars distinguish between the exclosure and control sites, respectively. Means are shown with standard error. For abbreviations of vegetation types, see Fig. 1.
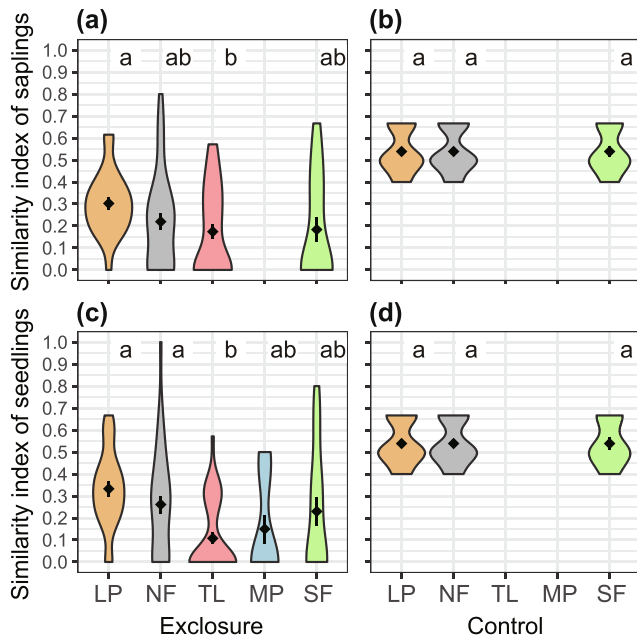

Fig. 5. Frequency distributions of the similarity index of saplings and seedlings, shown by violin plots. Results are based on a survey in 2013 (see Supplementary Fig. 8 for results from the 2018 survey). Similarity index based on species presence/absence data ranges from 0 to 1, indicating low and high similarity to the species composition of overstory NF. The black points and vertical lines indicate means and standard error, respectively. Different lower-case letters indicate significant differences between vegetation types in each regeneration stage and treatment type (*P* < 0.05). For abbreviations of vegetation types, see Fig. 1.

2004; Nishizawa et al., 2016), it is not a panacea given the multiple challenges for forest restoration. Specifically, synergistic influences between deer overgrazing and prevailing winds make restoration challenging in Shiretoko National Park. We found that fencing *L. kaempferi* plantations could have synergistically positive effects on the species richness of regenerating trees (Fig. 4). Additionally, our results show that the coverage of dwarf bamboo species in *L. kaempferi* plantations tended to be low (Fig. 6; Group 1 and 2). Dwarf bamboos are dominant species in the understory of many temperate forests in East Asia, including Japan (Franklin et al., 1979; Noguchi and Yoshida, 2005), as represented by MP and SF in this study (Supplementary Fig. 3). Their cover is recognized as an ecological filter for restoration, inhibiting tree regeneration through mechanisms such as high litter production and low light availability (Doležal et al., 2009). We also found that the cover of native tree species was high in alien plantations (Fig. 6; Group 1). This could be the result of functional differences between *L. kaempferi* and native species, such as leaf phenology (deciduous vs. evergreen) and

light requirement, as reported elsewhere (Lugo, 2004). Furthermore, *A. sachalinensis*, which can survive under low light because of its high shade tolerance, originally dominates the regeneration in *L. kaempferi* plantations. High densities of native tree species over different life stages (saplings, seedlings and forest floor plants) imply that monoculture plantations of alien species will likely be replaced by diverse stands of native species in the long term (cf. Aide et al., 2000). In addition to the turnover of native species, the failure of *L. kaempferi* individuals to regenerate further document that the alien tree species is not invasive in our study system (Blackburn et al., 2011).

