Doctoral thesis

Influences of abiotic and biotic factors on plant-plant facilitation toward forest restoration

（森林再生に関わる植物間の促進作用への非生物的・生物的要因の影響に関する研究）

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Abstract

Forests are among the most extensive terrestrial ecosystems, supporting diverse ecological functions. In recent decades, the increasing frequency of extreme climatic events driven by global climate change, coupled with disturbances from human activities, places forests at risk of degradation. After disturbance, the natural regeneration process begins with the recruitment of plant seedlings. The dynamics of the seedling stage are crucial for determining subsequent vegetation recovery patterns. However, seedlings are likely to be highly susceptible to harsh environments after disturbances. Furthermore, interactions among seedlings, influenced by both biotic and abiotic environmental factors, shape the trajectory of forest restoration and determine the composition and structure of future stands.

Facilitation among plants, either directly or indirectly, can enhance the performance of the interacting participants. Compared to natural forests, disturbed sites experience stronger environmental stress, under which plant facilitation is more likely to be critical for seedling colonization success and performance. Severe forest disturbance events, such as landslides and the ongoing soil erosion that follows, create new environmental conditions in the disturbed areas. However, whether facilitation occurs among newly recruited seedlings following disturbance, how such facilitation is shaped by environmental conditions, and its ecological consequence towards restoration remain unclear. In my doctoral research, I investigate how the new biotic and abiotic conditions following landslides influence the process of facilitation during seedling regeneration, aiming to uncover insights for forest restoration and management. Specifically, by combining field surveys and common garden experiments, I conducted the following three studies.

In Chapter 2, I am dedicated to clearly illustrating in the post-landslide area, how the initial spatial distribution of seedlings emerges, and how those abiotic and biotic environmental conditions, i.e. neighboring seedlings' interactions and rill erosion, influence seedling performance. Based on a replicated Artificial Landslide Experiment Sites (i.e., ALES), in the first growing season after the disturbance, I monitored the seedlings' performance and recorded the rill erosion. This study indicated that, in the post-landslide area, newly recruited seedlings primarily exhibited spatial clustering with conspecific neighbors and demonstrated significantly higher abundance around rills. At the scale of several centimeters, proximity to conspecific and heterospecific neighbors significantly enhanced focal seedling survival and growth. The survival of seedlings near rills decreased, and this response varied by species. Interactive effects of plant facilitation and rill erosion on tree seedling colonization toward restoration have been validated. The proximity of a seedling to heterospecific neighbors attenuated the negative influences of being near rills. This study suggests that there were conspecific and heterospecific facilitative effects on seedling survival at this post-landslide habitat, but the relative importance of conspecific and heterospecific facilitative effects could be dependent on the degree of rill erosion. This study inspired the understanding that the effects of plant-plant facilitation, together with the fine-scale geomorphological heterogeneity, shape seedling performance, thereby influencing the forest restoration process.

In Chapter 3, I aimed to elucidate the genetic properties of the newly recruited seedlings and their effects on seedling performance. In particular, the following questions were addressed: 1) are there population differentiations among spatially proximate disturbance sites after landslides, 2) how landslide scars and subsequent rill erosion shape the genetic structure of seedling populations, and 3) how genetic relatedness among seedlings influence their performance. By using the same ALES sites of Chapter 2, I examined the genetic structure of the dominant seedlings, *Abies sachalinensis* (F.Schmidt) Mast. (Pinaceae), in each landslide site. I extracted genomic DNA from 292 seedlings and performed MIG-seq analysis. This study indicated that the genetic structure of three spatially proximate seedling populations exhibited significant differentiation, suggesting strong dispersal limitations. These dispersal limitations, coupled with rill erosion within the patches, contributed to the low genetic diversity of the within-site seedling populations. The genetic distance between a focal seedling and its nearest neighbor significantly affects the focal seedling's growth, and this effect depends on their spatial distance. This study suggests that the restoration management of disturbed sites should consider the dispersal capacity of surrounding

tree species and the genetic structure of source populations. Considering the genetic diversity of restored populations may provide valuable insights for forest restoration.

In Chapter 4, I explored how species diversity-ecosystem functioning relationships are influenced by soil microorganisms and intraspecific genetic diversity. In parallel, how this species diversity, in turn, shapes the composition of soil microorganisms (i.e., fungi and bacteria). I conducted a common garden experiment to control intraspecific genetic diversity by combining seedlings from different origins and to regulate soil microorganisms by inoculating natural soil collected beneath maternal trees or commercial Akadama soil. In fact, the composition of microbe communities was significantly affected by the soil inoculation treatment. Both soil inoculation treatment and genetic diversity treatment influenced the sign and strength of species diversity effects on ecosystem functioning. The presence and absence of natural soil microorganisms affected the selection effects of species diversity. Moreover, increasing genetic diversity improved the complementarity effects of species diversity on ecosystem functioning. The effect of natural soil inoculation on the relationship between species diversity and ecosystem functioning was stronger than the effects of intraspecific diversity. Furthermore, changes in fungal community composition from the start to the end of the study were driven by whether planted tree seedlings were in polyculture or monoculture. My results indicated that plant species diversity could also play a critical role in the restoration of soil microbial communities, which may feedback to the subsequent ecosystem functioning. Overall, this common garden study suggests that an increase in the genetic diversity of plants could strengthen the positive association between species diversity and ecosystem functioning. It should also be noted that the management of soil inoculation or microbe communities could much enhance species diversity effects. Toward a long-term forest restoration project, soil properties should be tailored to the local plant community composition and the stage of restoration, as soil inoculation during the early successional stages may disproportionately boost the performance of dominant seedlings.

In summary, during the natural regeneration process of plants after disturbance, the fine-scale spatial and genetic structure of seedlings, small-scale topographic heterogeneity, and other ecosystem participants such as soil microorganisms collectively shape plant facilitation. Furthermore, my research pioneeringly reveals the interactive effects of plant species and genetic diversity on ecosystem functioning. Species diversity fosters plant-soil feedback, while increased genetic diversity further promotes the relationship between species diversity and ecosystem functioning. In future forest restoration management, natural regeneration of local populations, supplemented by the manipulation of new biotic and abiotic factors, will benefit the long-term development of restored communities.

CONTENTS

Chapter 1. General introduction

General introduction

Plants are usually surrounded by neighboring individuals in natural and managed environments, and plant-plant interactions influence both the performance of plant individuals and the functioning of ecosystems (Sato and Wuest, 2024). In terms of the consequences of interactions, facilitation occurs when one species positively impacts the fitness of another (Zélé et al., 2018). Facilitations can ameliorate environments through processes such as redistributing soil moisture (Zou et al., 2005), concentrating soil nutrients (Zhang et al., 2018), stabilizing substrate (Kéfi et al., 2016), moderating microclimate (Brigham and Suding, 2024), shielding neighbors from wind (Schöb et al., 2013) and water runoff (Mazal et al., 2021), and protecting from herbivory (Carroll and MacDougall, 2024), thereby shaping community productivity and stability (Montesinos, 2015; Soliveres and Maestre, 2014). Moreover, the effects of plant facilitation are considered to increase under the harshness of abiotic or biotic challenges (stress-gradient hypotheses) (Bertness and Callaway, 1994). However, we still lack an understanding of how newly emerged abiotic and biotic environmental factors influence plant facilitation, and subsequently modify the process of forest primary succession following severe disturbances.

Forests cover about one-third of the world's land area (Sánchez et al., 2019). Forest ecosystems perform multiple functions, such as carbon sinks (Pan et al., 2024), regulating climate (Thom et al., 2017), preventing soil erosion and degradation (Ren et al., 2024), supporting biodiversity (Brockerhoff et al., 2017), and providing resources for human societies (Köhl et al., 2015). A landslide in forest is a mass movement of materials, including soil, rock, and debris, down a slope, removing above- and below-ground biomass (van Westen et al., 2003). Landslides are often triggered by events such as heavy rainstorms (Liu et al., 2021) and earthquakes (Ito et al., 2021) and are some of the major causes of forest disturbance. In recent decades, the frequency of landslides worldwide has increased due to global climate change (Ozturk et al., 2022), combined with anthropogenic factors such as deforestation and land-use change (Pacheco Quevedo et al., 2023), making forest restoration in post-landslide areas an urgent and challenging issue.

In mountainous forests, major natural disturbances, such as landslides, often result in "stand-replacement" events (Swanson et al., 2011), followed by primary succession driven by pioneer species (Dalling, 2008). Natural regeneration plays a pivotal role in shaping the forest restoration trajectory and determining the composition and structure of future stands (Mejstřík et al., 2024). Unlike tree planting, the process of natural colonization of restoration is regarded as a passive and more ecologically sound approach (Bauld et al., 2023). It has gained significant attention for being more economical, efficient, and less risky for tree disease and pests (Di Sacco et al., 2021). In the long term, natural regeneration creates structural heterogeneity due to variations in age, tree species, and species composition, and gaps in forests can provide more habitats for flora and fauna, promoting biodiversity in restoration sites (Pedersen et al., 2023). However, the recruitment and colonization success of new seedlings in post-landslide areas face numerous uncertainties. While a growing body of work has focused on plant regeneration following landslides (Takaoka, 2019; Velázquez and Gómez-Sal, 2008; Yang et al., 2023), there is a lack of studies examining how spatial structures of newly recruited seedlings, i.e. the spatial distribution and spatial genetic structure, drive their colonization.

Landslides, along with the subsequent ongoing erosion, alter the abiotic environment of forests. The physical environment is greatly altered following a landslide (Walker and Shiels, 2012). Large subaerial landslides can have significant morphologic impacts on the Earth’s surface, causing slope retreat and leading to a loss of soil resources (Schuster and Highland, 2003). Furthermore, landslides create forest destruction. Widespread stripping of natural forests by mass movements has been noted in tropical areas as the result of large-scale, earthquake-induced landslide activity (Schuster and Highland, 2003). Furthermore, bare (vegetation-free) soil is often the immediate consequence of a landslide, and therefore the amount of post-landslide erosion that occurs on landslide slopes can be significant (Walker and Shiels, 2012). Erosion that occurs after a landslide event is often neglected, but high rates of soil erosion can happen even within months of the initial disturbance (Walker and Shiels, 2008), exerting complex and long-lasting effects on the geographical and biological aspects of the landscape. The ongoing soil erosion

following a landslide can affect substrate stability and fertility (carbon, nitrogen, phosphorus and potassium) (Walker and Shiels, 2008; Zarin and Johnson, 1995), thereby influencing vegetation development. Moreover, it also creates topographic heterogeneity in both erosion and depositional zones.

New biotic conditions created after the landslide influence seedling performance during the regeneration process. Seedlings of pioneer species (Brokaw, 1987) or dominant species (Connell and Slatyer, 1977) are likely to be dispersed from the adjusted forest and initially colonize the post-landslide area, resulting in low species richness. On the other hand, the physical barrier caused by the landslide, coupled with the disruption of pollinator and seed disperser communities, may block gene and seed flow among plant species, leading to potential differentiation of plant populations (Nazareno et al., 2021). These processes result in newly recruited seedlings experiencing intra- and interspecific interactions that differ from those in mature forests, with the relatively infertile resource conditions and ongoing soil erosion in the post-landslide areas, likely causing further differences in the interaction patterns. Additionally, the mechanisms of biodiversity-ecosystem functioning relationships underlying species interactions are also likely to change in these disturbed areas.

Shallow landslides typically involve surface soil failing approximately 50-cm depth on the slope (Dietrich et al., 2008), that harbors the highest biomass and the most active soil microbes (Lavahun et al., 1996). Soil microorganisms are microscopic life forms in soil, including bacteria, fungi, and other groups such as viruses and protists (Islam et al., 2022; Sala et al., 2017). Soil microorganisms are well known to enhance plant performance through direct or indirect interactions with plant roots (Artursson et al., 2006). Soil bacteria and fungi, through symbiotic relationships, can improve nutrient acquisition and resistance in plants (Lladó et al., 2017; Wahab et al., 2023). At the same time, they decompose litter and debris, improving soil resource availability (Rashid et al., 2016). In post-landslide areas, plant-soil interactions may change due to the disruption of soil structure, which can further impact plant-ecosystem functioning (Forero et al., 2021).

In my doctoral research, I investigated how the new abiotic and biotic factors following disturbance influence plant-plant interactions, aiming to uncover insights for forest restoration and management. By combining a natural setting experiment and a common garden experiment, I conducted three studies. Firstly, at a site that had recently experienced a severe forest landslide, I monitored the spatial distribution and performance of newly recruited seedlings during the first growing season, aiming to reveal the contribution of fine-scale spatial conditions of abiotic and biotic (neighbor) factors to seedling colonization. Secondly, building on the same natural setting experiment, I illustrated how a genetic approach sheds new light on the fine-scale spatial conditions of neighbor identity and genetic diversity, and their influences on plant performance. Finally, based on a well-manipulated common garden experiment, I further integrated biodiversity–ecosystem functioning (BEF) into forest restoration strategies. Fine-scale biotic conditions influence the performance of plant individuals, which consequently modifies the outcomes of BEF, laying the groundwork for developing effective forest restoration and management.

Specifically, in Chapter 2, my goal is to clearly illustrate how the initial spatial distribution of seedlings emerges, how rill erosion occurs at post-landslide stages, and how those environmental conditions influence seedling performance. The field survey was conducted within a replicated artificial landslide experiment, where slopes were artificially cleaned in mountainous forests to simulate the depositional zones formed after natural landslides. During the first growing season following the construction of the artificial landslides, I recorded the spatial distribution patterns of newly recruited seedlings of two dominant species and monitored their performance throughout the season.

In Chapter 3, I aimed to determine whether the newly recruited seedlings exhibit population differentiation tendencies after landslides, how landslide scars and subsequent rill erosion shape the genetic structure of seedling populations, and how genetic relatedness among seedlings drives their performance. I collected genomic DNA from leaf samples of the dominant species seedlings to analyze the genetic structure of the population.

In Chapter 4, I established a common garden experiment to explore how species diversity-ecosystem functioning relationships are influenced by the new biotic conditions introduced by landslides, namely genetic diversity and soil microorganisms. The natural regeneration of seedlings following landslides often involves multiple processes simultaneously shaping ecosystem functioning. Thus, this common garden experiment was designed to control intraspecific genetic diversity by combining seedlings from different origins and to regulate soil microorganisms by inoculating natural soil collected from beneath maternal trees.

Finally, in Chapter 5, I synthesize all findings across Chapters 2, 3, and 4 and discuss how the findings will contribute to the future management and restoration of forests in landslide-affected regions.

Chapter 2.

Post-landslide interactive effects of plant facilitation and rill erosion on tree seedling colonization toward restoration

1. Introduction

A landslide in the forest is a mass movement of materials, including soil, rock, and debris, down a slope, removing above- and below-ground biomass (Van Westen et al., 2003). Landslides are often triggered by events such as heavy rainstorms (Liu et al., 2021) and earthquakes (Ito et al., 2021) and are some of the major causes of forest disturbance (Garwood et al., 1979; Restrepo et al., 2009). Landslides can transform soil substrates (Blonska et al., 2018) and increase forest heterogeneity (Geertsema and Pojar, 2007; Hotta et al., 2024; Velázquez and Gómez-Sal, 2008), which dramatically impacts the biodiversity of forest ecosystems (Freund and Silman, 2023; Furusawa et al., 2023; Ohwaki et al., 2023). In recent decades, the frequency of landslides worldwide has increased due to global climate change (Ozturk et al., 2022), combined with anthropogenic factors such as deforestation and land-use change (Quevedo et al., 2023), making forest restoration in post-landslide areas an urgent and challenging issue (Chen et al., 2014; Hu et al., 2020). One of the key issues in forest restoration is the recruitment and colonization success of new seedlings (Bustamante-Sánchez et al., 2011; Thijs et al., 2014). While a growing body of work has focused on vegetation structure following landslides (Takaoka, 2019; Velázquez and Gómez-Sal, 2008; Yang et al., 2023), it remains poorly understood how post-landslide biotic and abiotic environmental conditions, such as the spatial distribution of newly recruited seedlings and soil erosion, govern the colonization success of seedlings.

Seed dispersal into a landslide area from surrounding forest trees and germination of these seeds make up the initial spatial distribution of seedlings. Initial spatial distribution patterns of newly recruited seedlings create new biotic conditions, which are likely to further affect the colonization success of later recruited individuals through positive and negative interactions between neighbors, such as competition and facilitation (Ben-Said et al., 2022; Bianchi et al., 2021). Resource competition among plants has been long considered to be the primary factor in regulating the dynamics of plant populations and communities (Craine and Dybzinski, 2013), while facilitation is more likely to be predominant under stressful, harsh conditions (Bertness and Callaway, 1994; Bonanomi et al., 2011). Facilitations can ameliorate

environments through processes such as redistributing soil moisture (Zou et al., 2005), concentrating soil nutrients (Zhang et al., 2018), stabilizing substrate (Kéfi et al., 2016), moderating microclimate (Brigham and Suding, 2024), shielding neighbors from wind (Schöb et al., 2013) and water runoff (Mazal et al., 2021), and protecting from herbivory (Carroll and MacDougall, 2024), thereby shaping community productivity and stability (Montesinos, 2015; Soliveres and Maestre, 2014). Post-landslide areas experience significant environmental stress (Velázquez et al., 2014), making facilitation potentially crucial for the successful colonization of seedlings. Nevertheless, both fine-scale spatial distribution of new seedlings (i.e., individual seedling scale) and its effects on seedling performance in post-landslide areas have remained to be elucidated.

Furthermore, following the landslide, subsequent erosion frequently occurs on the landslide scar (Larsen et al., 1999). In particular, the erosion caused by overland flow resulting from rain creates rills, which are small, intermittent watercourses with steep sides (Zheng and Gao, 2003), measuring 2 to 20 cm in width and depth (Ou et al., 2021). Rill erosion has been defined as the process of dispersing, scouring, and transporting soil during rill formation and development (Zheng and Gao, 2003), which could lead to further soil loss, nutrient degradation, and the prevention of seedling colonization in the disturbed area (Ou et al., 2021). Although previous studies highlighted the importance of rill erosion effects on geological morphology and hydrology in post-landslide areas (Tang et al., 2024), only limited research has focused on the impact of rill erosion on plant performance (Espigares et al., 2011; Wang et al., 2022). These studies have reported mixed results, in which rill erosions positively or negatively influenced seedling colonization, survival, and growth through changes in physical environments, including soil water and soil instability (Espigares et al., 2011; Wang et al., 2022). It should also be noted that in post-landslide areas, rill erosions emerge as a new abiotic environmental condition after disturbance, which may influence fine-scale distribution and performance of seedlings in complex ways.

Initial succession following natural landslides is a complex assemblage of both newly recruited seedlings and regenerated plants from remaining tissues (Hotta et al., 2024; Hu et al., 2018; Walker et al.,

2013). Also, natural landslides are stochastic events with highly heterogenous land structures (Takaoka, 2019). It is often difficult to clearly examine spatial interactions among seedlings and define rill erosion after landslides. Hence, in this study, we use a replicated artificial landslide experiment, where the initial environmental conditions were approximately homogeneous because of all tree stands, roots and surface soil were manually removed. This study is dedicated to clearly illustrating how the initial spatial distribution of seedlings emerges, how rill erosion (Fig. 1) occurs at post-landslide stages, and how those environmental conditions influence seedling performance. Specifically, we address the following questions: 1) how newly recruited seedlings form spatial distribution patterns (i.e., random, uniform, or clustered); 2) how the spatial distance between conspecific and heterospecific seedlings affect the survival and growth of seedlings; 3) what roles rill erosion plays in post-landslide sites on the process of seedling colonization; and 4) whether the distance of seedlings from neighbors and from the rill boundary interactively shapes seedling performance.

2. Material and Methods

2.1. Artificial landslide experiment and focal organisms

This study was conducted at the Artificial Landslide Experimental Sites (ALES) established in the three experimental forests of Hokkaido University in northern Hokkaido, Japan (Furusawa et al., 2023; Makoto et al., 2024). We prepared 30 artificial landslide sites in mountainous forest stands for ALES, and at each site, all trees in a 40 by 40 m area were harvested between December 2019 and March 2020. The remaining root systems, understory vegetation, and soil (approximately 50 cm in depth) were removed using bulldozers and power shovels in the summer of 2020 and 2021. Finally, the surface layers were contoured into a smooth slope. Details regarding the establishment and environments of ALES can be found in (Furusawa et al., 2023; Makoto et al., 2024). For this study, we selected three sites, which were completed in the summer of 2021 in the Nakagawa Experimental Forest (Site 1: 44.786° N, 142.252° E; Site 2: 44.783° N, 142.254° E; Site 3: 44.796° N, 142.249° E). The three sites were located in

natural forest stands mixed with conifers (e.g., *Abies sachalinensis* (Fr. Schm.) Masters) and broad-leaved trees (e.g., *Acer mono* Maxim. and *Betula ermanii* Cham.), with slope angles were 19°, 24.6° and 12°, at Site 1, 2 and 3, respectively (Furusawa et al., 2023).

In the late spring of 2022, nine 2 × 2 m survey plots were established at each site, located within the central area (30 × 30 m) of the ALES treatment, with a buffer zone greater than 10 m in width separating the plots from the surrounding natural forest. These plots were evenly spaced in a 3 × 3 grid, with a distance of 10 m between each plot and its adjacent plots. After the landslide treatment, rill erosion appeared on these bare slopes due to rainfall. The morphology of the rills at these 3 sites was approximately 5 cm deep and 10 cm wide, running from the top of the slope to the bottom (Fig. 1). There were 17 of 27 plots intersected by rills, with a percentage coverage area of 11.56 ± 5.10% (mean ± SD).

In the first growing season after the landslide treatment, seedlings of two species, *Abies sachalinensis* and *Acer mono,* mostly dominated. Both species are typically dominant in the local natural forests. *Abies sachalinensis* is an obligate seeder that depends on seed reproduction. Woody debris (such as fallen logs) is the primary regeneration site for its seedlings in the sub-boreal forests (Lian et al., 2008; Nakagawa et al., 2003), but ALES treatment removed all residual woody debris and potential seed banks (Makoto et al., 2024). The cones of *A. sachalinensis* contain numerous small seeds with wings developed from ovuliferous scales. *Acer mono* is capable of reproducing both by seeds and vegetatively. Seeds of *A. mono* are winged. The seeds of the current year tend to germinate in the following spring, so their recruitment is less dependent on the seed bank (Tanaka, 1995). Although adventitious roots occurred on the natural layering of trunks and branches for reproduction, it is generally more common in older trees of *A. mono*. However, we randomly excavated several *Acer mono* seedlings outside of the survey plots at these sites, as well as at other ALES sites, and confirmed that all *A. mono* seedlings originated from seeds rather than root and stem systems. Therefore, in the first year after the landslide, the seedlings of both species germinated from seeds that matured in the autumn of 2021 and were dispersed into the focal sites. Hereafter, we refer to *A. sachalinensis* as *Abies* and *A. mono* as *Acer*.

2.2. Surveys on spatial position and performance of seedlings

Our field surveys have been conducted three times (June, August, and October) on these 27 plots to monitor the recruitment, survival, and growth of seedlings. During the June survey, we individually marked all seedlings within the plots with labelled nails. Using a monopod, we manually took five digital photographs from a height of 2 m above the center of each plot, perpendicular to the slope, and the photo that most successfully captured the entire plot was selected for further processing (referred to as the "map" hereafter; Fig. 1). Preliminarily, we performed a test to examine an image distortion in a laboratory. We took photos of a measurement tape with a 1-mm scale from the same height. This preliminary test confirmed that the bias due to pixel distortion at the edges of the photos in comparison to the photo center was less than 1 mm.

Using ImageJ software (v1.53t), we manually determined the horizontal and vertical coordinates (unit: cm) of each of the seedlings. We also traced the edge of all rills within the survey plots on the digitized map. The Euclidean distance (unit: cm) of each seedling to the nearest neighboring seedling of both conspecifics and heterospecifics, as well as the distance of each seedling to the nearest edge of the rill, was measured using ImageJ. In subsequent surveys, all newly germinated seedlings were labelled and recorded on the maps.

The survival status of all seedlings was also recorded. Seedlings that disappeared or were uprooted were recorded as dead. Those that remained in place but lacked leaves or had only wilting leaves and stems were also recorded as dead. The height (unit: cm) of surviving seedlings, defined as the length from the ground level of the seedling to the tip of the highest leaf along the stem, was measured during each survey. Relative growth rates (RGR, unit: $cm \cdot cm^{-1}$) were calculated using Eq. (1).

$$RGR = (H_L - H_E)/H_E \quad (1)$$

where H_E is the height of the earlier month and H_L is the later month. Thus, growth rates were obtained for the periods of June to August, August to October, and June to August, respectively (Table S1). Continuous

erosion occurred on post-landslide slopes (Hu et al., 2020), which caused the instability of the soil surface and introduced observatory errors in our height measurements of seedlings (i.e., negative growth rates). To retain the most valid data, we used the growth rate from June to October for *Abies* and from June to August for *Acer,* as this period showed the lowest percentage of seedlings with negative growth rates (36.59% for *Abies* and 47.02% for *Acer*) (Table S1).

2.3. Spatial distribution pattern analysis

Generalized linear models (GLMs) were used to examine the difference in seedling abundance (unit: the number of individuals per plot) between rill-absent and rill-present plots. The response variable was the plot-level abundance, while the presence or absence of rill and the site ID were used as explanatory variables. These GLMs followed the Poisson error distribution and used a log link function.

For each of both rill-absent and rill-present plots, the Clark and Evans aggregation index *R* was used to estimate the spatial point patterns of all initially recruited seedlings that appeared during the first season (including dead individuals), differentiated by species. In a random distribution, *R* equals 1. The index of *R* less than 1 indicates a clustered distribution of points, with values closer to 0 reflecting higher degrees of clustering; *R* greater than 1 indicates a uniform distribution of points, with larger values indicating a greater tendency towards uniformity. *R* indices and *P*-values were calculated using the clarkevans.test function with default options implemented in the R package spatstat. Donnelly's method was applied for edge correction. The seedling abundance in our survey, especially for *Acer*, was extremely low in some plots (Table S3). Considering that a small sample size could introduce bias into spatial point analysis (Ben-Said, 2021), we only performed the Clark and Evans test on plots containing more than eight seedlings, which ensured relatively robust results while allowing for more than half of the plots to be included in the analysis.

We also assessed whether seedlings clustered around rills and were differentiated by species. The minimum distances of seedlings to the rill edge from all rill-present plots were combined, and we

computed an empirical cumulative distribution function (ECDF) of the observed data. Simultaneously, for all rill-present plots, we created 10 × 10 uniform grids with neighboring points spaced 20 cm apart and calculated the minimum distance from each grid intersection to the rill edge; the minimum distances of uniform points to the rill edge from all rill-present plots were combined, and the simulated null ECDF was computed. A Kolmogorov-Smirnov test was performed to compare the observed ECDF with the null ECDF to examine whether seedlings were clustered around rills.

2.4. Statistical analysis

To access the effects of new biotic and abiotic environmental conditions post-landslide, namely neighboring individuals and rill erosion, on seedling performance, generalized linear mixed models (GLMMs) were employed for both *Abies* and *Acer*, respectively. The GLMMs for seedling survival followed the binomial error distribution. For the growth rate of seedlings, the GLMMs followed a Gamma error distribution and used a log link function. A natural logarithmic transformation was performed for all the three distance indices.

Firstly, we employed GLMMs to examine potential interactive effects between the distance to the nearest neighbors and rill erosion on seedling performance. The survival and growth rates of *Abies* and *Acer* were used as the response variables in the model, respectively. The explanatory variables included the distance of each seedling to the nearest conspecific and heterospecific neighbors, the absence/presence of rills in each plot, the interactive effects between neighboring distance and rill presence, as well as the site ID, with the plot ID as a random intercept. lme4 package was used for GLMM and type II ANOVA tables were obtained with the Anova function implemented in the car package.

Next, to clearly describe the effects of neighboring individuals and rill erosion on seedling performance, separate GLMMs were bult for rill-absent and rill-present plots, respectively, and model selection was performed. For rill-absent plots, the explanatory variables included the distance of each seedling to the nearest conspecific and heterospecific neighbors, as well as the site ID, with the plot ID set

as a random intercept. For rill-present plots, the explanatory variables included the distance between conspecific and heterospecific individuals, the distance of the seedling to the nearest edge of the rill, as well as the site ID, with the plot ID as a random intercept. Then, the backward stepwise selection was conducted to obtain minimum adequate models (MAMs). The least significant variables were removed from a full model one after the other until the MAM based on the least AIC (Akaike Information Criterion; Akaike, 1974) value was obtained, or no variables were left in the model. All MAMs are shown in Table 1. All statistical analyses were conducted in R software version 4.3.1 (R development core team 2023).

3. Results

3.1. Spatial distribution pattern of seedlings

The abundance of *Abies* seedlings in rill-present plots was significantly higher than in rill-absent plots (Fig. 2a, Table S2), while the abundance of *Acer* seedlings showed no significant difference between rill-absent and rill-present plots (Fig. 2b, Table S2).

In most plots, *Abies* seedlings exhibited spatially clustered tendency, regardless of whether they were in rill-absent or rill-present plots (80% and 62.5%, respectively; Table S3). For *Acer*, seedlings were spatially clustered in all rill-absent plots, while spatially randomized patterns were shown in more than half of rill-present plots (70%) (Table S3). For the rill-present plots, seedlings showed different patterns in clustering around rills. The ECDF curve for *Abies* was significantly higher near the rill edges than the null ECDF (Fig. 3a), indicating a significant clustering of *Abies* seedlings around rills. In contrast, the ECDF curve for *Acer* did not differ significantly from the null ECDF (Fig. 3b), suggesting that *Acer* seedlings did not show a clustering tendency around rills.

3.2. Impacts of intra- and interspecific distance on survival and growth

For survival and growth rate, marginally significant interactions between conspecific/heterospecific distance and the presence of rills were detected (Table S4, Fig. 4). From here, we address the effects of intra- and interspecific distance on survival and growth in rill-absent plots or rill-present plots separately.

In rill-absent plots, the survival rates for *Abies* and *Acer* were 80.22% and 89.61%, respectively. For growth rates, the mean growth rate ($cm \cdot cm^{-1}$) for *Abies* was 0.35 ± 0.27 (mean ± SD), and for *Acer*, it was 0.25 ± 0.27. Effects of intra- and interspecific distance on survival and growth were tested by 10 plots where rills were absent. For *Abies*, seedlings exhibited a survival rate exceeding 80% when they were within 10 cm of conspecific neighbors. The survival significantly decreased with an increase in the nearest distance between conspecific seedlings (Fig. 4a, Table 1). For *Acer*, seedlings exhibited a survival rate exceeding 90% when they were within 10 cm of conspecific neighbors. The survival significantly decreased with an increase in the nearest distance between conspecific seedlings (Fig. 4b, Table 1).

The growth rate of *Abies* seedlings significantly decreased as they became further from heterospecific seedlings (Fig. 4c, Table 1), suggesting that heterospecific neighbors had a positive impact on the growth of *Abies* seedlings. For *Acer*, the growth rate significantly increased with an increase in the nearest distance between conspecific seedlings (Fig. 4d, Table 1).

3.3. Impacts of distance from rills on survival and growth

In rill-present plots, the survival rates for *Abies* and *Acer* were 73.93% and 82.69%, respectively. For growth rates, the mean growth rate ($cm \cdot cm^{-1}$) for *Abies* was 0.45 ± 0.44, and for *Acer*, it was 0.20 ± 0.22. Effects of distance from rills on survival and growth of seedlings were tested by 17 plots where rills were present. For *Abies*, survival was generally highest for individuals that were further from rills (Fig. 5a, Table 1). A survival rate higher than 80% was observed when the distance was > 50cm, indicating that the presence of nearby rills had a negative impact on the survival of *Abies* seedlings. The survival rate also tended to increase with a decrease in the nearest distance to heterospecific seedlings (Fig. 5b, Table

1), suggesting a trend that heterospecific neighbors had a positive impact on the survival of *Abies* under rill erosion. For *Acer* survival, the distances to the nearest conspecific and heterospecific neighbors, as well as the distance from the rill edge, had no significant influence (Table 1).

The growth rate of *Abies* seedlings was not influenced by the distance to the nearest conspecific and heterospecific neighbors, nor by the distance from the rill edge (Table 1). The growth rate of *Acer* was generally highest near the edge of rills (Fig. 5c, Table 1), indicating that rill proximity had a positive impact on the growth of *Acer* seedlings.

4. Discussion

This study clearly highlighted how post-landslide conditions of biotic and abiotic environments influenced initial seedling colonization with artificial landslide experiments. Both *Abies* and *Acer* seedlings showed a spatially clustered pattern in rill-absent plots, and *Abies* seedlings were clustered around rills in rill-present plots. The influence of conspecific and heterospecific neighbors on seedling performance may also depend on the presence of rills. In rill-absent plots, seedlings survive better when in proximity to conspecifics, and *Abies* seedlings grow faster when close to heterospecific neighbors. In rill-present plots, the survival of *Abies* significantly decreased with the nearest distance to rills, but this negative effect was likely to be attenuated by the presence of heterospecific neighbors. Furthermore, *Acer* seedlings showed a significantly higher growth rate when close to rills. To our knowledge, this is the first study that illustrates how biotic interactions and rill erosion interactively shape the colonization of new seedlings after landslide disturbance.

4.1. Initial spatial distribution patterns of newly recruited seedlings

The initial spatial distribution of newly recruited *Abies* seedlings after ALES treatment was clustered with or without rills (Fig. 3a, Table S2). This is likely due to 1) seed dispersal processes and/or 2)heterogeneity in the fine-scale physical environment. First, the dispersal limitation of seeds from adult

trees is considered to be a crucial factor in determining the spatial distribution of seedlings (Beyns et al., 2021; Lin et al., 2011; Masaki et al., 2019). The degree of spatial aggregation of seedlings sometimes declines as the distance from the mother tree increases (Zhang et al., 2013; Zong, 2018). Although there was no observed trend where seedling aggregation increased if the plot was closer to the boundary of the survey site, seed dispersal from surrounding mother trees with different distances and heights may create the clustered distribution of seeds. On the other hand, rainfall water flow is much stronger on the landslide surface than on undisturbed forest stands. Water flows may also be important transporting agents of seed dispersal, as water flowing through the upper natural forest could carry seeds into landslide scars, leading to the aggregation of seedlings around rills. Second, habitat heterogeneity, including topography, soil nutrients, and shading, may contribute to the initial spatial distribution of seedlings (Getzin et al., 2008; Lara-Romero et al., 2016; Patiño et al., 2021). Newly recruited seedlings are sensitive to habitat heterogeneity and can quickly establish in fine-scale patches with more favorable germination conditions, resulting in spatial aggregations (Li et al., 2009; Zong, 2018). According to the treatment of ALES, the initial condition within each landslide scar was presumed to be approximately homogenous, with consistent slope angles and a lack of nutrient-rich topsoil. However, physical heterogeneity in the soil would be triggered by rill erosion in terms of surface structure, soil deposition, water and nutrient distribution. This heterogeneity may at least partially influence the distribution pattern of seedlings.

Overall, both water flow transportation of seeds and rill-induced heterogeneity could play an important role in shaping the clustered *Abies* seedling distribution. This explains why the seedling abundance in rill-present plots was higher (Fig. 2a) and why they were clustered around rills (Fig. 3a). Our result aligns with the research of Wang et al. (2022), which showed a higher density and coverage of vegetation on rills than on bare slopes, highlighting the seed-trapping function of micro-topography. Therefore, habitat heterogeneity, primarily contributed by rill erosion, may be an important factor influencing the initial clustering pattern of *Abies* seedlings.

In addition, this notion can also explain why *Acer* seedlings exhibited less clustered distribution than *Abies*. *Acer* seeds are relatively flat, with greater mass and larger wings compared to *Abies* seeds. This is consistent with the research of Caravaca et al. (2002), which indicates that large, flat seeds experience lower removal rates under water erosion. Thus, the effects of water transportation with rill erosion should be weaker in *Acer* than those in *Abies*, explaining the lack of significantly higher seedling abundance in rill-present plots (Fig. 2b) and the absence of clustering around rills (Fig. 3b).

4.2. Plant-plant facilitations further promote seedlings clustering

Initial clustered distribution can increase the probability of neighboring interactions between conspecifics/heterospecifics. Our findings of positive effects of neighbors on survival and growth rates in the absence of rills suggest facilitation between seedlings. These facilitative interactions may be explained by the following mechanisms: 1) soil physical structure and 2) mycorrhizal networks.

The increased likelihood of survival (Fig. 4a, 4b) may be attributed to changes in soil physical structure due to neighboring conspecific seedlings (Gilland and McCarthy, 2014; Jones et al., 1994). Plant root systems can generate tensile stress at the soil-root interface, leading to the formation of soil aggregates, as well as secrete mucilage to make soil particles adhere (Materechera et al., 1992; Poirier et al., 2018). Also, plant root systems can create pore space between aggregates, thus improving gas exchange between soil and atmosphere (Angers and Caron, 1998; Fernández et al., 2019). *Acer* especially exhibits a stronger and more extensive root system during the first growing season after a landslide (Fang, personal observation). Its roots are also predicted to have stronger tensile strength (Zeng and Makoto, 2023), which helps it resist the movement of the soil surface. The extensive root system of *Acer* seedlings was likely to promote soil stabilization, leading to the improvement of survival.

Common mycorrhizal networks (CMNs) may also contribute to the greater survival of nearby conspecific seedlings (Figueiredo et al., 2021; Liang et al., 2021). It has been demonstrated that naturally regenerating *Abies* seedlings could form symbiosis with Ectomycorrhizal (EcM) fungi (Obase et al.,

2022; Policelli et al., 2019). Also, EcM fungi colonization has been observed on the root of the 1st -year naturally recruited *Abies* in ALES sites (*Cenococcum*, *Amanita*, *Thelephola*, *Tomentella*; Utsumi, unpublished data). EcM may improve seedling survival due to pathogen protection, nutrient allocations, and improved soil substrate (Bennett et al., 2017; Branco et al., 2022; Caravaca et al., 2002; Liang et al., 2021). We speculate that the EcM-dominated CMN network mediates the facilitation between *Abies* and conspecific neighbors, thereby promoting their survival. However, the increased likelihood of survival for *Acer* near conspecific seedlings (Fig. 4b) may not be attributed to mycorrhizal facilitation, though some members of the family *Aceraceae* could form arbuscular mycorrhizae (AM) (Brundrett et al., 1990; Gorzelak et al., 2015). Especially in bare sites, current-year seedlings of *A. mono* may not be obligatory mycorrhizal (Yoshida et al., 2011). Regarding growth rates, the higher growth of *Abies* around heterospecific neighbors (Fig. 4c) could also be explained by soil physical properties, as discussed above. Additionally, niche partitioning between species may be able to enhance the positive effects of such soil physical properties on the growth of newly recruited seedlings. This notion could also explain why *Acer* displayed a greater growth rate with a longer distance than a neighbor conspecific seedling (Fig. 4d).

4.3. Interactive effects of rill erosion and plant interactions

Rill erosion negatively affects seedling survival (Espigares et al., 2011; Pang et al., 2018). Thus, the negative effects of rill distance on the survival of *Abies* in rill-present plots (Fig. 5a) were likely due to rill erosion disturbance. However, this effect is species-specific, and this influence was not detected in *Acer* seedlings. The differential response of these two species to rill erosion is associated with their functional traits. As we discussed in section 4.2., *Abies* seedlings are smaller and have softer stems and shallower roots with fewer lateral root branches than *Acer*, making them more suspectable to being buried or washed away by soil movement. In fact, the main cause of death of *Abies* in our survey was disappearance, rather than wilting, supporting this explanation. Conversely, newly recruited *Acer* seedlings are much more robust, with larger height and stronger above- and belowground morphology,

which could counteract the disturbance of rill erosion. Our results are consistent with the study by Wang et al. (2014), in which seedlings of smaller species were more susceptible to rainfall erosion, while seedlings of larger species having deeper and stronger roots had a reduced risk of being washed away by precipitation-induced erosion.

However, interestingly, the mortality of *Abies* was potentially mitigated by heterospecific neighbors (Fig. 5b). We discussed conspecific and heterospecific facilitative effects through soil physical properties in section 4.2. In the presence of rill erosion, *Acer*'s protective effects on *Abies* based on the interspecific differences in functional traits were likely to be more prominent than in the absence of rill. Overall, there were conspecific and heterospecific facilitative effects on seedling survival at a post-landslide habitat, but the relative importance of the two effects could be dependent on the degree of rill erosion.

Moreover, we detected that *Acer* seedlings tended to grow faster when closer to the rill (Table 1, Fig. 5c), which may be attributed to the resource enrichment of soil deposited around as well as increased soil moisture. Although direct evidence is lacking in this study, the soil around rills is presumed to be more fertile (Pang et al., 2018; Wang et al., 2022) as it originates from the topsoil of the upper mature forest, washed down by rainwater. *Acer*, due to its more robust morphology, offsets the disturbance of soil movement and acquires more nutrients from the deposited soil, resulting in higher growth rates. Therefore, rill erosion potentially contributes to the enrichment of nutrients and water, creating resource heterogeneity, which may promote spatial clustering of seedlings over the next few growing seasons.

5. Conclusion

This study found that newly recruited seedlings exhibited spatial clustering after landslides, promoting the possibility of plant-plant interactions among neighbors. At a scale of several centimeters, seedlings exhibited higher performance when co-occurring with conspecific and heterospecific neighbors, which may be attributed to plant facilitation. Rill erosion represents critical fine-scale heterogeneity in

post-landslide areas, attracting more seedlings with species-specific impacts on their performance. Notably, plant facilitation partially attenuated the disturbances caused by soil movement due to rill erosion, which may demonstrate the interactive effects of plant facilitation and rill erosion on seedling performance. In post-landslide areas, fine-scale plant facilitation, together with habitat heterogeneity, will continue to shape future spatial distribution patterns of seedlings. Our results suggest that during forest restoration after landslides, careful consideration of the fine-scale spatial structure of neighboring species and rill erosion will promote successful seedling colonization and establishment. Future research should focus on a more quantitative description of fine-scale heterogeneity in post-landslide areas, such as soil characteristics, soil microbial communities, and geomorphologies, toward a more comprehensive understanding of the regulation of forest restoration.

Table 1. Minimum adequate models for survival and growth rates of newly recruited seedlings.

			Explanatory variables							
			Heterospecific distance		Conspecific distance		Distance from rill edge		Site ID	
Rill erosion	Species	Response	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Rill-absent	*Abies*	Survival	(-)		-0.716	**0.031**			(-)	
		Growth rate	-0.369	**0.033**	(-)				(-)	
	Acer	Survival	(-)		-1.060	**0.049**			(-)	
		Growth rate	(-)		1.430	**< 0.001**				
Rill-present	*Abies*	Survival	-0.316	**0.078**	(-)		0.432	**< 0.001**	(-)	
		Growth rate	(-)		(-)		(-)		(-)	
	Acer	Survival	(-)		(-)		(-)			**0.024**
		Growth rate	(-)		(-)		-0.145	**< 0.001**		**< 0.001**

Note: The log-transformed explanatory variables 'Heterospecific distance', 'Conspecific distance', and 'Distance from rill edge' were used in the above models. '(-)' indicates a variable removed during the model selection process. *P*-values less than 0.1 are marked in bold.

Table S1. The percentage of seedlings with negative growth rates and the mean growth rate within each sampling interval.

Species	Sampling time interval	Percentage of seedlings with negative relative growth rate	Mean relative growth rate ($cm \cdot cm^{-1}$) (mean ± SD)
Abies	June - August	41.18%	0.50 ± 0.53
	August – October	54.36%	0.32 ± 0.42
	June - October	36.59%	0.43 ± 0.41
Acer	June - August	47.02%	0.22 ± 0.24
	August – October	76.44%	0.25 ± 0.57
	June - October	64.60%	0.18 ± 0.18

Note: The mean growth rate within each sampling interval is based solely on positive values.

Table S2. The GLMs examining the difference in seedlings' abundance between rill-absent and rill-present plots.

		Explanatory variables	
		Rill presence	Site ID
Species	Response	*P*	*P*
Abies	No. seedlings per plot	**< 0.001**	**< 0.001**
Acer	No. seedlings per plot	0.666	**< 0.001**

Note: *P*-values less than 0.1 are marked in bold.