The introduction of alien species often results in the emergence of novel ecosystems (Hobbs et al., 2006) with potentially irreversible consequences (Hallett et al., 2013; Hobbs et al., 2014). Our study system can be classified as a hybrid ecosystem, mixing new and old components (Hobbs et al., 2009). Ecological filters that limit the success of forest regeneration might result from no-analog conditions, such as disturbance frequencies modified by anthropogenic effects. Shiretoko National Park might return towards its historical state, because *L. kaempferi* relaxes those filters, while not successfully regenerating itself. However, some caveats of our study have to be considered when interpreting our results. First, we did not evaluate alien species impacts at the landscape scale, yet alien species might perform differently under a range of environmental conditions (Felton et al., 2013). Second, we lack long-term quantitative data on *L. kaempferi* in our system, restricting our ability to predict whether *L. kaempferi* plantations will indeed be replaced by native species. Third, we did not assess the effects of alien species on other taxonomic groups (e.g., mammals and birds) as well as on ecosystem processes (e.g., nutrient cycling and net primary production). *Larix* spp. have been reported to be potentially invasive (Nuñez et al., 2011; Richardson and Rejmánek, 2004). In Hokkaido, naturally established *L. kaempferi* has also been observed in disturbed areas, for instance, sites affected by volcanic eruptions undergoing primary succession (Akasaka and Tsuyuzaki, 2009; Kondo and Tsuyuzaki, 1999) and abandoned fields (Nakagawa, 2014). In our study, however, no *L. kaempferi* saplings and seedlings emerged between the two observation points, suggesting that an invasion of the species into undisturbed areas is unlikely (Mortenson and Mack, 2006; Peterken, 2001). Evidence is accumulating that alien species could make an important contribution to supporting desired compositional and functional characteristics of ecosystems (Gawel et al., 2018; Maclagan et al., 2018; Mascaro et al., 2012). An earlier study in this area found that *L. kaempferi* plantations facilitated a novel interaction between brown bears and cicada nymphs as alternative food resources (Tomita and Hiura, 2019). However, further research is required to evaluate the long-term consequences of alien species such as *L. kaempferi*.

Given the limited resources available for biological conservation, it is increasingly required to achieve multiple goals simultaneously with restoration measures (Brancalion et al., 2018; Matos et al., 2020). The potential utility of alien species for forest restoration has also been reported for other systems. For instance, in the tropical region where restoration activities play a central role in global restoration programs
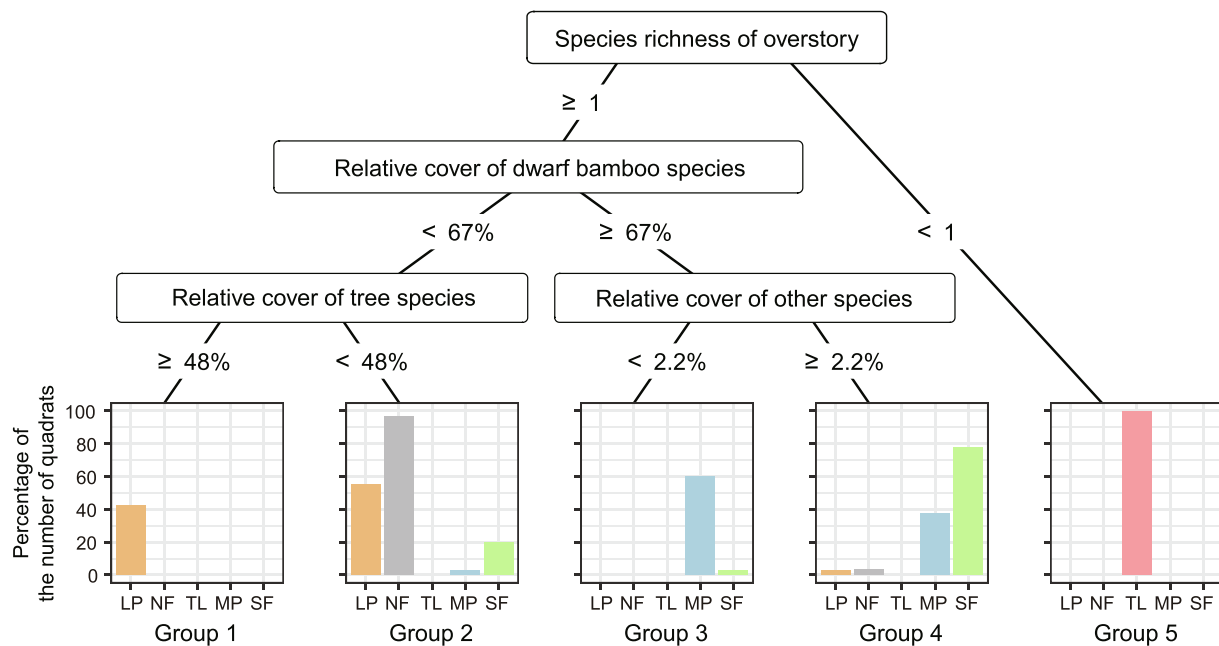
Fig. 6. Classification tree model to identify the key environmental conditions for understory vegetation among vegetation types. Results are based on a survey in 2013 (see Supplementary Fig. 9 for results from the 2018 survey). Bars indicate the percentages of the number of quadrats classified in the respective vegetation type. There were 40 quadrats in each of LP, MP and SF, and 60 quadrats in each of NF and TL vegetation types. For abbreviations of vegetation types, see Fig. 1.