Table S3. Spatial point pattern analysis of newly recruited seedlings

		Abies				*Acer*			
Rill erosion	Plot ID	Density (No. / m^2)	R	*P*	Spatial pattern	Density (No. / m^2)	R	*P*	Spatial pattern
Rill-absent	1-t-5	2	0.725	**0.077**	C	1.5			
	1-t-15	1.5				3	0.414	**<0.001**	C
	1-t-25	1.25				2.5	0.475	**<0.001**	C
	2-b-5	6.5	0.785	**0.022**	C	7.25	0.695	**<0.001**	C
	2-t-5	4.5	0.594	**<0.001**	C	3.25	0.740	**0.041**	C
	2-t-25	2	0.776	0.150	R	0.75			
	3-b-15	2.5	0.746	**0.074**	C	1			
	3-m-5	0.75				0			
	3-t-5	1.75				0			
	3-t-15	0				0			
Rill-present	1-b-5	2.25	0.689	**0.036**	C	2.25	0.609	**0.008**	C
	1-b-15	3.75	0.576	**<0.001**	C	1.75			
	1-b-25	2.5	0.992	0.955	R	3.5	0.937	0.607	R
	1-m-5	2.75	0.629	**0.007**	C	4	0.863	0.238	R
	1-m-15	1.75				2	1.004	0.979	R
	1-m-25	2	0.929	0.648	R	1.75			
	2-b-15	5.25	0.637	**<0.001**	C	5.75	0.746	**0.010**	C
	2-b-25	5.5	0.677	**0.001**	C	2.25	1.048	0.748	R
	2-m-5	6	0.841	0.101	R	4.5	0.924	0.491	R
	2-m-15	4.25	1.085	0.454	R	2.25	0.710	**0.051**	C
	2-m-25	5.75	0.866	0.176	R	2.25	0.996	0.976	R
	2-t-15	4.25	0.846	0.173	R	2.25	1.085	0.569	R
	3-b-5	9.25	0.720	**<0.001**	C	0.5			
	3-b-25	4	0.618	**0.001**	C	1.25			
	3-m-15	3.75	0.761	**0.046**	C	1			
	3-m-25	6.25	0.633	**<0.001**	C	0.5			
	3-t-25	6.5	0.727	**0.004**	C	1.25			

Note: 'C': Clustered; 'R': Random. *P*-values less than 0.1 are marked in bold.

Table S4. The GLMMs examining interactive effects between the distance to the nearest neighbors and rill erosion on seedling performance

		Explanatory variables											
		Heterospecific distance		Conspecific distance		Rill presence		Site ID		Heterospecific distance × Rill presence		Conspecific distance × Rill presence	
Species	Response	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Abies	Survival	0.013	0.275	-0.655	0.256		0.339		0.374	-0.280	0.442	0.577	0.156
	Growth rate	-0.291	0.912	-0.086	0.361		0.153		0.737	0.400	**0.061**	0.007	0.973
Acer	Survival	0.447	0.231	-1.069	0.450		0.644		**0.006**	-0.114	0.865	1.126	**0.099**
	Growth rate	-0.429	0.766	0.599	0.274		0.468		0.151	0.494	0.176	-0.622	**0.063**

Note: The log-transformed explanatory variables 'Heterospecific distance' and 'Conspecific distance' were used in this models. *P*-values less than 0.1 are marked in bold.

FIGURE LEGENDS

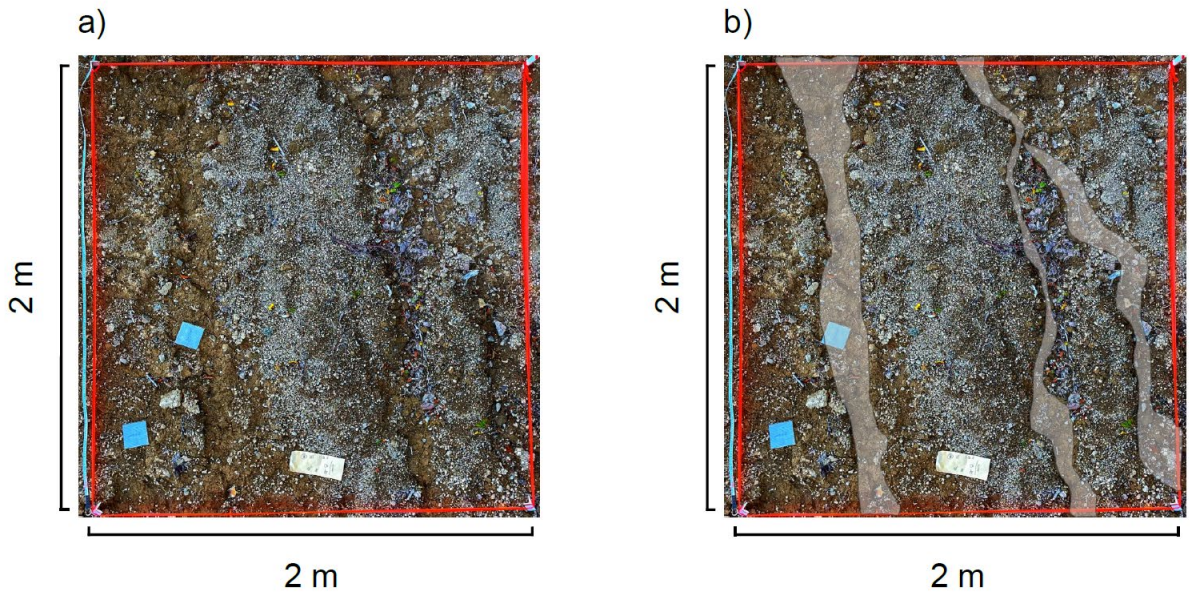
Figure 1. An example of a plot showing rill erosion. This example is a plot from ALES-Site 1. (a) the original photograph of this plot, (b) the rills are shown in light grey.

Figure 2. A comparison of seedling abundance between rill-absent and rill-present plots. a) represents *Abies* and b) represents *Acer*.

Figure 3. Empirical cumulative distribution function (ECDF) of the two species in rill-present plots, representing a distribution of a minimum distance to a rill from each seedling of a) *Abies* and b) *Acer*. The grey dashed lines represent the simulated null ECDFs generated using uniform distribution points in each plot.

Figure 4. Impacts of intra- and interspecific distance on survival and growth in rill-absent plots. Each point represents raw data of seedlings. a) Impacts of the minimum conspecific distance on the survival of *Abies*; b) Impacts of the minimum conspecific distance on the survival of *Acer*; c) Impacts of the minimum heterospecific distance on the growth rate of *Abies*; d) Impacts of the minimum conspecific distance on the growth rate of *Acer*. The fitted curves in the figure are calculated based on only the fixed effects. Significance (*P*-value) calculations are derived on MAMs (Table 1).

Figure 5. Impacts of neighboring seedlings and rill erosion on survival and growth in rill-present plots. Each point represents raw data of seedlings. a) Impacts of the minimum distance to the rill edge on the survival of *Abies*; b) Impacts of minimum heterospecific distance on the survival of *Abies*; c) Impacts of the minimum distance to the rill edge on the survival of *Abies*. The fitted curves in the figure are calculated based on only the fixed effects. Significance (*P*-value) calculations are derived on MAMs (Table 1)



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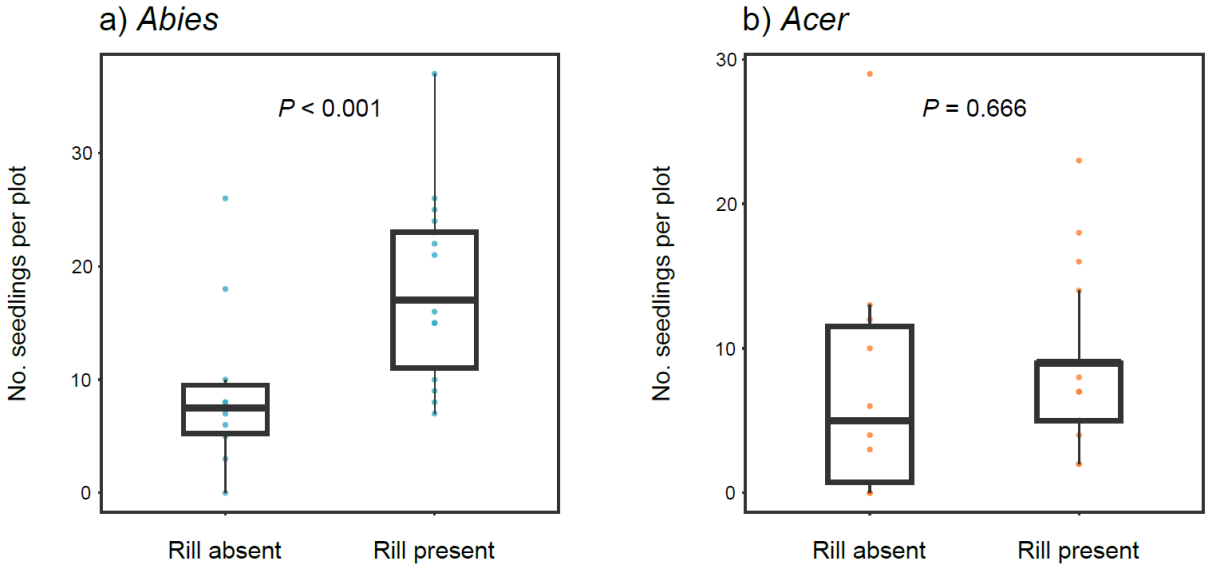

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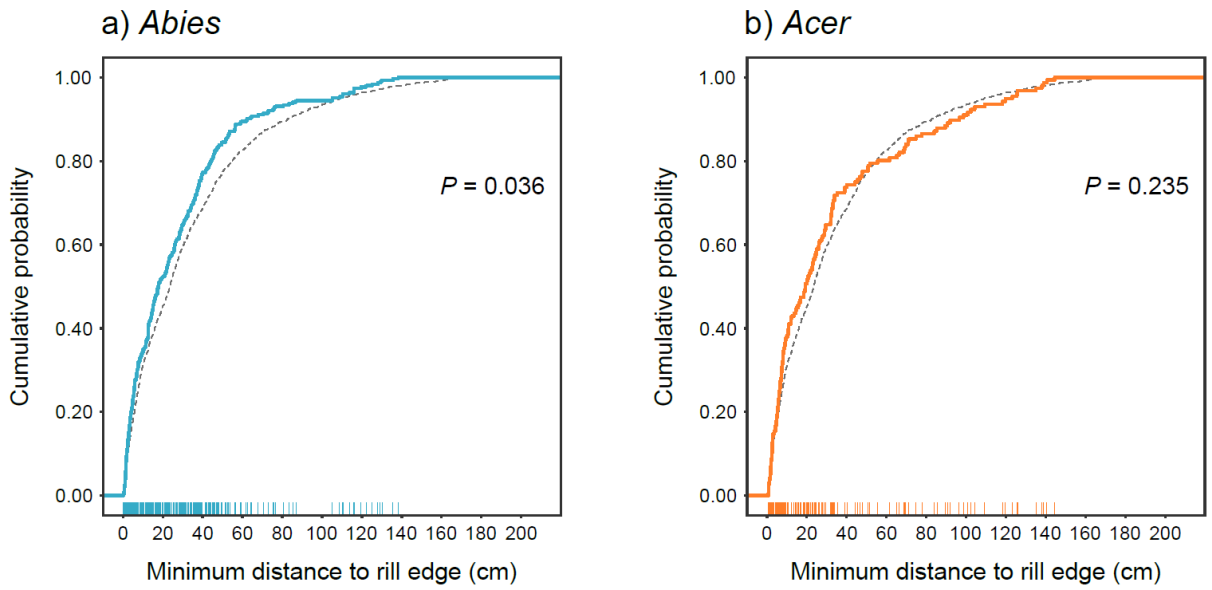

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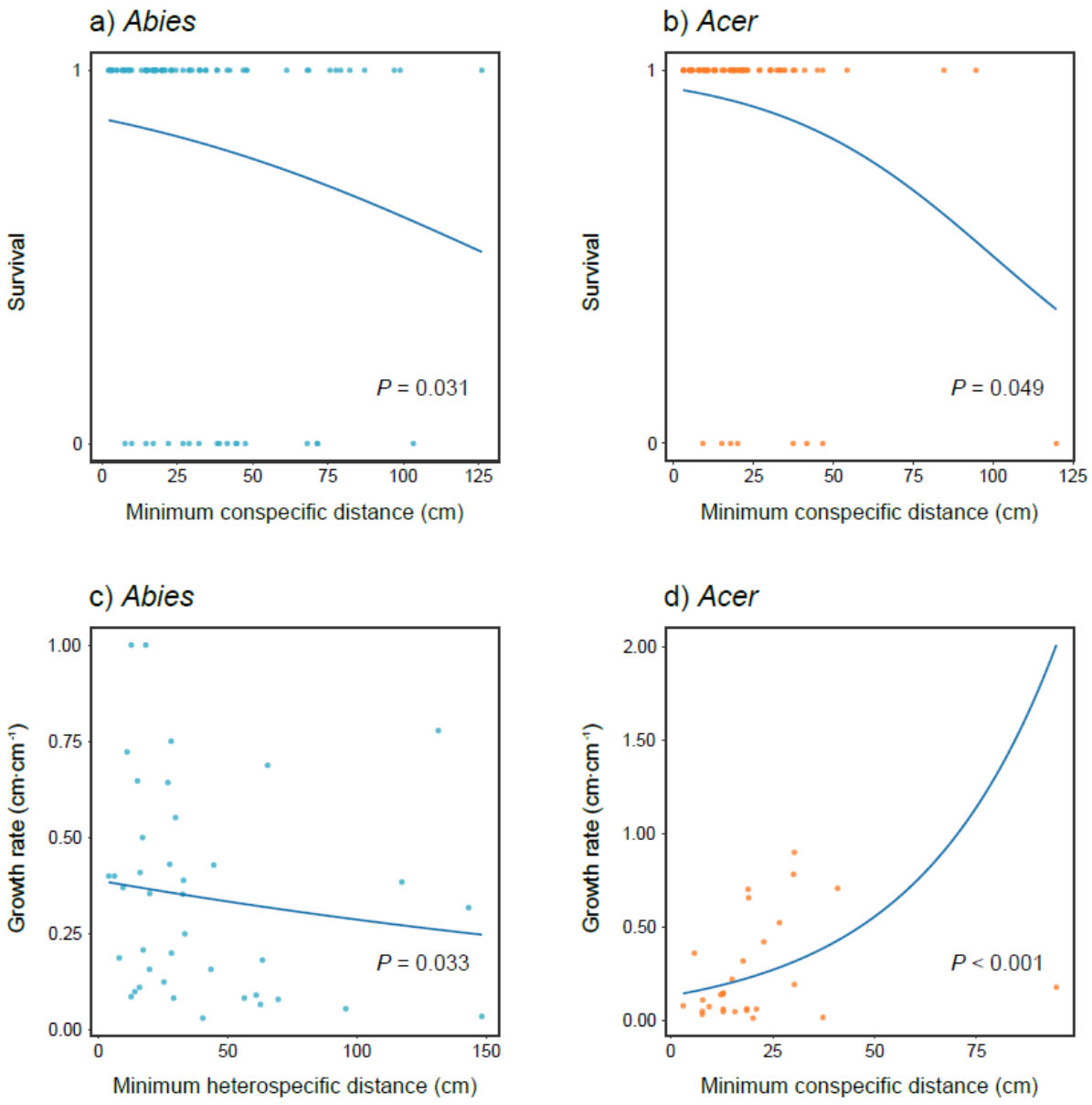

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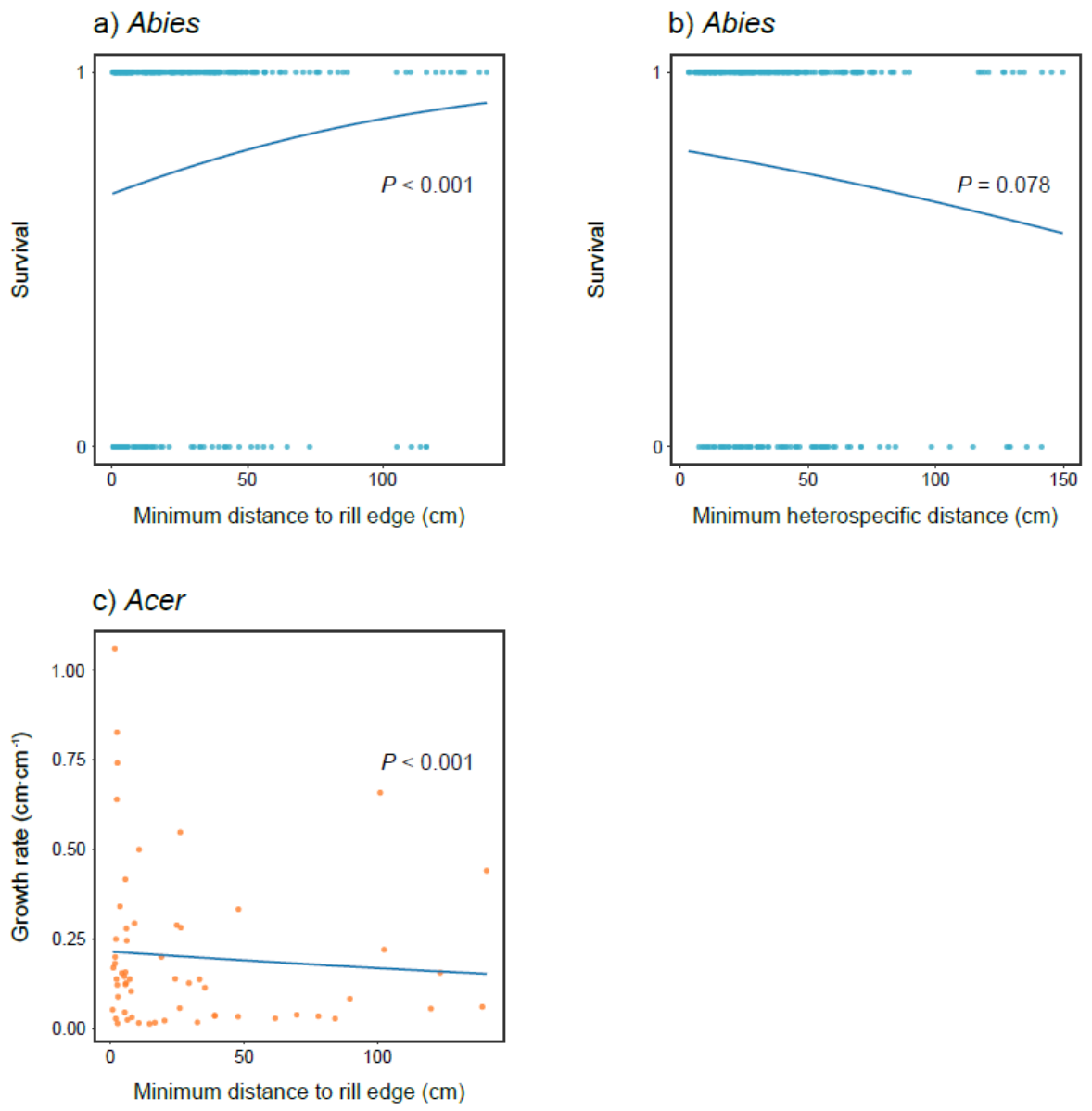

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Chapter 3.

The genetic structure of newly recruited populations in post-landslide areas is shaped by rill erosion and drives the outcomes of intraspecific interactions

Abbreviations:

ISSR: inter-simple sequence repeat

MIG-seq: multiplexed ISSR genotyping by sequencing

PCR: polymerase chain reaction

SPRI: solid-phase reversible immobilization

SNP: single-nucleotide polymorphism

IBS: identity-by-state

1. Introduction

Major natural disturbances, such as wildfires and landslides, often result in "stand-replacement" events in forests (Swanson et al., 2011), followed by primary succession driven by pioneer species (Dalling, 2008). The genetic differentiation among populations recruited in newly disturbed patches may result from various ecological processes (Litrico et al., 2005), while the genetic identity and diversity of the population are potentially critical for shaping the performance of population members (Wan et al., 2022). The genetic properties of seedling populations following disturbance have long been underappreciated. Global climate change is increasing disturbance risks to forests (Dale et al., 2001), highlighting the need for ecological genetics insights into the colonization processes of pioneer tree species to tackle the growing challenges of forest restoration.

The dispersal ability of plants has important consequences for the establishment, persistence, and range dynamics of species (Major et al., 2021). Notably, dispersal initiates plant recolonization after disturbances (Reid et al., 2015) and largely determines the genetic differentiation among and within disturbed patches. If dispersal ability is high, newly recruited seedlings can originate from multiple adult trees, resulting in higher diversity within newly colonized populations in a patch and weaker genetic differentiation between patches (Suárez et al., 2022). Conversely, in the presence of strong dispersal limitation, newly recruited seedlings will likely originate from only a few seed sources at the edge of mature forests (Litrico et al., 2005). This results in a founder effect within patches, leading to relatively homogeneous genetic composition within newly established populations, while genetic differentiation between patches becomes more pronounced (Litrico et al., 2005). However, during the primary succession after disturbance, the extent of the population’s genetic differentiation among and within adjacent patches remains poorly understood.

Spatial genetic structure (SGS), defined as the non-random spatial distribution of genotypes, characterizes the relationship of relatedness estimates between pairs of individuals and their physical proximity (Mazal et al., 2021). Dispersal of pollen and seeds plays a crucial role in shaping spatial genetic

structure (Banks et al., 2013; Mazal et al., 2021). During the succession following disturbances, complex conditions may also shape SGS, including processes such as the initial spatial distribution pattern of seedlings (Daniels, 1978), ongoing soil erosion (Ou et al., 2021), and seed redistribution caused by soil or water movement (i.e. rill erosion in post-landslide area, Chapter 2). Moreover, at fine scales, within which plants can interact with their immediate neighbors ('zones of influence', Stoll and Weiner (2000)), SGS likely modify the genetic identities of neighboring seedlings. Genetic relatedness potentially influences the outcome of intraspecific interactions, such as resource competition (Husain Jaafry et al., 2020) and facilitation (Ehlers et al., 2016; Fajardo and McIntire, 2011). There are no studies that address genetic-performance relationships among newly-colonized neighbor seedlings at the early phase of primary succession, while this knowledge can provide significant insight for forest restoration.

This study is dedicated to illustrating the genetic structure among and within adjacent sites after a severe disturbance, and how genetic structure within a population shapes the outcome of intraspecific interactions. Artificial Landslide Experimental Sites (ALES) simulated the natural shallow landslide disturbances in mountainous forests by artificially creating well-cleaned patches with replications (Furusawa et al., 2023; Makoto et al., 2024). Therefore, ALES provides an excellent opportunity to study the associations between the genetic issues among and within newly colonized plant populations, and ecological processes during the primary succession following disturbance. The following questions were addressed: 1) are there population differentiations among spatially proximate disturbance sites after landslides, 2) how do landslide scars and subsequent rill erosion shape the genetic structure of seedling populations, and 3) how does genetic relatedness among seedlings influence their performance.

2. Material and Methods

2.1. Artificial landslide experiment and focal organisms

This study was conducted at three sites from the project of the Artificial Landslide Experimental Sites (ALES) established in the Nakagawa Experimental Forest of Hokkaido University in northern

Hokkaido, Japan (Fig. 1, Site 1: 44.786° N, 142.252° E; Site 2: 44.783° N, 142.254° E; Site 3: 44.796° N, 142.249° E). The plant stand, root systems, and approximately 50 cm of topsoil were removed at each site using bulldozers and power shovels, contouring the surface layers into a smooth slope. The centre area of ALES measures 30 × 30 m, surrounded by a 5-meter-wide buffer zone. The buffer zone prevented any woody debris or vegetative structures, such as adventitious roots, from entering the post-landslide area, ensuring that the seedlings originated solely from seed reproduction. All ALES treatments of these three sites were completed in the summer of 2021 (Furusawa et al., 2023; Makoto et al., 2024). In the late spring of 2022, the first growing season after the landslide treatment, nine 2 × 2m survey plots were established, evenly spaced in a 3 × 3 grid, with a distance of 10 m between each plot and its adjacent plots.

Seedlings of the species, *Abies sachalinensis* and *Acer mono*, mostly dominated. *A. sachalinensis* is commonly distributed at elevations below 1000 m (Forest Research and Management Organization, Japan) and is one of the dominant conifer species in the natural forests of Hokkaido. *A. sachalinensis* is a diploid (2n = 24, (Hizume et al., 2016)), monoecious species and an obligate seeder, depending on seed reproduction. Seeds of *A. sachalinensis* are mainly dispersed by gravity and wind. *A. sachalinensis* can also regenerate on woody debris in the sub-boreal forest (Lian et al., 2008), and may be dispersed through the food storage behavior of birds and small mammals (Lobo, 2014). ALES removed the soil seed bank and all woody debris, and no signs of mammals caching seeds were observed in the central area. Therefore, we assume that all *A. sachalinensis* seedlings dispersed from the surrounding mature forest. Hereafter we refer to *A. sachalinensis* as *Abies.* Details of the experimental forests, ALES treatment and target plants can be found in Chapter 2.

2.2. Survey, measurement and sampling

From June to October 2022, we monitored the performance of newly recruited seedlings at the three sites. Combining field photography with laboratory image analysis using ImageJ (v1.53t), we

extracted the coordinates of seedlings and rill edges within each plot. The Euclidean distance (unit: cm) of each *Abies* seedling to the nearest conspecific neighbor within each plot was measured based on the seedlings' spatial coordinates, and the percentage of rill erosion in each plot was calculated as the ratio of the rill area (a polygon enclosed by rill edges in the field photo) to the plot area. Furthermore, the height (unit: cm) of surviving seedlings, defined as the length from the ground level of the seedling to the tip of the highest leaf along the stem, was measured during each survey. The relative growth rate (unit: $cm \cdot cm^{-1}$) of *Abies* is defined as the change in seedling height, calculated by dividing the difference between the height in October and June by the height in June (Chapter 2). 36.59% of the *Abies* growth rate data were excluded because their values were below zero, due to measurement errors caused by unstable slope surface during continuous erosion. The survey and the measurement of seedling performance were detailed in Chapter 2.

We collected five healthy needles from the shoot at the middle position of each of the marked *Abies* seedlings. It should be noted that tiny seedlings or seedlings without fully unfolded buds were avoided. The sampled needle was at least 5 mm in length, and older or rust-spotted needles were avoided. Scissors were used for sampling, and it was bleached with a sodium hypochlorite solution (KANEYO SOAP Co., Ltd, Arakawa City, Tokyo, Japan) after each use. The collected needles were immediately stored in a cool box and transferred to a -20°C freezer on the same day. I kept the sample at -20°C until genomic DNA extraction.

2.3. Library preparation for MIG-seq

A total of 292 *Abies* individuals were collected from these three sites. DNA extraction was performed with Abies needles using the protocols described by Gupta et al. (2020). The MIG-seq library was prepared as previously described by Suyama and Matsuki (2015). First, a multiplexed 1st PCR was performed using MIG-seq primer set-1 (Suyama and Matsuki, 2015) to amplify the ISSR. Next, a 2nd PCR was performed to attach index sequences and Illumina sequencing adapters. Subsequently, we

employed SPRI-based purification to remove too-large and small fragments from the 2nd PCR products (Double Size Selection, Backman Coulter, inc., Brea, CA, USA). The concentration of purified products was quantified, after which 4 ng of DNA from each sample was pooled to create the library. Sequencing was performed using the MiSeq Reagent Kit v3 (300 cycles, Illumina) on an Illumina MiSeq sequencer (Illumina, San Diego, CA, USA).

2.4. SNPs detection

SNP detection was performed using ipyrad (v0.9.93) (Eaton and Overcast, 2020). For each sample, the first 15 bases of R1 and R2 were trimmed, as they were part of the sequences of the MIG-seq primer. The filter for adapters/primers was set at 2. The clustering threshold for de novo assembly was set at 90% and the minimum depth at 5. All settings except for these have been set to defaults. SNP locus and read depth information formatted as a .vcf file output by ipyrad were used for further downstream analysis.

Quality control of SNP locus was performed by Tassel (v5.2.93) (Bradbury et al., 2007). It was required that an allele not be unknown (N) in at least 50% (146 / 292) of the seedlings. Otherwise, the locus was excluded. SNPs calling resulted in the selection of 2854 SNPs.

2.5. Genetic structure analysis and statistical analysis

Exploration of the genetic structure of the *Abies* population was done using discriminant analysis of principal components (DAPC, Jombart et al. (2010)). Using ‘adegenet’ package. Moreover, pair-wise and overall F_{ST} was calculated by GenAlEx (v6.51b2) (Peakall and Smouse, 2012).

Isolation-by-distance (IBD) has been tested within each Site. Specifically, a Mantel test (based on Pearson's product-moment correlation) was used to assess the correlation between the IBS genetic distance matrix and the spatial distance matrix of all individuals within a site, with the significance of the

correlation evaluated using 999 permutations. The mantel function in the 'vegan' package was used for the Mantel test.

At the plot level, we used linear mixed models (LMMs) to assess the effect of fine-scale habitat heterogeneity, i.e. rill erosion, on the genetic diversity of seedlings. Nucleotide diversity (π) within each plot was the response variable, while the coverage percentage of rill erosion within the plot and the Site ID were the explanatory variables. Seedling abundance (unit: No. seedlings) within each plot was treated as random effects. The lmer function in the lme4 package was used for the LMM.

The generalized linear mixed models (GLMMs) were used to assess the relationship between the growth rate and genetic relatedness of neighboring seedlings. First, based on the minimum conspecific distance (Chapter 2), the focal seedlings and their spatially nearest conspecific neighbors were identified. Second, seedlings with positive growth rates and estimated genetic identities were selected. Third, the genetic distance between the target seedlings and their closest neighbors was extracted from the genetic distance matrix. In the GLMM, the growth rate of a focal seedling was set as the response variable. The genetic and spatial distance between this focal seedling and its spatially nearest neighbor, and their interactive factor were set as explanatory variables. The explanatory variables were centered and standardized to eliminate the influence of their scales on model fitting. It should be noted that some seedlings were spatially nearest neighbors to each other. The explanatory variables of such seedling pairs completely overlapped when these two were treated as focal seedlings respectively. To eliminate collinearity, we included a 'Pair ID' for such seedling pairs as a random effect in the model. Furthermore, the Plot ID was set as the random effect. The GLMMs followed a Gamma error distribution and used a log link function. The glmer function in the lme4 package was used for the GLMM.

The significance of all mixed models was evaluated using the Type II Wald chi-square test. Unless otherwise stated, all statistical analyses were conducted in R software version 4.3.1 (R development core team 2023).

3. Results

3.1. Genetic structure of the Abies population

The genetic structure of *Abies* populations shown by DAPC indicated that these three populations generally clustered according to Sites, with a few individuals positioned between clusters (Fig. 2). This pattern aligns with the relative geographic locations of the three sites (Fig. 1). Pair-wise and overall F_{ST} values among *Abies* populations were all significantly different from 0, indicating a significant genetic differentiation between Sites (Table 1).

3.2. Isolation-by-distance of the Abies population

The abundance of *Abies* populations from Site 1 to Site 3 was 53, 138 and 101, respectively (Table 2). The Mantel test showed a significant positive correlation between the genetic and spatial distance matrices in Site 1, with a correlation coefficient of 0.167 (P = 0.001, Table 2). This indicated the IBD structure, in which genetic similarity decreases with increasing spatial distance between individuals in this Site. However, no correlation between genetic and spatial distances was found in the populations of Site 2 and Site 3. (Table 2)

3.3. Impacts of fine-scale habitat heterogeneity on seedlings' genetic diversity

The average nucleotide diversity (π) of surveyed plots was 0.061 $\pm$ 0.004 (mean $\pm$ SD), and the mean abundance of *Abies* seedlings was 11.8 $\pm$ 6.4 (No. seedlings per plot). The π tended to decrease with an increase in the rill coverage percentage (P = 0.064, Fig. 3, Table 3). The plot with the most severe rill erosion (rill coverage > 20%) exhibited the lowest nucleotide diversity, with a π of approximately 0.06 (Fig. 3).

3.4. Impacts of genetic distance between the nearest neighbors on growth

72 *Abies* seedlings with extracted genomic DNA and valid growth rate were detected (see Section 2.5), with an average intraspecific distance of 22.5 ± 13.7 cm. The GLMM results indicated that two factors of genetic and spatial distances exhibit an interactive effect on focal seedlings' growth, indicating that the genetic distance between focal seedlings and their nearest neighbors on the growth of focal seedlings significantly depends on their spatial distance ($P = 0.007$, Table 4). When the spatial distance between a focal seedling and its nearest neighbor is at its minimum (3.409 cm), the growth rate decreases with an increase in the genetic distance to its nearest neighbor. However, this negative pattern weakens as the spatial distance increases. Once the spatial distance exceeds 12 cm, the growth rate begins to increase with a greater genetic distance to the nearest neighbor (Fig. 4).

4. Discussion

Significant genetic differentiation was estimated among *Abies* populations across three spatially proximate disturbed patches. Within *Abies* populations, a weak but significant fine-scale spatial genetic structure was detected at least in one site. This finding suggests that dispersal limitation can work for *Abies* even at this small spatial scale (i.e., 40 x 40 m). This can also explain why genetic differentiation between all pairs of three sites was detected. Furthermore, stronger rill erosion following the landslide reduced genetic diversity in the *Abies* population. Interestingly, the influence of the genetic distance between focal seedlings and their nearest neighbors on the growth of the focal seedlings significantly depends on their spatial distance. The higher genetic relatedness promoted the growth of focal seedlings within close spatial distance, while this relationship reversed when the spatial distance increased. To our knowledge, this is the first evidence of the among- and within-patch genetic structure of newly colonized seedlings and how it shapes seedling growth at the early stage of primary succession following a heavy disturbance.

4.1. Genetic differentiation of Abies populations among adjacent disturbed patches

ALES removed all plant material, woody debris, and potential seed banks in the three Sites. Therefore, these three newly colonized *Abies* seedlings in the first growing season originated by seed dispersal from adjacent natural forests. Although the maximum geographic distance among the three Sites is only 1.5 km, F_{ST} and DAPC analysis indicate significant genetic differentiation (Table 1, Fig. 2). The limited dispersal ability of *Abies* may explain this genetic differentiation among adjacent patches. According to Zou et al. (2007), the congeneric species *Abies fargesii* exhibits seed dispersal limitation in natural communities, with seed rain primarily concentrated beneath the canopy and long-distance seed dispersal (greater than 20 m) rarely observed. The strong dispersal limitation of *Abies* suggests that the seedlings colonizing disturbed patches are likely derived primarily from a few mother trees at the patch edges. The limited seed sources create a founder effect, leading to significant genetic differentiation among patches, while genetic diversity within patches remains relatively low.

Our results contrast with the study of Litrico et al. (2005), which reported low genetic differentiation among early-succession populations, attributing this to colonization from multiple nearby source populations, facilitated by the proximity of forest fragments to lava flows. Meanwhile, our finding is partially consistent with the result of Vandepitte et al. (2012). They found that the colonization of orchid populations in vacant sites was mainly dispersed from a few nearby extant populations, with very limited inflow from outside the spatially isolated reserve which reduced population diversity and promoted genetic divergence among populations. In the current study, the newly colonizing *Abies* populations within patches primarily originated from seed dispersal from nearby natural forests, with a lack of other seedling recruitment processes (e.g., from soil seed bank). Given the likely limited seed dispersal ability, this resulted in significant genetic differentiation among populations.

4.2. Fine-scale genetic structure and effects of rill erosion

We found that one of the three Sites newly colonizing *Abies* populations exhibited a pattern of isolation-by-distance at the scale of the post-landslide area (tens of meters), where the genetic distance

between seedlings increased with increasing spatial distance. These patterns of fine-scale genetic structures in seedling populations are mainly related to the genetic structure of source populations in the surrounding natural forest.

Considering the dispersal limitations of *Abies*, spatial genetic structures may have existed within its populations during the long-term development of local natural forests. The spatial genetic structure in natural forests, "genetic groups", shows stronger genetic identity-relatedness among individuals within groups and genetic differentiation between groups. Based on survey-site information (Fig. 1) and DAPC analysis (Fig. 2), we infer that Site 1 is located at the boundary between two genetic groups in the natural forest, where the surrounding adult trees exhibit higher diversity. In contrast, Site 2 and Site 3 are situated within a single genetic group, with adult trees in their vicinity showing greater genetic homogeneity. As discussed in Section 4.1, the newly established seedlings in disturbed patches originate from seeds dispersed by mother trees at the patch edges. Consequently, genetic structure, IBD, was detected in the seedling population at Site 1, whereas no such structure was found in Site 2 and Site 3 populations.

Furthermore, the environmental heterogeneity caused by ongoing rill erosion following the landslide may also contribute to the genetic structure within populations in disturbed patches. Under strong rill erosion, i.e., in plots with higher rill coverage, the π value was significantly lower (Fig. 3), which suggests the secondary seed distribution process (Vander Wall et al., 2005) caused by rill erosion contributed to shaping the genetic structure of the population. After seeds disperse into the post-landslide area, water flows, soil movement and mixing during the rill erosion may redistribute seeds, thus weakening fine-scale genetic structures. Plots in Site 1 experienced the mildest rill erosion in our survey, with rills on average covering 8.6% of the total plot area (Table 2). At Site 1, the seed redistribution process caused by rill erosion was relatively weak, which may provide another explanation for the significant genetic structure observed in the population.

4.3. Effects of the genetic relatedness among conspecific neighbors

The dispersal limitation of *Abies* species, combined with the persistent rill erosion in the post-landslide area, may have collectively contributed to the relatively low genetic diversity of newly colonized populations within the site. Therefore, seedlings are more likely to interact with genetically similar neighbors, modifying their performance. The growth-genetic distance relationships between the focal seedling and its spatially nearest neighbor may result from the combined effects of three processes including (1) conspecific competition, (2) competition avoidance among kin individuals, and (3) conspecific facilitation mediated by mycorrhiza networks. The spatial ranges of these three processes likely differ, leading to the growth-genetic distance relationship being significantly dependent on the spatial distance between focal seedlings and their nearest neighbors (Fig. 4).

As discussed above, strong dispersal limitation results in a genetically non-diverse seedling population, leading to highly related seedlings only occurring in a site. High relatedness, i.e. lower genetic distance, among seedlings may indicate substantial niche overlap, meaning their resource requirements are highly similar, which could intensify conspecific competition (Adler et al., 2018; File et al., 2011). However, if related neighbors are in very close spatial proximity, the outcomes of competition may be influenced by certain facilitative processes. For instance, mechanisms of competition avoidance have been demonstrated among coexisting genetically related individuals, particularly root competition avoidance, reduced cost of competition, thereby facilitate the accumulation of more aboveground biomass (Tomiolo et al., 2021). Furthermore, common mycorrhizal networks can also contribute to conspecific facilitation (Chapter 2). We speculate that these two processes outweigh intraspecific competition at very close distances, which leads to higher genetic relatedness promoting the growth of focal seedlings within close spatial distances. However, the effects of these two processes diminish as spatial distance increases, resulting in growth-relatedness relationships reversed. When the spatial distance between the focal seedling and its nearest neighbor exceeds approximately 12 cm, the growth of the focal seedling is promoted by their greater genetic distance, which may be a result of intraspecific niche differentiation (Sandhu et al., 2013).

5. Conclusion

This study determined the dispersal limitation of the species *Abies sachalinensis* during early succession following disturbance. This explains the genetic differentiation among *Abies* populations across three spatially proximate patches and serves as a major driver of fine-scale spatial genetic structure within the population. Stronger rill erosion reduces genetic diversity and may also mitigate genetic structure within populations. Interestingly, the growth-genetic distance relationships between the focal seedling and its spatially nearest neighbor may result from the combined effects of multiple processes. The spatial scales at which these processes operate differ, leading to the outcomes of the growth-genetic distance relationships that depend on the spatial distance. Our results suggest that a deeper understanding of the among- and within-patch genetic structure of newly colonized seedlings and its influence on seedling growth at the early stage of primary succession will provide valuable insights for guiding post-disturbance forest restoration and management projects. In the future, prioritizing long-term monitoring of the genetic structure of newly colonized populations and their interactions with community members, such as herbivores, as populations develop, will contribute to a more comprehensive understanding of forest restoration regulation.

Table 1. The pair-wise and overall F_{ST} between newly colonized *Abies* populations

	F_{ST}	P
Site 1 vs Site 2	0.079	**0.001**
Site 1 vs Site 3	0.087	**0.001**
Site 2 vs Site 3	0.040	**0.001**
Overall	0.060	**0.001**

Note: *P*-values less than 0.1 are marked in bold.

Table 2. Mantel analysis between spatial and genetic distance matrix within populations.

	r	*P*	Abundance	Rill percentage
Site 1	0.167	**0.001**	53	8.6%
Site 2	0.009	0.34	138	13.16%
Site 3	0.018	0.217	101	10.2%

Note: Abundance refers to the number of seedlings detected for SNPs within each Site. Rill percentage was calculated as the average coverage percentage of plots covered by rills within each Site. *P*-values less than 0.1 are marked in bold.

Table 3. A linear mixed model (LMM) for the average nucleotide diversity (π).

	Explanatory variables			
	Rill percentage (%)		Site ID	
Response	Estimate	*P*	Estimate	*P*
π	-0.024	**0.048**	-0.002	**0.013**

Note: *P*-values less than 0.1 are marked in bold.

Table 4. A generalized linear mixed model (GLMM) for the growth rate of focal seedlings.

	Explanatory variables					
	Genetic distance		Spatial distance (cm)		Genetic distance × Spatial distance	
Response	Estimate	*P*	Estimate	*P*	Estimate	*P*
Growth rate	0.199	**0.074**	-0.166	**0.002**	0.301	**0.007**

Note: The spatial and genetic distances were centered and standardized for modelling. *P*-values less than 0.1 are marked in bold.

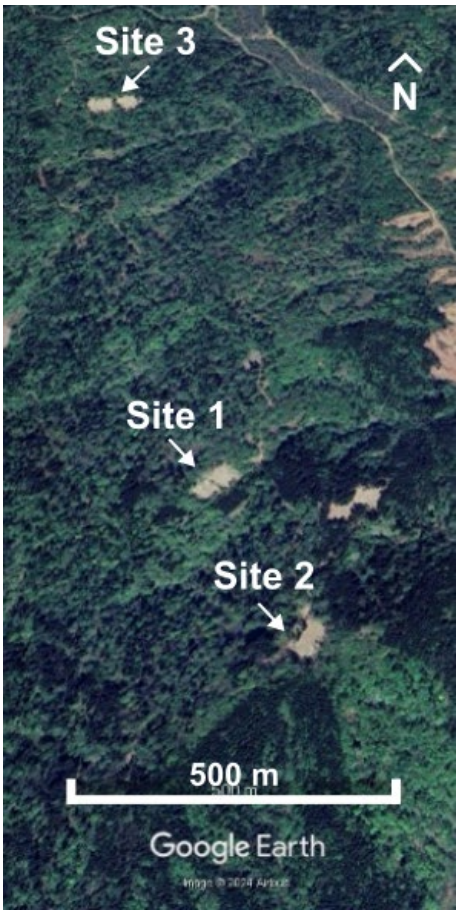
FIGURE LEGENDS

Figure 1. A geographical distribution map of the three Artificial Landslide Experimental Sites.

Figure 2. Discriminant analysis of principal components (DAPC) of the genetic structure of newly established *Abies* populations across the three ALES sites based on SNPs. Each point represents a seedling. F_{ST} represents the overall value derived from Table 1.

Figure 3. A linear mixed model (LMM) of the influence of plot-level rill coverage percentage (%) on the Average nucleotide diversity (π). Each point represents the π value of a plot. The fitted curves in the figure are calculated based on only the fixed effect. The *P*-value is derived from Table 3.

Figure 4. A generalized linear mixed model (GLMM) exploring the interactive effect of spatial and genetic distances between focal seedlings and their nearest neighbors on the growth rate of focal seedlings. Each point represents the growth rate of a seedling. The lines represent the predicted growth rates as a function of genetic distance at different levels of spatial distance, based on the original data. The *P*-value is derived from Table 4, where spatial and genetic distances were centered and standardized for modelling.