such as Forest and Landscape Restoration (FLR) and the Reducing Emissions from Deforestation and Forest Degradation (REDD+) program, novel mangrove forests can support both carbon storage and sediment retention in coastal ecosystems, expecting to be a buffer for sea level rise under climate change (Soper et al., 2019). Recently, "Nature-based Solutions" (NbS), which is a framework working with and enhancing nature to help address societal challenges, such as climate-change mitigation and biodiversity protection, has received increasing attention (Cohen-Shacham et al., 2016; Seddon et al., 2020b). Although FLR is framed under the NbS umbrella (Cohen-Shacham et al., 2019), planting non-native trees has been regarded as an undesirable component in supporting naturally functioning forests (Seddon et al., 2020a). New species combinations in novel or hybrid ecosystems are more likely to arise in a rapidly changing world, inter alia due to increasing disturbance activity (Seidl et al., 2020). This highlights the importance of knowledge regarding the potential effects of alien species at the local scale in different ecosystems around the globe. Our results underscore that accepting alien species as part of ecosystem (Hobbs et al., 2014) in the short term can promote native species in the long term. We note, however, that the removal of alien species needs to be considered whenever they are invasive, i.e., where they successfully establish themselves and spread widely (Blackburn et al., 2011). While we do not advocate for the proactive introduction of alien species, managers need to carefully examine the potential of alien species in areas where they have already been introduced and established. Assessing whether naturally regenerating forests can be sustained even in no-analog assemblages could be a suitable approach to make restoration more cost-effective and successful.

5. Conclusion

Combining remote sensing and vegetation inventory in diverse vegetation types we revealed a positive relationship between an alien tree species (*L. kaempferi*) and the growth and regeneration of native tree assemblages. First, *L. kaempferi* plantations act as windbreaks and protect native species from predominant winds, likely because of their rapid growth and cold tolerance. Second, *L. kaempferi* canopies tend to promote a higher abundance and species richness in understory tree species

than other vegetation types, possibly because of functional differences between *L. kaempferi* and native species. We conclude that alien species can act as nurse plants, facilitating the long-term restoration of native tree assemblages. As long as alien species are not invasive, alien species can provide co-benefits between several goals of restoration such as increasing carbon stocks and fostering biodiversity conservation. Managers should thus consider flexible options such as temporarily accepting alien species as an ecological tool for supporting a transition towards naturally regenerating forests, especially when novel species combinations are already present.

CRediT authorship contribution statement

Kureha F. Suzuki: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Writing - original draft, Writing - review & editing, Visualization. **Yuta Kobayashi:** Conceptualization, Investigation, Writing - review & editing. **Rupert Seidl:** Conceptualization, Writing - review & editing. **Cornelius Senf:** Conceptualization, Software, Writing - review & editing. **Shinichi Tatsumi:** Investigation, Writing - review & editing. **Dai Koide:** Investigation, Writing - review & editing. **Wakana A. Azuma:** Investigation, Writing - review & editing. **Motoki Higa:** Investigation, Writing - review & editing. **Tomoyo F. Koyanagi:** Investigation, Writing - review & editing. **Shenhua Qian:** Investigation, Writing - review & editing. **Yuji Kusano:** Resources. **Ryota Matsubayashi:** Resources. **Akira S. Mori:** Conceptualization, Investigation, Writing - review & editing, Funding acquisition, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119253.

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