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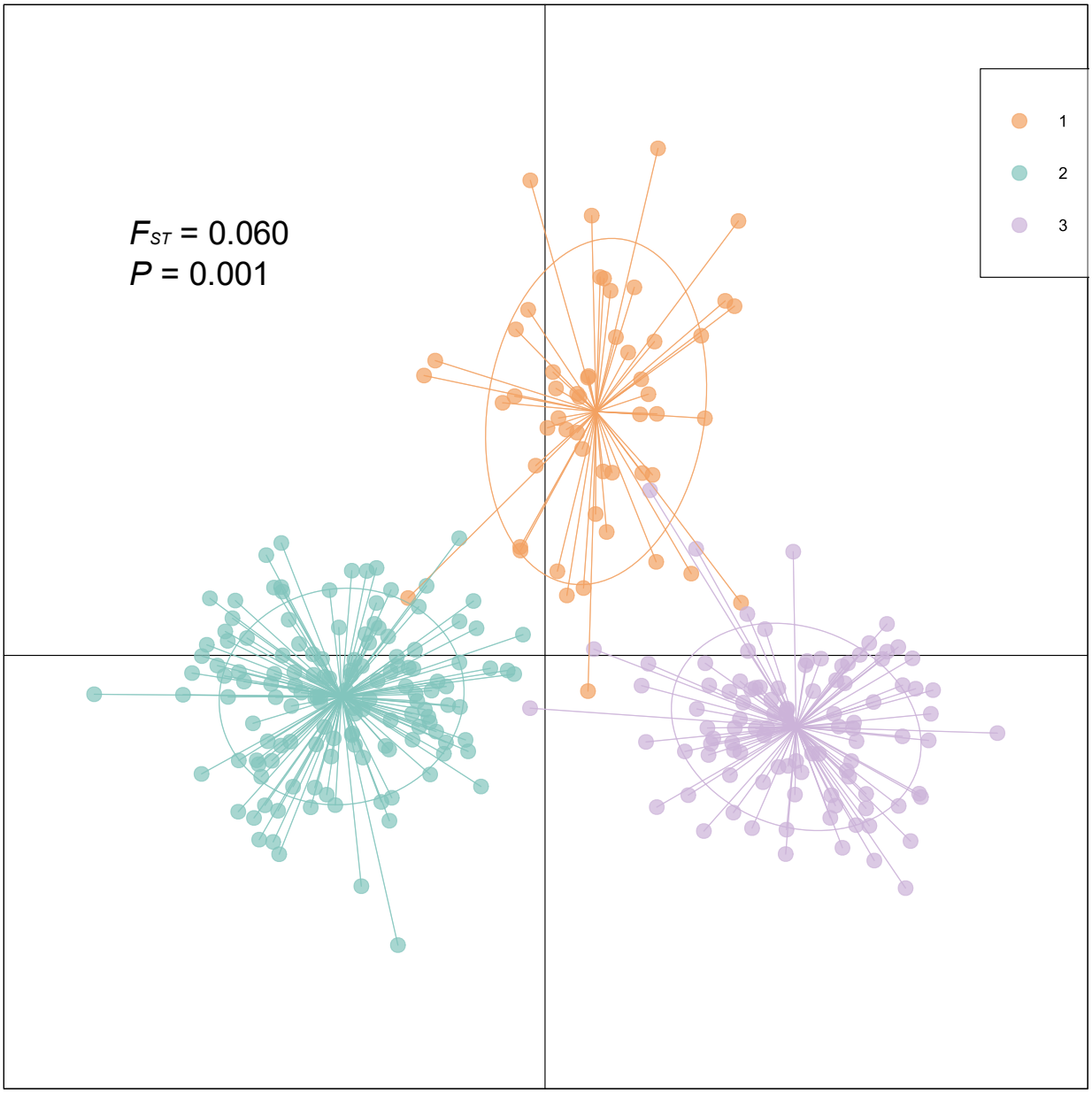

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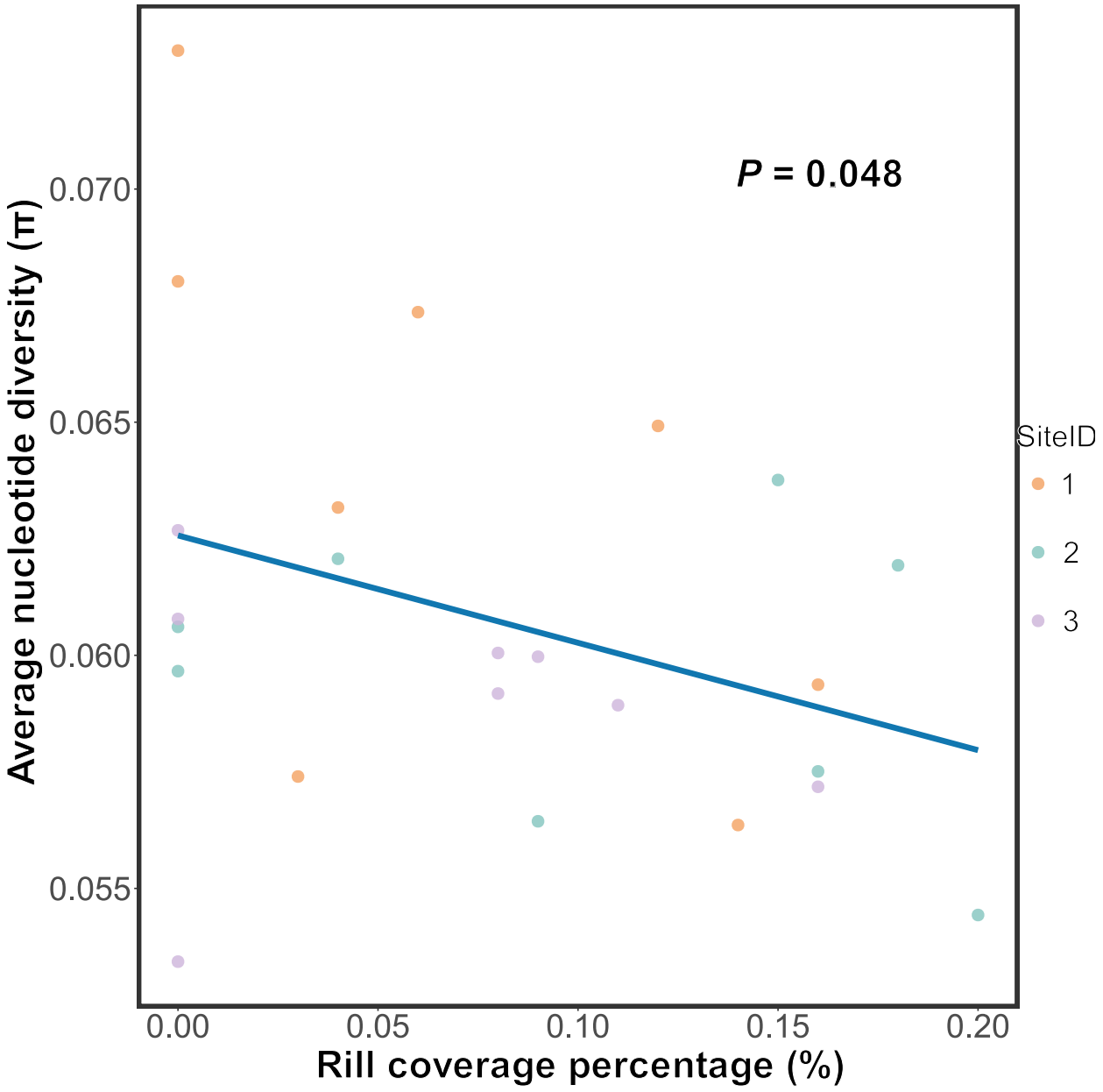

Figure 3. A linear mixed model (LMM) of the influence of plot-level rill coverage percentage (%) on the Average nucleotide diversity (π). Each point represents the π value of a plot. The fitted curves in the figure are calculated based on only the fixed effect. The *P*-value is derived from Table 3.

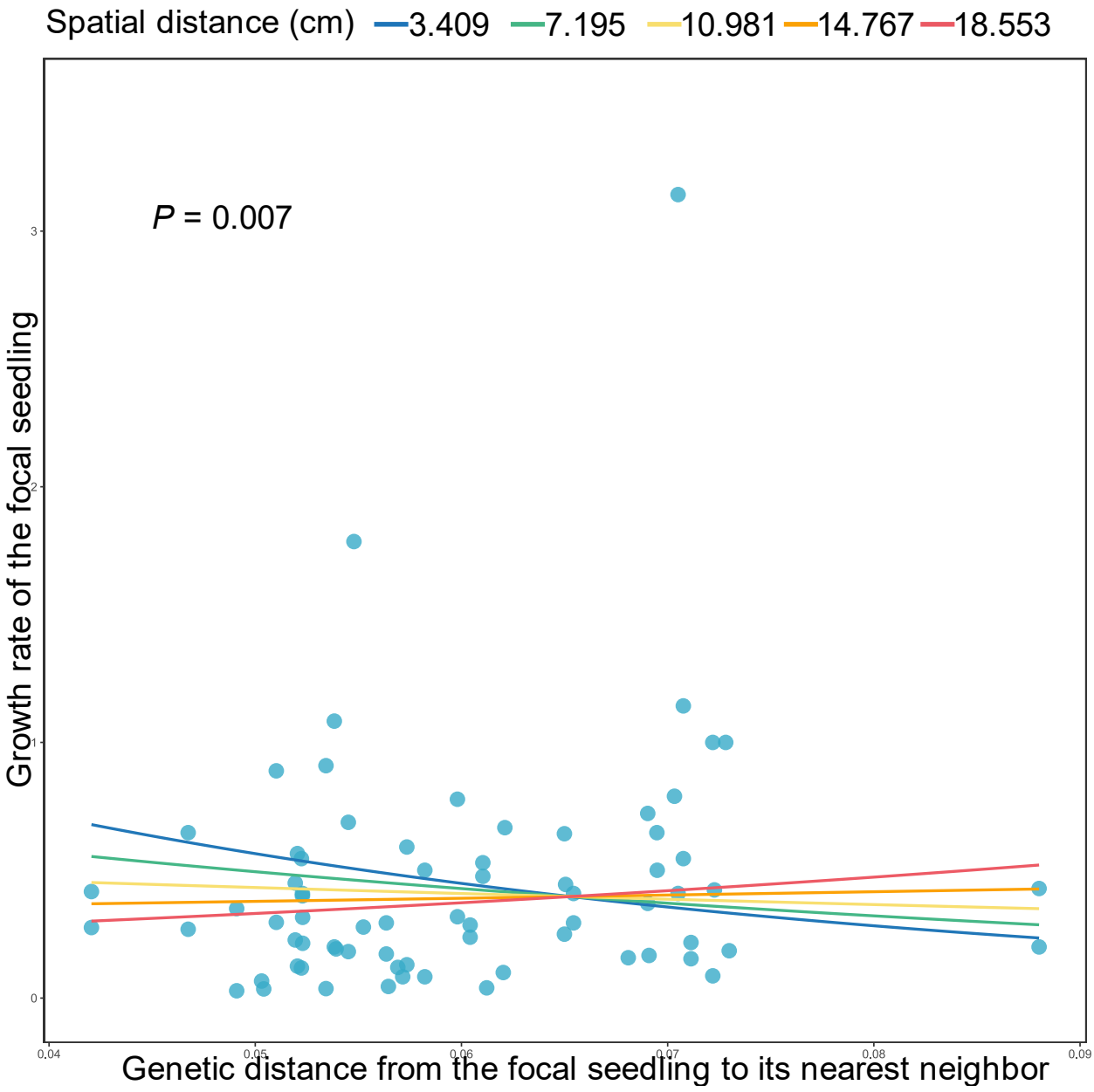

Figure 4. A generalized linear mixed model (GLMM) exploring the interactive effect of spatial and genetic distances between focal seedlings and their nearest neighbors on the growth rate of focal seedlings. Each point represents the growth rate of a seedling. The lines represent the predicted growth rates as a function of genetic distance at different levels of spatial distance, based on the original data. The *P*-value is derived from Table 4, where spatial and genetic distances were centered and standardized for modelling.

Chapter 4.

Soil microorganisms and intraspecific genetic diversity influence relationships between species diversity and ecosystem functioning

1. Introduction

Ecosystem functions include the physicochemical and biological processes that occur within the ecosystem to maintain terrestrial life (Trivedi et al., 2018), and the subject of biodiversity-ecosystem functioning (BEF) focuses on how biodiversity and ecosystem functioning are interrelated (Ali, 2023; Loreau, 2000; Loreau and Hector, 2001; Naeem and Li, 1997; Tilman, 2001). Forests perform vital ecosystem functions (i.e. productivity: Hao et al., 2020; herbivory resistance: van Schrojenstein Lantman et al., 2018; carbon balance: Lladó et al., 2017), and their conservation and restoration are crucial for regulating climate and mitigating global biodiversity loss (Trogisch et al., 2021). Previous studies have revealed positive influences of plant species diversity on multiple ecosystem functions (Jiang et al., 2009; van der Plas et al., 2016). The explanations for the mechanisms behind positive biodiversity-functioning relationships can be partitioned into two main categories: complementarity effects and selection effects, the former arises from niche differentiation and/or facilitation among species, while the latter results from the dominance by species with particular traits, leading to improved functioning (Loreau and Hector, 2001). In recent decades, global climate change (Seidl et al., 2017), coupled with the impact of human activities (FAO, 2000), has led to more frequent disturbances in forests (forest fire: Cannon et al., 2017; landslides: Scheidl et al., 2020; and introduced species: Dale et al., 2001). Due to urgent demands for more efficient forest restoration under these recent disturbance conditions, it is crucial to better understand how biodiversity-functioning relationships in newly recruited seedling communities vary with other ecological factors. In particular, both soil microorganism community and intraspecific diversity may be largely affected by large-scale forest disturbance but how both alter the relationships between tree species diversity and ecosystem functioning remains to be elucidated.

Soil microorganisms are microscopic life forms in soil, including bacteria, fungi, and other groups such as viruses and protists (Islam et al., 2022; Sala et al., 2017). Soil microorganisms are well known to enhance plant performance through direct or indirect interactions with plants (Artursson et al., 2006). Soil bacteria and fungi, through symbiotic relationships, can improve nutrient acquisition and

herbivory resistance in plants (Lladó et al., 2017; Wahab et al., 2023). At the same time, they decompose litter and debris, improving soil nutrient availability (Rashid et al., 2016). Plant-ecosystem functioning could be explained by plant-soil interactions (Forero et al., 2021). Under climate change, landslides triggered by heavy rainfall, remove topsoil and significantly alter soil microbial composition (Yamanaka et al., 2022). However, the effects of changes in soil microbial composition on the BEF relationships in seedling communities have not been sufficiently studied (see Raynaud et al. (2021)).

In BEF research, plant species diversity was initially the primary focus (Guo et al., 2019; Kunz et al., 2019; Morin et al., 2011). Recently, the recognition of how multiple facets of biodiversity influence biomass productivity and other functions has gradually increased (Ali, 2023). The influences of biodiversity's intraspecific (genetic) facet on ecosystem functioning are similar to that of species diversity (Fargeot et al., 2024; Wan et al., 2022). Increased genetic diversity can enhance productivity (Reiss and Drinkwater, 2018), suppress herbivory damage (Tooker and Frank, 2012), and improve the potential adaptability of wild species to environmental changes (Hoban et al., 2021). However, there are no studies exploring how genetic diversity influences the association between species diversity and ecosystem functioning. Forest disturbances or fragmentation could reduce plant genetic variation through altering habitat size and seed dispersal patterns (Lehouck et al., 2009; Patiño et al., 2010). How changes in genetic diversity affect plant communities' functioning, and how it interacts with species diversity, remain unresolved.

Due to the complex structure of the natural forest, there are still few available BEF findings from manipulation experiments in young tree communities (Tobner et al., 2016), while the dynamics of the seedling stage are considered crucial in determining later vegetation patterns (Harper, 1977). To illustrate how the new biotic conditions following forest disturbances affect the functioning of newly recruited plant communities, we established a common garden experiment using seedlings of dominant species from natural forests in northern Japan. The presence or absence of natural soil microorganisms and the genetic diversity of seedlings were manipulated. Specifically, we address the following questions: 1) how

species diversity-ecosystem functioning relationships are influenced by soil microorganisms and intraspecific genetic diversity? 2) how this species diversity, in turn, shapes the composition of soil microorganisms (i.e., fungi and bacteria)?

2. Material and Methods

2.1 Plant materials

Two species, *Alnus hirsuta* Turcz. and *Betula ermanii* Cham., both belonging to Betulaceae, were used to establish a common garden. Both species are deciduous broad-leaved trees widely distributed in the native natural forests of Hokkaido and can serve as pioneer species following disturbances. *Alnus hirsuta* is a nitrogen-fixing tree capable of forming root nodules in symbiosis with *Frankia* bacteria and has been suggested for use in landslide restoration (Kagiya and Utsumi, 2020; Makoto et al., 2024). *Betula ermanii* is known for its rapid presence in forest gaps and post-disturbance sites (Tabata, 1966). Hereafter, we refer to *A. hirsuta* as *Alnus* and *B. ermanii* as *Betula*.

The experimental seedlings were grown from seeds collected from four experimental forests of the Field Science Center for Northern Biosphere, Hokkaido University. The experimental forests, from north to south, include Teshio (TS), Nakagawa (NK), Uryu (UR), and Tomakomai (TMK). The average annual temperatures of the first three forests range from 3 to 5°C, with a maximum snow depth exceeding 200 cm. The experimental forest TMK is located in the suburbs of Tomakomai, a coastal industrial city. The average annual temperature of the forest TMK is around 7°C, and the maximum snow depth is approximately 70 cm. *Alnus* consists of one population sourced from TS, while *Betula* includes three populations collected from NK, UR, and TMK. Since the distances between these origins are significantly greater than the seed collection ranges within each origin, the *Betula* populations are considered to have genetic variables. Seeds were collected from those origins in autumn 2020, immediately washed with ethanol and water, dried at room temperature. And then, the seeds were sterilized with 15% hydrogen peroxide for 20 minutes, and were wrapped with wet filter papers and stored at 4°C until sowing.

In January 2022, seeds of *Alnus* and *Betula* were sown in seedling trays in the glasshouse of the Sapporo Experimental Forest, Hokkaido University. Five seeds of each species (population) were planted in each cell. Commercial gardening soil (Akadama soil, made from a type of volcanic clay) was used for seed germination (MORI SANGYO Co., Ltd., Shihoro Town, Hokkaido, Japan). The seeds began germinating in March 2022. We selected the largest seedlings in April and removed the remaining individuals from each cell. When the height of the aboveground part of the seedlings reached approximately 5 cm, we transplanted them from the seedling trays into separate pots (7.5 cm in diameter and 6.5 cm in height). The pots were placed in a glasshouse for two weeks before being moved outdoors until transplanted and combined in the common garden experiment. From seed germination until the start of the common garden experiment, the seedlings were watered thoroughly twice a week and protected from herbivory using insect mesh.

The natural soil used for inoculation was collected from UR in July 2022. The soil was classified as brown forest soil. Approximately 30 L of soil were separately collected from beneath mature *Alnus* and *Betula* tree crowns in the natural forest. Natural soil were collected from the ground surface down to a depth of approximately 20 cm. The collected soil was then transported back to the laboratory at ambient temperature. Plant tissues and soil animals were removed from both soil samples, which were then combined, sieved through a 2 mm mesh, and stored at 4°C.

2.2 Common garden establishments

The common garden experiment was conducted from July 2022 to October 2023. In July 2022, the common garden experiment was conducted in the open air of the cultivation field of Sapporo Experimental Forest. This field is located in the urban area of Sapporo, where the average annual temperature is 9.5°C and the maximum snow depth is 94 cm, calculated as the average from records spanning 2001 to 2020 (Japan Meteorological Agency).

We selected a 10 × 10 m area within the cultivation field. The above-ground weeds in this area were removed, and plastic mats were laid down to prevent the re-establishment of weeds and to ensure that the ground beneath all pots was homogeneous. The experimental zone was designated as a 16 × 16 grid, with each cell measuring 50 cm on each side. A 1 m wide buffer zone surrounded the experimental zone.

The common garden was established using pots with a diameter and depth of 30 cm, which were bleached with a 1% sodium hypochlorite solution (KANEYO SOAP Co., Ltd., Arakawa City, Tokyo, Japan) before use. Each pot was filled with approximately 9 kg of commercial Akadama soil (KATO SANGYO Co., Ltd, Kanuma City, Tochigi, Japan), a commonly used Japanese horticultural substrate made from dried volcanic clay. Diversity treatments were implemented by transplanting different combinations of seedlings into common garden pots. Four seedlings were transplanted into each pot, and combinations for the diversity treatment included: the *Alnus* monoculture; monocultures of *Betula* with 1, 2, and 3 mixed populations; and polycultures of *Alnus* with 1, 2, and 3 *Betula* populations (see Table S1 for the details of combinations and the number of replicates). The transplanted seedlings were spaced at least 15 cm apart. The soil was washed off the roots with tap water, and all *Alnus* had already formed root nodules through symbiosis with *Frankia* bacteria before transplantation.

Furthermore, an equal number of pots were inoculated with the sieved natural soil to compare the effects of the presence or absence of natural soil microbial communities on the host plants. The natural soil was inoculated at a ratio of 1:49 (natural soil: Akadama soil on the weight basis), which has been expected to alter the soil microbial community without increasing mineral nutrient availability (Luo et al., 2017). Before transplanting the seedlings, the natural soil was evenly spread over the Akadama soil, and an additional layer of the Akadama soil was placed on top. In summary, 226 pots were randomly placed at the center of each 0.5 × 0.5 m cell. During the experiment, we weeded every two months during the growing season and only watered during prolonged drought periods, defined as more than 10 consecutive days without rain.

2.3 Plant performance measurements

The percentage of leaf area loss has been used as the index of plant herbivory damage. For each seedling, the leaf area loss caused by insect feeding was assessed on-site by visual estimation for the 2nd, 3rd, and 4th mature leaves from the top (excluding the top leaf if it was not fully expanded). The average of the three leaves was calculated to represent the herbivory damage of each individual. Before this census, as a reference for estimation, we collected 20 *Betula* leaves outside of the experimental zone, scanned each leaf, and used ImageJ (v1.53t) to quantify the area consumed by insect herbivory (Utsumi et al., 2013). The percentage of leaf area loss was categorized into the following ranges: <1%, 1–2.5%, 2.5–5%, 5–7.5%, 7.5–10%, 10–25%, 25–50%, 50–75%, and 75–100% (Lincoln and Mooney, 1984). All seedlings were assessed for herbivory damage in mid-July 2023, the peak activity period for local herbivorous insects during the growing season.

The difference in a seedling's aboveground biomass at the start and end of the experiment was used as an index of productivity (unit: g). Productivity at the population or community level was calculated as the sum of the productivity of all seedlings within a pot (unit: g).

The height and diameter of all seedlings were measured at the start and end of the common garden experiment. Seedling height was defined as the length from the base of the seedling to the tip of the highest leaf along the stem, while diameter measurements were taken at the base, with two measurements averaged. Aboveground biomass of experimental seedlings was fitted using Eq. (1),

$$\boldsymbol{B} = -0.082261 + 0.011049\boldsymbol{H} + 0.053617\boldsymbol{D};\ P < 0.001, R^2 = 0.770 \quad \textbf{Eq. (1)}$$

where B is the above-ground biomass (unit: g), H is the height (unit: cm) and D (unit: mm) is the basal diameter of a focal seedling. This regression was based on measurements from an additional 155 same-aged *Betula* seedlings (30 from NK, 71 from UR and 54 from TMK), which were kept under the same germination and cultivation conditions as the experimental seedlings before they were transplanted into the common garden pots. We measured the height and diameter of these seedlings in their separated pots

and measured dried aboveground biomass in the laboratory (70°C, 72 h). The same regression model was used for *Alnus* and the three *Betula* populations, because both species belong to the Betulaceae family and have similar morphology, especially during the seedling stage.

2.4 Soil sampling and DNA extraction

In September 2022 and October 2023, corresponding to the start and end of the common garden experiment, I collected soil samples from all pots. Specifically, 40 mL of soil was collected from the centre of each pot. Approximately 2 cm of surface soil was removed, and samples were taken from a 2 – 10 cm depth. The surface soil was then replaced. Samples were collected using a sterilized spoon and placed in 50 mL centrifuge tubes. The collected samples were immediately stored in a cool box and transferred to a -30°C freezer on the same day.

Soil samples for the analysis of the microorganism community were chosen from a total of 25 pots of *Alnus* monoculture, *Betula* monoculture, and species polyculture (see Table S2 for the list of soil sample selections). Since each pot was sampled at both the initial and the end stages of the experiment, a total of 50 samples were selected.

Soil DNA was extracted and purified using an ISOIL Beads Beating kit (NIPPON GENE Co., Ltd., Chiyoda City, Tokyo, Japan) with a few modifications to the original protocol by the manufacturer. 0.5 g of soil sample was taken and transferred into the supplied 2 mL tube, followed by the addition of two types of Lysis Solution (BB and 20S) and 20 mg of Skim Milk (NACALAI TESQUE, INC., Kyoto, Japan). The sample was pulverized using the SpeedMill PLUS system (Analytik Jena GmbH + Co. KG, Jena, Thuringia, Germany) for 50 s, and then centrifuged (12000 × g, 1 min, ambient temperature). The extracted DNA was air-dried, dissolved with 50 ml TE buffer (pH 8.0), and stored at −20°C until further processing.

2.5 PCR and sequencing

We used a two-step PCR approach for the library preparation for MiSeq sequencing. The first-round PCR (1st PCR) was conducted to amplify the 16s rRNA regions and the ITS2 region using primers specific to bacteria (515F – 860R, Caporaso et al. 2011) and fungi (gITS7 – ITS4, Ihrmark et al. 2012), respectively. For both bacteria and fungi, the volume of the 1st PCR reaction mixture was 25 µl, containing 2 µl of template DNA, 0.5 µl of forward and reverse 1st PCR primers (with the concentration of 10 µM), 12.5 µl of Platinum Hot Start PCR Master Mix (Thermo Fisher Scientific Inc., Waltham, Massachusetts, USA), and 9.5 µl of Milli-Q water. A negative control was included in the 1st PCR, where 2 µL of template DNA was replaced with an equal volume of Milli-Q water, while the rest of the reaction mixture was identical to that of the samples. The 1st PCR was performed under the following conditions: initial activation at 94°C for 3 mins; 35 cycles at 94°C for 45 s (denaturation), 50°C for 60 s (annealing of primers), and 72°C for 90 s (extension), and a final incubation at 72°C for 10 min.

The second-round PCR (2nd PCR) was carried out to append indices for different samples for sequencing with MiSeq. For both bacteria and fungi, the volume of the 2nd PCR reaction mixture was 25 µl, containing 2.5 µl of template DNA (1st PCR products, without diluted), 2.5 µl of forward and reverse index primers (with the concentration of 5 µM), 12.5 µl of KAPA HiFi HotStart ReadyMix (NIPPON Genetics Co, Ltd., Bunkyo City, Tokyo, Japan), and 5 µl of Milli-Q water. A negative control was included in the 2nd PCR, where 2.5 µL of template DNA was replaced with an equal volume of Milli-Q water, while the rest of the reaction mixture was identical to that of the samples. 2nd PCR was performed under the following conditions: initial activation at 95°C for 3 mins; 8 cycles at 95°C for 30s (denaturation), 55°C for 30s (annealing of primers) and 72°C for 30s (extension), and a final incubation at 72°C for 5 min. The second PCR products were then pooled for each of the 16S rRNA and fungal ITS2 regions after a purification step using the AMPure XP Bead-Based Reagent (Beckman Coulter, Inc., Brea, California, USA). The DNA library was paired-end sequenced (2 × 300 bp) on the MiSeq platform (Illumina, San Diego, California, USA) using the MiSeq Reagent Kit v3 (600 cycle, Illumina, San Diego, CA, USA). SimpliAmp Thermal Cycler (A24812, Thermo Fisher Scientific Inc.)

2.6 Bioinformatics

The sequencing data were analyzed in R using "DADA2" (Callahan et al., 2016). Prior to the bioinformatics pipeline in DADA2, I used the "fastp" and "cutadapt" software to remove primers from the data and ensured that the data set comprises demultiplexed, paired-end fastq files. I applied the core sample inference algorithm to the trimmed and filtered data using "dada" function, and then forward and reverse reads were merged to obtain the full denoised sequences (the "mergePairs" function in the package DADA2). After the removal of the chimeras (the "removeBimeraDenovo" function), I applied taxonomic assignment to ASV data. Each ASV was taxonomically assigned using the IDTAXA machine learning algorithm (the "IdTaxa" function in DECIPHER; Murali et al. 2018), which is better than the long-time standard set by the native Bayesian classifier. The RDP v18 classifier reference database, and the UNITE 2024 database were used as training data sets with known taxonomy for bacteria and archaea, and for fungi, respectively.

2.7 Statistical analysis

The species diversity effects of species polyculture pots (Groups 4, 5 and 6 in Table S1) were statistically partitioned into complementarity and selection effects, and the net diversity effects were calculated as the sum of the complementary and selection effects (Loreau and Hector, 2001). For the two treatments in this experiment, namely the presence or absence of natural soil inoculation (y or n) in pots and the genetic diversity of *Betula* seedlings (with population combinations of 1, 2, or 3), we calculated the species diversity effects separately for each treatment. Two-sided t-tests were used to compare the significant differences in diversity effects (complementarity, selection and net effects) from zero for each treatment. The ANOVA was used to compare whether there are significant differences among different levels within treatments.

To visualize the pot difference in the microbial composition we performed the statistic of t-distributed stochastic neighbor embedding (t-SNE). Additionally, we applied permutational multivariate analysis of variance (PERMANOVA) to analyze whether species diversity, live soil inoculation and experimental stage (initial or end stage of the common garden experiment) significantly affect the Bray-Curtis dissimilarity distance of soil microbial community. The R package tsnemicrobiota was used to perform t-SNE analysis, and the package vegan was used to perform PERMANOVA.

Soil bacteria and fungi were analyzed separately. First, we grouped the pots based on the natural soil inoculation and their experimental stage, using t-SNE for visualization. PERMANOVA was applied to analysis whether species diversity, natural soil inoculation, experimental stage, and the interactions of these three factors significantly affected microbial composition as measured by Bray-Curtis distance. Second, we performed t-SNE-based visualization of microbial composition separately for the initial and end stages of the experiment, grouping the pots by species diversity and natural soil inoculation. PERMANOVA was applied to analysis in different experimental stages, whether species diversity, natural soil inoculation and their interactional effects affected the Bray-Curtis distance of microbial communities.

All statistical analyses were conducted in R software version 4.3.1 (R development core team 2023). The following packages were also used: ‘car’, ‘multcomp’ besides the above packages.

3. Results

3.1 Natural soil inoculation influenced species diversity - ecosystem functioning relationships

For communities with natural soil inoculation, the complementarity effect, selection effect or net effect of species diversity on herbivory damage showed no significant difference from zero (Fig. 1a, Table 2). For communities without natural soil inoculation, both the selection effect and net effect of species diversity on herbivory damage were significantly less than zero (Fig. 1a, Table 2). The selection effect and the net effect were significantly higher in communities with natural soil inoculation compared to those without natural soil inoculation (Fig. 1a, Table 1).

For communities with natural soil inoculation, the selection effect and net effect of species diversity on productivity were significantly less than zero (Fig. 1b, Table 2). For communities without natural soil inoculation, the selection effect of species diversity on productivity was significantly greater than zero (Fig. 1b, Table 2). The selection effect and net effect of species diversity on productivity were significantly lower in communities with natural soil inoculation compared to those without natural soil inoculation (Fig. 1b, Table 1).

3.2 Genetic diversity influenced species diversity - ecosystem functioning relationships

For communities with a single *Betula* population, a marginally negative net effect of species diversity on herbivory damage was detected (Fig. 2a, Table 2). For communities with three *Betula* populations, the complementarity effect and net effect of species diversity on herbivory damage were significantly less than zero (Fig. 2a, Table 2). There were no significant differences between the number of *Betula* populations in the complementary, selection and net effects of species diversity on herbivory damage (Fig. 2a, Table 1).

For communities with one *Betula* population, the complementarity effect and net effect of species diversity on productivity were less than zero (Fig. 2b, Table 2). For communities with two *Betula* populations, the selection effect of species diversity on productivity was significantly less than zero (Fig. 2b, Table 2). The complementarity effect of species diversity on productivity significantly increased with the number of *Betula* populations, the complementarity effect in communities with three *Betula* populations was higher than that in communities with only one population (Tukey's multiple comparisons: $P = 0.088$; Fig. 2b, Table 1).

3.3 Compositions of soil bacterial and fungal communities.

For soil bacterial communities, in pots with only Akadama soil, the dominant classes in their composition at both the initial and end stage of the common garden experiment were *Actinobacteria*,

Alphaproteobacteria, *Betaproteobacteria*, *Chitinophagia and Gemmatimonadetes* (Fig. 3). In pots with natural soil inoculation, for both the initial and end stage, the dominant class in soil bacterial communities were *Acidobacteria*, *Betaproteobacteria*, *Chitinophagia*, and *Spartobacteria* (Fig. 3).

For soil fungal communities, the dominant classes in their composition at both the initial and end stages, in pots with Akadama soil or natural soil inoculation, were *Agaricomycetes*, *Dothideomycetes*, *Leotiomycetes*, and *Mortierellomycetes* (Fig. 4).

The experimental stage, natural soil inoculation, and their interactional effect significantly influenced the composition of bacterial communities (Table 3, Fig. 5a). Specifically, at both the initial and the end stage, the inoculation with natural soil significantly influenced the bacterial community composition (Table 3, Fig. 5b). Interestingly, at the end of the experiment, seedling species diversity also affected bacterial community composition, though this effect was marginally significant (Table 3, Fig. 5c).

The experimental stage, natural soil inoculation, the interactional effect between experimental stage and soil inoculation, as well as the three factors' interactive effect between seedling species diversity, experimental stage and soil inoculation significantly influenced the composition of fungal communities (Table 3, Fig. 6a). Similar with bacterial communities, at both the initial and the end stage, the inoculation with natural soil significantly influenced the fungal community composition (Table 3, Fig. 6b & 6c). At the end of the experiment, seedling species diversity significantly influenced bacterial community composition (Table 3, Fig. 6c).

4. Discussion

This study clearly illustrated that how soil microbial communities, and the genetic diversity of component species modified species diversity–ecosystem functioning relationships. Natural soil inoculation altered the composition of soil bacterial and fungal communities, and this effect was significant from the beginning to the end of the experiment. Both soil inoculation and the genetic

diversity of *Betula* influenced the net effect of species diversity on functioning, while the processes involved were different. Soil inoculation significantly altered the net effect of species diversity by changing the selection effect, while genetic diversity influenced the net effect of species diversity by altering the complementarity effect. Interestingly, at the end of the study, the modification of soil bacterial and fungal communities by plant species diversity was detected.

4.1 Soil microorganisms modified the dominance of seedlings in species polyculture communities

The significant net effect on reducing herbivory damage in communities (i.e., species diversity suppressed herbivory damage) without natural soil inoculation was detected, while natural soil inoculation significantly eliminated this effect (i.e., herbivory damage was not significantly different from the expectation based on species monocultures, Fig. 1(a)). On the other hand, the significant net effect of under-yielding (negative net species diversity effect on productivity) in natural soil inoculated communities was found, in contrast to the absence of this effect in communities without natural soil inoculation (i.e., productivity was not significantly different from the expectation based on species monocultures, Fig. 1(b)). Interestingly, the influence of natural soil inoculation on the aforementioned net effects was mediated through driving the selection effect of species diversity (Fig. 1). Considering the significant differences in bacterial and fungal community composition between pots with or without natural soil inoculation (Table 3(a)), I suggest that the soil microorganisms significantly modified the dominance of seedlings within the plant community.

Natural microbial communities may change palatability and competitive advantage of seedlings within the community. Regarding herbivory damage, we infer that natural soil inoculation altered seedling palatability by modifying nutrient acquisition efficiency (Kempel et al., 2009). Natural soil inoculation made *Alnus* more susceptible to damage compared to *Betula*, which may be attributed to the tripartite interaction among *Alnus*, root-nodule bacteria of *Frankia*, and ectomycorrhizal fungi (Yamanaka et al., 2022). Additionally, the enhancement of *Alnus* seedling palatability due to natural microbial inoculation is

expected to be greater than that for *Betula*. This is supported by the outbreak of the *Alnus*-specialist herbivore *Agelastica coerulea* observed in the field (my personal observation). Consequently, responses of seedlings to herbivory shifted from associational protection in the absence of natural microorganisms, where the presence of less palatable *Betula* dominated the overall low damage, to near susceptibility in the presence of natural microorganisms, where the presence of more palatable *Alnus* altered the selection effect from significantly negative to positive (although insignificant).

In the case of productivity, the natural soil inoculation may alter the competitive advantage between coexistent *Alnus* and *Betula* seedlings. Negative selection effects occur when species with relatively minor functional roles in monoculture increasingly dominate diverse communities (Jiang et al., 2008; Loreau, 2000). We speculate that natural microbial inoculation enhanced the competitive ability of *Betula*, giving it a competitive advantage in polyculture, thereby exhibiting the negative selection effect. Furthermore, differences in community soil microbiomes may also explain the negative net biodiversity effect on productivity under natural soil inoculation treatments. Pathogens can reduce plant productivity, as has been widely demonstrated in both forestry and agriculture (Chakraborty et al., 2008). In this experiment, the relative abundance of the fungal class *Tremellomycetes* increased in the natural soil, which includes several yield-reducing pathogens (Gkoutselis et al., 2024). Since the natural soil was collected from beneath the canopies of mature *Alnus* and *Betula* in natural forests, and given the significantly negative selection effect of species diversity on productivity, we infer the presence of species-specific pathogens in the natural soil targeting the seedlings of these two species. During the experiment, community species diversity also shaped the composition of soil bacterial and fungal communities, which might be the consequence of plants promoting the dominance of specific microorganisms.

4.2 Genetic diversity of seedlings facilitates the relationship of species diversity – ecosystem functioning

The significant net effect on reducing herbivory damage in communities (i.e., species diversity suppressed herbivory damage) with the highest *Betula* genetic diversity was detected, while this effect in the other two genetic diversity levels was not found (i.e., herbivory damage was not significantly different from the expectation based on species monocultures, Fig. 2(a)). On the other hand, the significant net effect of under-yielding (negative net species diversity effect on productivity) in the lowest *Betula* diversity was found. This effect diminished with increasing genetic diversity (i.e., productivity was not significantly different from the expectation based on species monocultures, Fig. 2(b)). Interestingly, the influence of *Betula* genetic diversity on the aforementioned net effects was mediated by driving the complementarity effect of species diversity (Fig. 2). These findings indicated that increased *Betula* genetic diversity within a community enhances the positive impact of species diversity on ecosystem functions.

Higher genetic diversity of *Betula* seedings in the community may enhance intraspecific facilitation, thus increasing the functioning of the community. Referring to the process of local adaptation (Lind et al., 2018), herbivorous insects may be more likely to prefer seedlings with traits similar to those of the local food resource (i.e., the common garden place), leading to greater damage. Because the native environmental conditions of the TMK forest are most similar to those in the common garden, i.e. a similar climate and both being situated around the city, we suspect that seedlings from the TMK population is more susceptible to local herbivory. The presence of the TMK population may attract more local herbivores (Fernandez-Conradi et al., 2017), thereby indirectly reducing the damage experienced by other members of the community and consequently decreasing overall community damage.

In the case of productivity, high genetic diversity enhances nutrient use efficiency in seedlings, leading to a trend of overyielding (positive net effect on productivity, although not significant). The occurrence of the complementarity effect is presumed to result from positive intraspecific interactions among seedlings, arising from resource partitioning between individuals with greater genetic distances (Subrahmaniam et al., 2021).

The current study has certain limitations. First, our exploration of BEF relationships is based solely on young seedlings, which may influence the effects of soil microorganisms and genetic diversity on species diversity–ecosystem functioning relationships, as plant life history traits often depend on their growth stage (Metz et al., 2023). Second, this experiment lasted only one year, whereas establishing associations between plants and soil microorganisms, particularly fungi, often requires a longer duration (Castillo-Bautista et al., 2024). Moreover, not only dominant species but also other tree species in the forest contribute to ecosystem functioning, which was not considered in this study. For instance, the niche under the canopy of local forests is extensively occupied by perennial herbs like *Lophatherum gracile*, which could threaten seedling survival under natural conditions (Watanabe et al., 2016).

5. Conclusion

This is the first research emphasizing that soil microorganisms and plant genetic diversity influence species diversity–ecosystem functioning relationships. Natural soil inoculation significantly altered the net effect of species diversity by changing the selection effect, indicating soil microorganisms could modify the dominance of component species within the community. The genetic diversity levels of *Betula* influenced the net effect of species diversity by altering the complementarity effect, suggesting that the intraspecific facilitation of *Betula* enhanced the functioning of the community. In post-disturbance forest management, the inoculation of soil microbial communities from mature forests should be implemented with caution, as natural soil can enhance the selection effect within plant communities, leading to a stronger dominance of certain species, which may hinder the maintenance of forest species diversity. Although this selection effect is stronger than complementarity effects (i.e., intraspecific diversity) on the relationship between species diversity and ecosystem functioning, increasing the genetic diversity of tree species could be an effective strategy facilitating BEF toward forest restoration.

Table 1. ANOVA for differences in species diversity effects (complementarity, selection, and net effects) between treatments

		Ecosystem functioning	
		Herbivory damage (%)	Productivity (g)
Treatment	Species diversity effect	*P*	*P*
Natural soil inoculation	Complementarity effect	0.403	0.753
	Selection effect	**0.012**	**< 0.001**
	Net effect	**0.003**	**< 0.001**
Genetic diversity of *Betula*	Complementarity effect	0.946	**0.042**
	Selection effect	0.361	0.113
	Net effect	0.727	0.391

Note: *P*-values less than 0.1 are marked in bold.

Table 2. Two-sided t-tests for differences in species diversity effects (complementarity, selection, and net effects) from zero across treatments

		Ecosystem functioning	
Treatment	Species diversity effect	Herbivory damage (%)	Productivity (g)
Natural soil inoculation	Complementarity effect	*P*	*P*
	Akadama	0.276	0.569
	Natural soil	0.989	0.981
	Selection effect	*P*	*P*
	Akadama	**0.019**	**0.016**
	Natural soil	0.505	**< 0.001**
	Net effect	*P*	*P*
	Akadama	**< 0.001**	0.438
	Natural soil	0.779	**< 0.001**
Genetic diversity of *Betula*	Complementarity effect	*P*	*P*
	1 *Betula* population	0.114	**0.093**
	2 *Betula* populations	0.624	0.197
	3 *Betula* populations	**0.013**	0.317
	Selection effect	*P*	*P*
	1 *Betula* population	0.241	0.240
	2 *Betula* populations	0.145	**0.002**
	3 *Betula* populations	0.457	0.164
	Net effect	*P*	*P*
	1 *Betula* population	**0.056**	**0.010**
	2 *Betula* populations	0.457	0.143

3 *Betula* populations	**< 0.001**	0.790

Note: *P*-values less than 0.1 are marked in bold.

Table 3. Permutational multivariate analysis of variance (PERMANOVA) for analyzing whether species diversity (Sp.Div), live soil inoculation (Soil) and experimental stage (Stage, initial or end) significantly affect the Bray-Curtis dissimilarity distance of soil microbial community. (a) microbial composition of all pots in all experimental stages, (b) microbial composition in the initial stage, and (c) microbial composition in the end stage.

		Explanatory variable	*P*
Bacteria	(a)	Sp.Div	NS
		Stage	**< 0.001**
		Soil	**< 0.001**
		Sp.Div × Stage	NS
		Sp.Div × Soil	NS
		Stage × Soil	**< 0.001**
		Sp.Div × Stage × Soil	NS
	(b)	Sp.Div	NS
		Soil	**< 0.05**
		Sp.Div × Soil	NS
	(c)	Sp.Div	**< 0.1**
		Soil	**< 0.001**
		Sp.Div × Soil	NS
Fungi	(a)	Sp.Div	NS
		Stage	**< 0.01**
		Soil	**< 0.001**
		Sp.Div × Stage	NS
		Sp.Div × Soil	NS
		Stage × Soil	**< 0.05**
		Sp.Div × Stage × Soil	**< 0.05**

(b)	Sp.Div	NS
	Soil	**< 0.05**
	Sp.Div × Soil	NS
(c)	Sp.Div	**< 0.05**
	Soil	**< 0.001**
	Sp.Div × Soil	NS

Note: NS: $P > 0.1$.

Table S1. Seedlings combination of common garden experiment

	Alnus	*Betula*			
		NK	*UR*	*TMK*	Replication
GROUP 1	4	0	0	0	7
	0	4	0	0	7
	0	0	4	0	7
	0	0	0	4	7
GROUP 2	0	2	2	0	7
	0	2	0	2	7
	0	0	2	2	7
GROUP 3	0	2	1	1	5
	0	1	2	1	5
	0	1	1	1	5
GROUP 4	2	2	0	0	7
	2	0	2	0	7
	2	0	0	2	7
GROUP 5	2	1	1	0	7
	2	1	0	1	7
	2	0	1	1	7
GROUP 6	1	1	1	1	7
Total					**113 Pots**

Note: GROUP 1, 2, 3: *Alnus* monoculture with 1 population, and *Betula* monoculture with 1, 2, or 3 populations. GROUP 4, 5, 6: *Alnus*-*Betula* polyculture with 1,2 or 3 *Betula* populations. B.NK: *Betula* population from experimental forest; B.UR: *Betula* population from Uryu experimental forest; B.TMK: *Betula* population from Tomakomai experimental forest. The number in the columns *Alnus, B.NK, B.UR and B.TMK* represent the abundance of seedlings of this population.

Table S2. List of samples for soil microbial analysis

No.	Pot ID	Species diversity	Soil treatment	Experimental stage
1	170	*Betula* monoculture	Akadama	Initial
2	145	*Betula* monoculture	Akadama	Initial
3	91	Species polyculture	Natural soil	End
4	226	Species polyculture	Akadama	End
5	113	Species polyculture	Natural soil	End
6	220	Species polyculture	Akadama	End
7	90	Species polyculture	Natural soil	Initial
8	204	Species polyculture	Akadama	Initial
9	34	*Betula* monoculture	Natural soil	Initial
10	50	*Betula* monoculture	Natural soil	End
11	163	*Betula* monoculture	Akadama	Initial
12	147	*Betula* monoculture	Akadama	End
13	204	Species polyculture	Akadama	End
14	146	*Betula* monoculture	Akadama	Initial
15	60	*Betula* monoculture	Natural soil	End
16	51	*Betula* monoculture	Natural soil	Initial
17	110	Species polyculture	Natural soil	Initial
18	30	*Betula* monoculture	Natural soil	End
19	29	*Betula* monoculture	Natural soil	End
20	29	*Betula* monoculture	Natural soil	Initial
21	220	Species polyculture	Akadama	Initial
22	112	Species polyculture	Natural soil	Initial
23	147	*Betula* monoculture	Akadama	Initial

24	163	*Betula* monoculture	Akadama	End
25	225	Species polyculture	Akadama	Initial
26	60	*Betula* monoculture	Natural soil	Initial
27	205	Species polyculture	Akadama	End
28	205	Species polyculture	Akadama	Initial
29	30	*Betula* monoculture	Natural soil	Initial
30	89	Species polyculture	Natural soil	End
31	51	*Betula* monoculture	Natural soil	End
32	221	Species polyculture	Akadama	End
33	91	Species polyculture	Natural soil	Initial
34	146	*Betula* monoculture	Akadama	End
35	112	Species polyculture	Natural soil	End
36	50	*Betula* monoculture	Natural soil	Initial
37	90	Species polyculture	Natural soil	End
38	226	Species polyculture	Akadama	Initial
39	110	Species polyculture	Natural soil	End
40	89	Species polyculture	Natural soil	Initial
41	145	*Betula* monoculture	Akadama	End
42	176	*Betula* monoculture	Akadama	End
43	221	Species polyculture	Akadama	Initial
44	34	*Betula* monoculture	Natural soil	End
45	225	Species polyculture	Akadama	End
46	202	Species polyculture	Akadama	End
47	170	*Betula* monoculture	Akadama	End

48	113	Species polyculture	Natural soil	Initial
49	176	*Betula* monoculture	Akadama	Initial
50	202	Species polyculture	Akadama	Initial

Note: No.: ID for soil microbial analysis. Pot ID: Pot ID was randomized in sequence.
Soil treatment: Akadama soil only or Natural soil inoculation.

Figure Legends

Figure 1. Effects of natural soil inoculation on the ecosystem functions of polycultures composed of *Alnus* and *Betula*. The deviations from the expected values based on monocultures are shown. (a) for the herbivory damage (%) and (b) for productivity (g). CE: complementarity effects; SE: selection effects; NE: net effects. The significance of each bar represents the significance difference between 0 (Table 2). The *P*-value under each panel indicates the significance of the difference between with or without natural soil inoculation (Table 1).

Figure 2. Effects of genetic diversity of *Betula* on the ecosystem functions of polycultures composed of *Alnus* and *Betula*. The deviations from the expected values based on monocultures are shown. (a) for the herbivory damage (%) and (b) for productivity (g). CE: complementarity effects; SE: selection effects; NE: net effects. The significance of each bar represents the significance difference between 0 (Table 2). The *P*-value under each panel indicates the significance of the difference between genetic diversity levels (Table 1).

Figure 3. Soil bacteria community composition and the relative abundance of each bacteria class.

Figure 4. Soil fungal community composition and the relative abundance of each fungal class.

Figure 5. t-SNE analysis of soil bacteria community composition. (a) the bacteria community structure in all pots, as well as at the initial and final stages. (b) and (c) represent the bacteria community at the initial and final stages. The significance of the treatments was calculated using PERMANOVA (Table 3).

Figure 6. t-SNE analysis of soil fungal community composition. (a) the fungal community structure in all pots, as well as at the initial and final stages. (b) and (c) represent the fungal community at the initial and final stages. The significance of the treatments was calculated using PERMANOVA (Table 3).

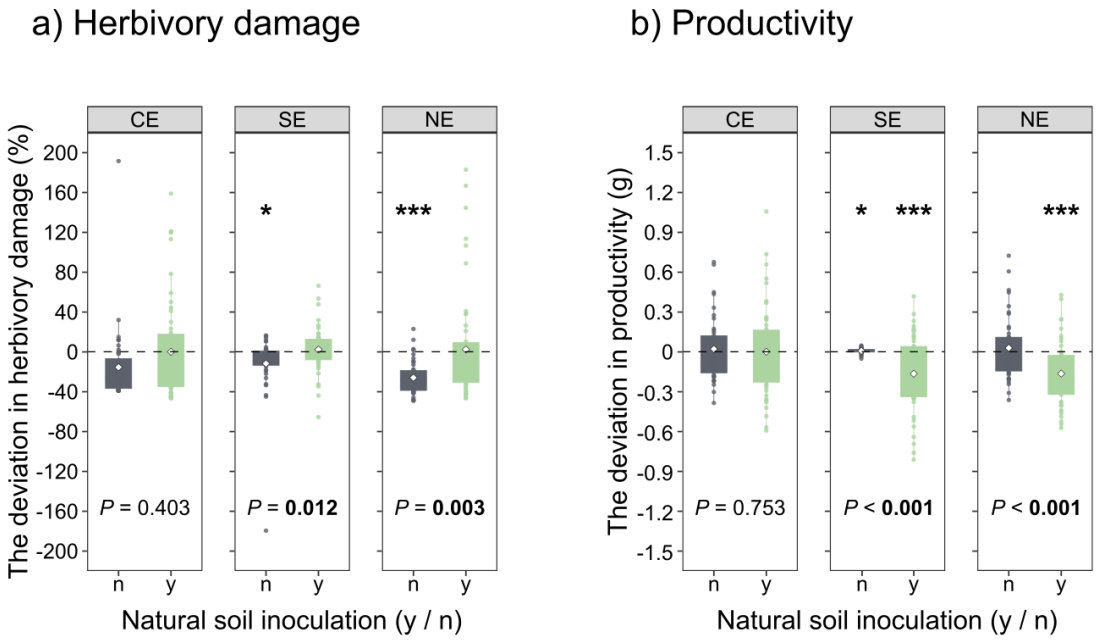

Figure 1. Effects of natural soil inoculation on the ecosystem functions of polycultures composed of *Alnus* and *Betula*. The deviations from the expected values based on monocultures are shown. (a) for the herbivory damage (%) and (b) for productivity (g). CE: complementarity effects; SE: selection effects; NE: net effects. The significance of each bar represents the significance difference between 0 (Table 2). The *P*-value under each panel indicates the significance of the difference between with or without natural soil inoculation (Table 1).

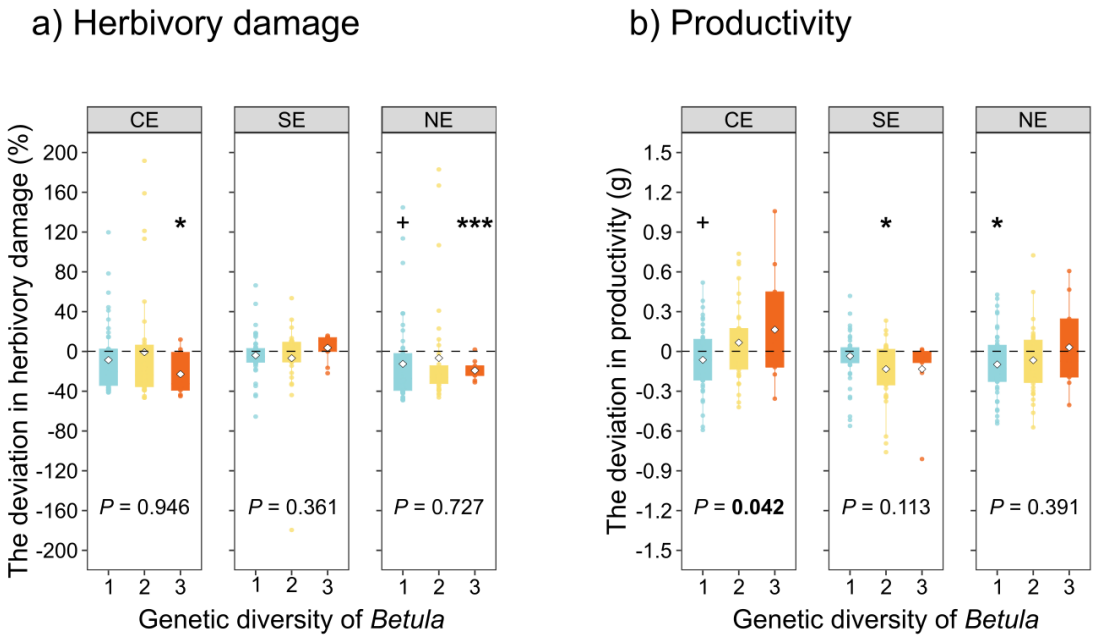

Figure 2. Effects of genetic diversity of *Betula* on the ecosystem functions of polycultures composed of *Alnus* and *Betula*. The deviations from the expected values based on monocultures are shown. (a) for the herbivory damage (%) and (b) for productivity (g). CE: complementarity effects; SE: selection effects; NE: net effects. The significance of each bar represents the significance difference between 0 (Table 2). The *P*-value under each panel indicates the significance of the difference between genetic diversity levels (Table 1).

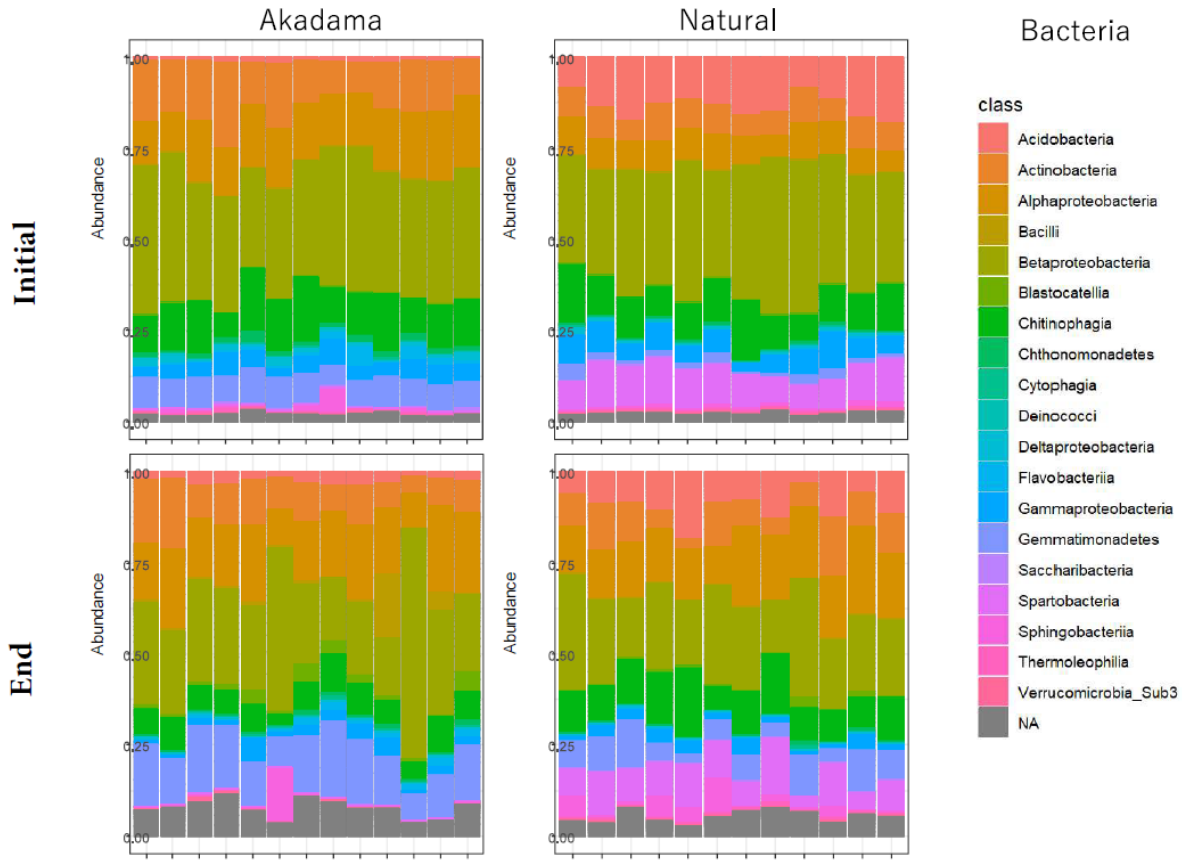

Figure 3. Soil bacteria community composition and the relative abundance of each bacteria class.

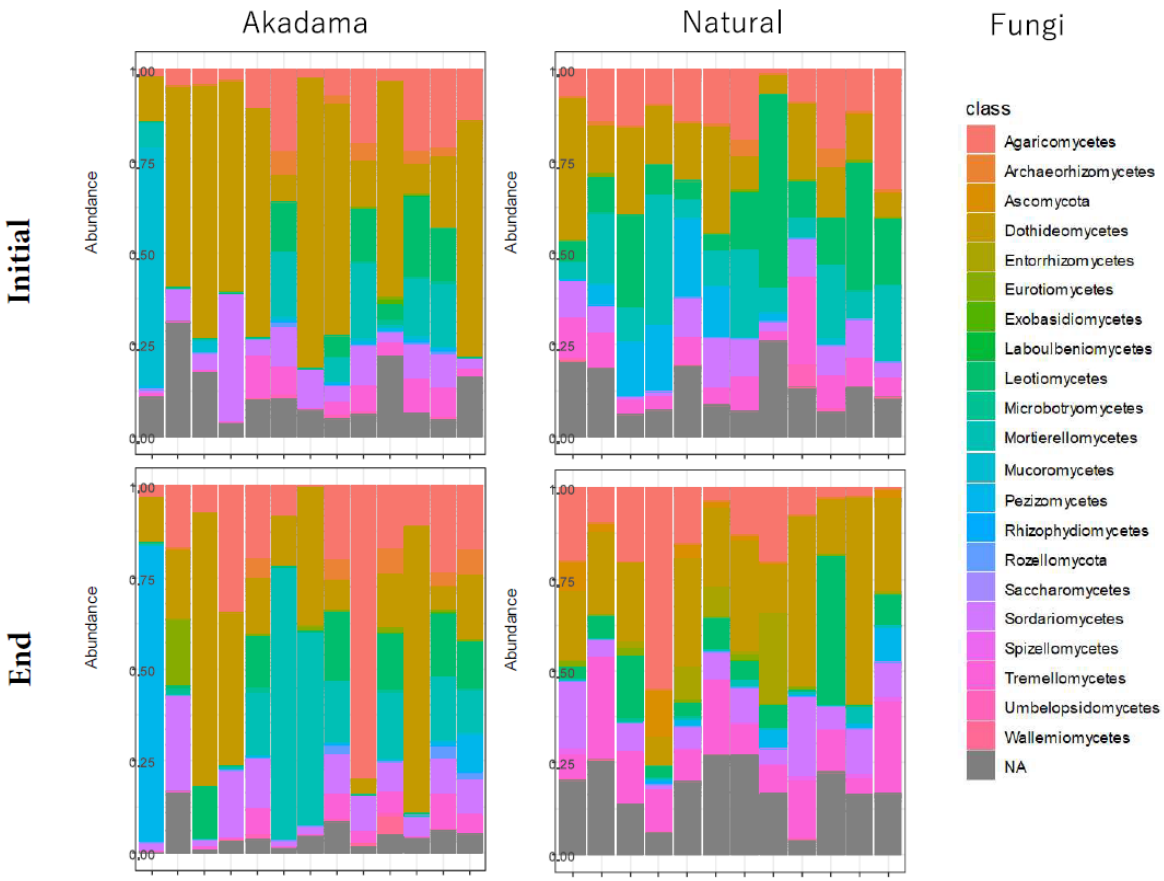

Figure 4. Soil fungal community composition and the relative abundance of each fungal class.

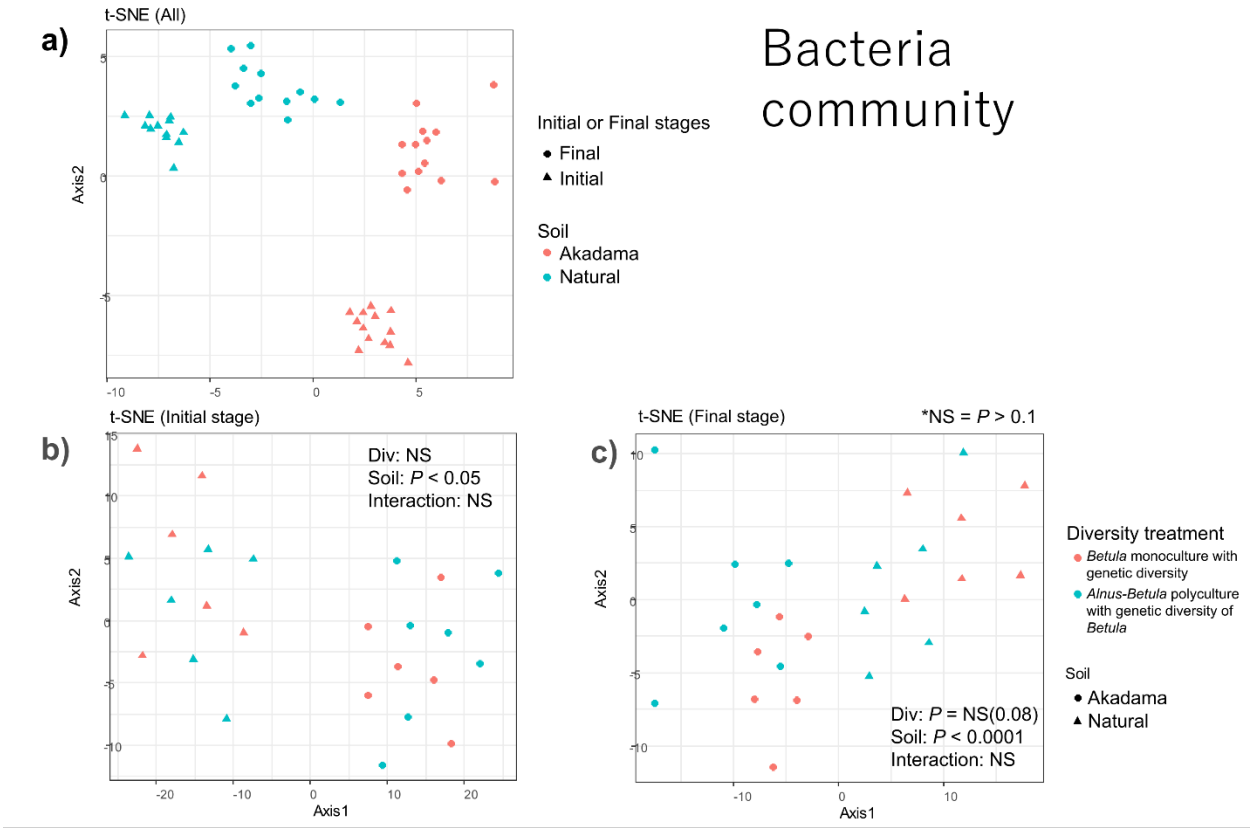

Figure 5. t-SNE analysis of soil bacteria community composition. (a) the bacteria community structure in all pots, as well as at the initial and final stages. (b) and (c) represent the bacteria community at the initial and final stages. The significance of the treatments was calculated using PERMANOVA (Table 3).

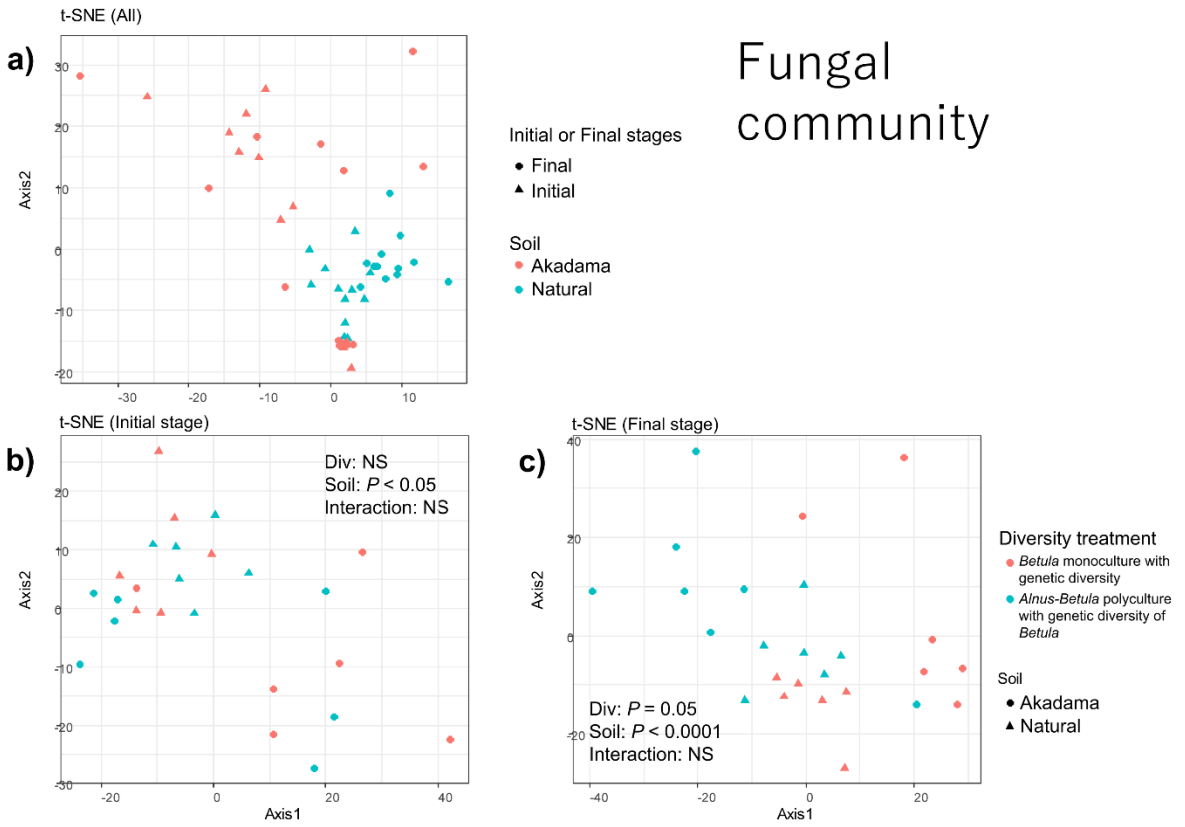

Figure 6. t-SNE analysis of soil fungal community composition. (a) the fungal community structure in all pots, as well as at the initial and final stages. (b) and (c) represent the fungal community at the initial and final stages. The significance of the treatments was calculated using PERMANOVA (Table 3).

Chapter 5. General discussion

General discussion

My research elucidates how various biotic and abiotic factors emerging after forest disturbances modified the pattern of plant-plant facilitation. In this chapter, I will first summarize the findings of each study, followed by a discussion of their implications for forest restoration projects.

In Chapter 2, I am dedicated to clearly illustrating in the post-landslide area, how the initial spatial distribution of seedlings emerges, and how those abiotic and biotic environmental conditions, i.e. neighboring seedlings' interactions and rill erosion, influence seedling performance. Based on a replicated artificial landslide experiment (i.e., ALES), in the first growing season after the disturbance, I monitored the seedlings' performance and recorded the rill erosion. This study indicated that, in the post-landslide area, newly recruited seedlings primarily exhibited spatial clustering with conspecific neighbors and demonstrated significantly higher abundance around rills. At the scale of several centimeters, proximity to conspecific and heterospecific neighbors significantly enhanced focal seedling survival and growth. The survival of seedlings near rills decreased, and this response varied by species. Interactive effects of plant facilitation and rill erosion on tree seedling colonization toward restoration have been validated. The proximity of a seedling to heterospecific neighbors attenuated the negative influences of being near rills. This study suggests that there were conspecific and heterospecific facilitative effects on seedling survival at this post-landslide habitat, but the relative importance of the two effects could be dependent on the degree of rill erosion. This study inspired the understanding that the effects of plant-plant facilitation, together with the fine-scale geomorphological heterogeneity, shape seedling performance, thereby influencing the forest restoration process.

In Chapter 3, I aimed to elucidate genetic properties of the newly recruited seedlings and their effects on seedling performance. In particular, the following questions were addressed: 1) are there population differentiations among spatially proximate disturbance sites after landslides, 2) how landslide scars and subsequent rill erosion shape the genetic structure of seedling populations, and 3) how genetic relatedness among seedlings influence their performance. By using the same ALES sites of Chapter 2, I

examined the genetic structure of the dominant seedlings, *Abies sachalinensis*, in each landslide site. This study determined the clear genetic differentiation among closely located sites, which was likely to be the dispersal limitation of the species *Abies* during early succession following disturbance. Interestingly, the growth-genetic distance relationships between the focal seedling and its spatially nearest neighbor may result from the combined effects of multiple processes. The spatial scales at which these processes operate differ, leading to the outcomes of the growth-genetic distance relationships that depend on the spatial distance. This study suggests that the restoration management of disturbed sites should consider the dispersal capacity of surrounding tree species and the genetic structure of source populations. Building upon natural succession, and supplementing it with strategies to control the genetic diversity of restored populations may provide valuable insights for forest restoration.

In Chapter 4, I explored how soil microbial communities and the genetic diversity of component species modify species diversity–ecosystem functioning relationships. In parallel, how this species diversity, in turn, shapes the composition of soil microorganisms (i.e., fungi and bacteria). I conducted a common garden experiment to control intraspecific genetic diversity by combining seedlings from different origins and to regulate soil microorganisms by inoculating natural soil collected from beneath maternal trees or commercial Akadama soil. Natural soil inoculation altered the composition of soil bacterial and fungal communities, and this effect was significant from the beginning to the end of our study. Both soil inoculation and the genetic diversity influenced the net effect of species diversity on functioning, while the processes involved were different. Natural soil inoculation significantly altered the net effect of species diversity by changing the selection effect, indicating soil microorganisms could modify the dominance of component species within the community. The genetic diversity levels influenced the net effect of species diversity by altering the complementarity effect, suggesting that the intraspecific facilitation enhanced the functioning of the community. This study suggests that in post-disturbance forest management, the inoculation of soil microbial communities from mature forests should be conducted with caution, as natural soil can enhance the selection effect within plant communities,

leading to a stronger dominance of certain species, which may hinder the maintenance of forest species diversity. This effect is stronger than intraspecific diversity effects on the relationship between species diversity and ecosystem functioning. Moreover, increasing the genetic diversity of tree species could be a constantly effective strategy toward restoration.

The insights gained from fine-scale structures towards forest restoration

The fine-scale spatial and genetic structure has been overlooked in restoration studies and programs. However, this thesis highlights the importance based on both a large-scale disturbance experiment in a natural forest and a well-manipulated common garden experiment. In this thesis, the two fine-scale structures—soil issues and neighbor's identity—provide insights into forest restoration.

Fine-scale soil issues including ongoing rill erosion following landslides in mountainous forests and soil microbial communities under natural forest canopies. Rill erosion disrupts the survival of newly recruited seedlings but may also concentrate water and nutrients around the rills (Chapter 2). Additionally, rill erosion drives the redistribution of seeds, shaping seedling abundance and genetic structure (Chapter 3). It is worth noting that seedlings' responses to rill erosion vary across species. Small-seeded seedlings are more susceptible to disturbance from rill erosion, while large-seeded seedlings can benefit from it. This indicates that rill erosion acts as an environmental filter in post-landslide areas, preventing specific seedlings from dominating newly established communities. Natural soil inoculation significantly altered the net effect of species diversity by changing the selection effect, indicating soil microorganisms could modify the dominance of component species within the community (Chapter 4). Although the facilitative role of soil microbes on plants has been studied extensively in forestry and agriculture, it may not always be compelling, particularly for seedling communities. Natural soil microbes exhibit complexity, with specialized pathogens potentially having negative effects on plant performance during the seedling stage.

Identities of neighboring seedlings at fine scales, which form the foundation of genetic and species diversity of population/community, largely influence seedling performance. Fine-scale genetic

structure is a short-term outcome of dispersal limitation, leading to genetically similar individuals being spatially closer to each other. For newly recruited seedlings, this proximity results in greater resource overlap, which negatively affects individual growth. However, this effect can be partially alleviated by various other spatially distance-dependent processes. (Chapter 3). Fine-scale species diversity creates opportunities for interspecific interactions, and facilitation between heterospecific seedlings has been demonstrated in this study to enhance the performance of neighboring species, for instance, by improving substrate stability (Chapter 2). Moreover, it was found that species diversity effects were modified by genetic diversity, with higher genetic diversity enhancing the net effects of species diversity on ecosystem functioning, leading to increased herbivory resistance and productivity in the community (Chapter 4). These findings suggest that integrating the manipulation of genetic diversity and species diversity may contribute to future forest restoration efforts. For plant communities newly established after disturbance, genetic and species diversity is related to the plasticity and adaptability (Boulding, 2008). During the restoration process, the adaptive potential of tree communities is expected to be positively correlated with their genetic and species diversity. Restoration efforts should aim to create appropriate conditions that facilitate the interaction and re-establishment of connections between species and genotypes. This will improve the success rate of restoration and promote associated biodiversity benefits.

Integration as future direction

Higher species diversity has been widely recognized for its promotion of ecosystem functioning (Cardinale et al., 2002; Isbell et al., 2011; Loreau, 2000). Meanwhile, the importance of genetic diversity, as well as its comparison with species diversity effects, has been less explored over the past two decades (Fourtune et al., 2016; Wehenkel et al., 2006). However, this study is the first to reveal the interactive effects of species and genetic diversity on ecosystem functioning. In the future, whether investigating naturally colonized vegetation or conducting well-manipulated planting practices, integrating genetic and species diversity will provide deeper insights into biodiversity-ecosystem functioning and forest

restoration processes. Furthermore, this study also provides ideas for plant-soil feedback. These feedbacks encompass both the physical aspect, where plant root systems stabilize soil structure and thereby enhance the performance of neighboring seedlings, and the ecological aspect, where species diversity shapes soil microbial communities, potentially influencing ecosystem functioning. Although this study did not detect the effect of plant genetic diversity on shaping soil microbial communities, many previous studies have demonstrated that plant genetic identity can influence soil microbes (Bolin and Lau, 2022; Kagiya and Utsumi, 2020; Schweitzer et al., 2011). Therefore, integrating species and genetic diversity while focusing plant-soil feedback processes would be highly beneficial for future restoration studies.

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Reference

Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., Meiners, J. M., Tredennick, A. T., Veblen, K. E. (2018). Competition and coexistence in plant communities: intraspecific competition is stronger than interspecific competition. *Ecology Letters*, 21, 1319-1329. doi:10.1111/ele.13098

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19, 716-723. doi:10.1109/TAC.1974.1100705

Ali, A. (2023). Biodiversity–ecosystem functioning research: brief history, major trends and perspectives. *Biological Conservation*, 285, 110210. doi:10.1016/j.biocon.2023.110210

Angers, D. A., Caron, J. (1998). Plant-induced changes in soil structure: processes and feedbacks. *Biogeochemistry*, 42, 55-72. doi:10.1023/A:1005944025343

Artursson, V., Finlay, R. D., Jansson, J. K. (2006). Interactions between arbuscular mycorrhizal fungi and bacteria and their potential for stimulating plant growth. *Environmental Microbiology*, 8, 1-10. doi:10.1111/j.1462-2920.2005.00942.x

Banks, S. C., Cary, G. J., Smith, A. L., Davies, I. D., Driscoll, D. A., Gill, A. M., Lindenmayer, D. B., Peakall, R. (2013). How does ecological disturbance influence genetic diversity? *Trends in Ecology & Evolution*, 28, 670-679. doi:10.1016/j.tree.2013.08.005

Bauld, J., Guy, M., Hughes, S., Forster, J., Watts, K. (2023). Assessing the use of natural colonization to create new forests within temperate agriculturally dominated landscapes. *Restoration Ecology*, 31, e14004. doi:10.1111/rec.14004

Ben-Said, M. (2021). Spatial point-pattern analysis as a powerful tool in identifying pattern-process relationships in plant ecology: an updated review. *Ecological Processes*, 10, 56. doi:10.1186/s13717-021-00314-4

Ben-Said, M., Linares, J. C., Carreira, J. A., Taïqui, L. (2022). Spatial patterns and species coexistence in mixed *Abies marocana-Cedrus atlantica* forest in Talassemtane National Park. *Forest Ecology and Management*, 506, 119967. doi:10.1016/j.foreco.2021.119967

Bennett, J. A., Maherali, H., Reinhart, K. O., Lekberg, Y., Hart, M. M., Klironomos, J. (2017). Plant-soil feedbacks and mycorrhizal type influence temperate forest population dynamics. *Science*, 35, 181-184. doi:10.1126/science.aai8212

Bertness, M. D., Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution*, 9, 191-193. doi:10.1016/0169-5347(94)90088-4

Beyns, R., Bauman, D., Drouet, T. (2021). Fine-scale tree spatial patterns are shaped by dispersal limitation which correlates with functional traits in a natural temperate forest. *Journal of Vegetation Science*, 32, e13070. doi:10.1111/jvs.13070

Bianchi, E., Bugmann, H., Hobi, M. L., Bigler, C. (2021). Spatial patterns of living and dead small trees in subalpine Norway spruce forest reserves in Switzerland. *Forest Ecology and Management*, 494, 119315. doi:10.1016/j.foreco.2021.119315

Blonska, E., Lasota, J., Piaszczyk, W., Wiechec, M., Klamerus-Iwan, A. (2018). The effect of landslide on soil organic carbon stock and biochemical properties of soil. *Journal of Soils and Sediments*, 18, 2727-2737. doi:10.1007/s11368-017-1775-4

Bolin, L. G., Lau, J. A. (2022). Linking genetic diversity and species diversity through plant–soil feedback. *Ecology*, 103, e3692. doi:10.1002/ecy.3692

Bonanomi, G., Incerti, G., Mazzoleni, S. (2011). Assessing occurrence, specificity, and mechanisms of plant facilitation in terrestrial ecosystems. *Plant Ecology*, 212, 1777-1790. doi:10.1007/s11258-011-9948-5

Boulding, E. G. (2008). Genetic diversity, adaptive potential, and population viability in changing environments. In: Carroll, S. P., Fox, C. W. (Eds.), *Conservation biology: evolution in action.* Oxford, United Kingdom: Oxford University Press, 199-219.

Bradbury, P. J., Zhang, Z., Kroon, D. E., Casstevens, T. M., Ramdoss, Y., Buckler, E. S. (2007). TASSEL: software for association mapping of complex traits in diverse samples. *Bioinformatics*, 23, 2633-2635. doi:10.1093/bioinformatics/btm308

Branco, S., Schauster, A., Liao, H. L., Ruytinx, J. (2022). Mechanisms of stress tolerance and their effects on the ecology and evolution of mycorrhizal fungi. *New Phytologist*, 235, 2158-2175. doi:10.1111/nph.18308

Brigham, L. M., N. Suding, K. (2024). Cross-scale facilitation: a framework for microclimate moderation of climate change. *Oikos*, 2024, e10241. doi:10.1111/oik.10241

Brockerhoff, E. G., Barbaro, L., Castagneyrol, B., Forrester, D. I., Gardiner, B., González-Olabarria, J. R., Lyver, P. O. B., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I. D., van der Plas, F., Jactel, H. (2017). Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation*, 26, 3005-3035. doi:10.1007/s10531-017-1453-2

Brokaw, N. V. L. (1987). Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology*, 75, 9-19. doi:10.2307/2260533

Brundrett, M., Murase, G., Kendrick, B. (1990). Comparative anayomy of roots and mycorrhizae of common Ontario trees. *Canadian Journal of Botany-Revue Canadienne De Botanique*, 68, 551-578. doi:10.1139/b90-076

Bustamante-Sánchez, M. A., Armesto, J. J., Halpern, C. B. (2011). Biotic and abiotic controls on tree colonization in three early successional communities of Chiloe Island, Chile. *Journal of Ecology*, 99, 288-299. doi:10.1111/j.1365-2745.2010.01737.x

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., Holmes, S. P. (2016). DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, 13, 581-583. doi:10.1038/nmeth.3869

Cannon, J. B., Peterson, C. J., O'Brien, J. J., Brewer, J. S. (2017). A review and classification of interactions between forest disturbance from wind and fire. *Forest Ecology and Management*, 406, 381-390. doi:10.1016/j.foreco.2017.07.035

Caporaso, J. G., Lauber, C. L., Walters, W. A., Berg-Lyons, D., Lozupone, C. A., Turnbaugh, P. J., Fierer, N., Knight, R. (2011). Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. *Proceedings of the National Academy of Sciences*, 108, 4516-4522. doi:10.1073/pnas.1000080107

Caravaca, F., Garcia, C., Hernández, M. T., Roldán, A. (2002). Aggregate stability changes after organic amendment and mycorrhizal inoculation in the afforestation of a semiarid site with *Pinus halepensis*. *Applied Soil Ecology*, 19, 199-208. doi:10.1016/S0929-1393(01)00189-5

Cardinale, B. J., Palmer, M. A., Collins, S. L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 415, 426-429. doi:10.1038/415426a

Carroll, O., MacDougall, A. S. (2024). Facilitation against herbivory more important than resource-based niche differences for plant coexistence in a field experiment. *Journal of Ecology*, 112, 1200-1209. doi:10.1111/1365-2745.14283

Castillo-Bautista, M. P., Rugeles-Silva, P. A., Armbrecht, I. (2024). Inoculation with rhizospheric microorganisms in tropical dry forests restoration increased microbial diversity but had no effect on seedling growth. *Restoration Ecology*, 32, e14111. doi:10.1111/rec.14111

Chen, Y. C., Wu, C. F., Lin, S. H. (2014). Mechanisms of forest restoration in landslide treatment areas. *Sustainability*, 6, 6766-6780. doi:10.3390/su6106766.

Connell, J. H., Slatyer, R. O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, 111, 1119-1144. doi:10.1086/283241

Craine, J. M., Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and light. *Functional Ecology*, 27, 833-840. doi:10.1111/1365-2435.12081

Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., Hanson, P. J., Irland, L. C., Lugo, A. E., Peterson, C. J., Simberloff, D., Swanson, F. J., Stocks, B. J., Wotton, B. M.

(2001). Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience*, 51, 723-734. doi:10.1641/0006-3568(2001)051[0723:CCAFD]2.0.CO;2

Dalling, J. W. (2008). Pioneer Species. In: Fath, B. (Ed.), *Encyclopedia of Ecology (Second Edition)*. Oxford, United Kingdom: Elsevier, 181-184.

Daniels, R. F. (1978). Spatial patterns and distance distributions in young seeded loblolly pine stands. *Forest Science*, 24, 260-266. doi:10.1093/forestscience/24.2.260

Di Sacco, A., Hardwick, K. A., Blakesley, D., Brancalion, P. H. S., Breman, E., Cecilio Rebola, L., Chomba, S., Dixon, K., Elliott, S., Ruyonga, G., Shaw, K., Smith, P., Smith, R. J., Antonelli, A. (2021). Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Global Change Biology*, 27, 1328-1348. doi:10.1111/gcb.15498

Dietrich, W., McKean, J., Bellugi, D., Perron, T. (2008). The prediction of shallow landslide location and size using a multidimensional landslide analysis in a digital terrain model. In: Chen, C. L., Major, J.J. (Eds.), *Proceedings of the Fourth International Conference on Debris-Flow Hazards Mitigation: Mechanics, Prediction, and Assessment (DFHM-4)*. Amsterdam, Netherlands: IOS press, 12.

Eaton, D. A. R., Overcast, I. (2020). ipyrad: interactive assembly and analysis of RADseq datasets. *Bioinformatics*, 36, 2592-2594. doi:10.1093/bioinformatics/btz966

Ehlers, B. K., Damgaard, C. F., Laroche, F. (2016). Intraspecific genetic variation and species coexistence in plant communities. *Biology Letter*, 12, 20150853. doi:10.1098/rsbl.2015.0853

Espigares, T., Moreno-de las Heras, M., Nicolau, J. M. (2011). Performance of vegetation in reclaimed slopes affected by soil erosion. *Restoration Ecology*, 19, 35-44. doi:10.1111/j.1526-100X.2009.00546.x

Fajardo, A., McIntire, E. J. B. (2011). Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology*, 99, 642-650. doi:10.1111/j.1365-2745.2010.01771.x

FAO 2000 On definitions of forest and forest change. FRA working paper 33. Rome: Food and Agriculture Organization of the UN.

Fargeot, L., Poesy, C., Lefort, M., Prunier, J. G., Krick, M., Verdonck, R., Veyssière, C., Richard, M., Legrand, D., Loot, G., Blanchet, S. (2024). Genetic diversity affects ecosystem functions across trophic levels as much as species diversity, but in an opposite direction. bioRxiv, 2024-03. doi:10.7554/elife.100041.1

Fernández, J. L. F., Rubin, L., Hartmann, P., Puhlmann, H., von Wilpert, K. (2019). Initial recovery of soil structure of a compacted forest soil can be enhanced by technical treatments and planting. *Forest Ecology and Management*, 431, 54-62. doi:10.1016/j.foreco.2018.04.045

Fernandez-Conradi, P., Jactel, H., Hampe, A., Leiva, M. J., Castagneyrol, B. (2017). The effect of tree genetic diversity on insect herbivory varies with insect abundance. *Ecosphere*, 8, e01637. doi:10.1002/ecs2.1637

File, A. L., Murphy, G. P., Dudley, S. A. (2011). Fitness consequences of plants growing with siblings: reconciling kin selection, niche partitioning and competitive ability. *Proceedings of the Royal Society B: Biological Sciences*, 279, 209-218. doi:10.1098/rspb.2011.1995

Figueiredo, A. F., Boy, J., Guggenberger, G. (2021). Common mycorrhizae network: a review of the theories and mechanisms behind underground interactions. *Frontiers in Fungal Biology*, 2, 735299. doi:10.3389/ffunb.2021.735299

Forero, L. E., Kulmatiski, A., Grenzer, J., Norton, J. M. (2021). Plant-soil feedbacks help explain biodiversity-productivity relationships. *Communications Biology*, 4, 789. doi:10.1038/s42003-021-02329-1

Fourtune, L., Paz-Vinas, I., Loot, G., Prunier, J. G., Blanchet, S. (2016). Lessons from the fish: a multi-species analysis reveals common processes underlying similar species-genetic diversity correlations. *Freshwater Biology*, 61, 1830-1845. doi: 10.1111/fwb.12826

Freund, C. A., Silman, M. R. (2023). Developing a more complete understanding of tropical montane forest disturbance ecology through landslide research. *Frontiers in Forests and Global Change*, 6, 1091387. doi:10.3389/ffgc.2023.1091387

Furusawa, J., Makoto, K., Utsumi, S. (2023). A large-scale field experiment of artificially caused landslides with replications revealed the response of the ground-dwelling beetle community to landslides. *Ecology and Evolution*, 13, e9939. doi:10.1002/ece3.9939

Garwood, N. C., Janos, D. P., Brokaw, N. (1979). Earthquake-caused landslides: a major disturbance to tropical forests. *Science*, 205, 997-999. doi:10.1126/science.205.4410.997

Geertsema, M., Pojar, J. J. (2007). Influence of landslides on biophysical diversity - a perspective from British Columbia. *Geomorphology*, 89, 55-69. doi:10.1016/j.geomorph.2006.07.019

Getzin, S., Wiegand, T., Wiegand, K., He, F. L. (2008). Heterogeneity influences spatial patterns and demographics in forest stands. *Journal of Ecology*, 96, 807-820. doi:10.1111/j.1365-2745.2008.01377.x

Gilland, K. E., McCarthy, B. C. (2014). Microtopography influences early successional plant communities on experimental coal surface mine land reclamation. *Restoration Ecology*, 22, 232-239. doi:10.1111/rec.12066

Gkoutselis, G., Rohrbach, S., Harjes, J., Brachmann, A., Horn, M. A., Rambold, G. (2024). Plastiphily is linked to generic virulence traits of important human pathogenic fungi. *Communications Earth & Environment*, 5, 51. doi:10.1038/s43247-023-01127-3

Gorzelak, M. A., Asay, A. K., Pickles, B. J., Simard, S. W. (2015). Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. *AoB Plants*, 7, plv050. doi:10.1093/aobpla/plv050

Guo, Y., Schöb, C., Ma, W., Mohammat, A., Liu, H., Yu, S., Jiang, Y., Schmid, B., Tang, Z. (2019). Increasing water availability and facilitation weaken biodiversity–biomass relationships in shrublands. *Ecology*, 100, e02624. doi:10.1002/ecy.2624

Gupta, P., Salava, H., Sreelakshmi, Y., Sharma, R. (2020). A low-cost high-throughput method for plant genomic DNA isolation. In: Vaschetto, L. M. (Ed.), *Cereal Genomics: Methods and Protocols*. New York, NY: Humana Press, 1-7.

Hao, M., Messier, C., Geng, Y., Zhang, C., Zhao, X., von Gadow, K. (2020). Functional traits influence biomass and productivity through multiple mechanisms in a temperate secondary forest. *European Journal of Forest Research*, 139, 959-968. doi:10.1007/s10342-020-01298-0

Harper, J. L. (1977). *Population Biology of Plants*. London, United Kindom: Academic Press.

Hizume, M., Yamasaki, Y., Kan, M. (2016). Fluorescent chromosome banding patterns in six species of *Abies*, Pinaceae. *CYTOLOGIA*, 81, 61-67. doi:10.1508/cytologia.81.61

Hoban, S., Campbell, C. D., da Silva, J. M., Ekblom, R., Funk, W. C., Garner, B. A., Godoy, J. A., Kershaw, F., MacDonald, A. J., Mergeay, J., Minter, M., O'Brien, D., Vinas, I. P., Pearson, S. K., Pérez-Espona, S., Potter, K. M., Russo, I.-R. M., Segelbacher, G., Vernesi, C., Hunter, M. E. (2021). Genetic diversity is considered important but interpreted narrowly in country reports to the Convention on Biological Diversity: current actions and indicators are insufficient. *Biological Conservation*, 261, 109233. doi:10.1016/j.biocon.2021.109233

Hotta, W., Morimoto, J., Yanai, S., Uchida, Y., Nakamura, F. (2024). Environmental heterogeneity on landslide slopes affects the long-term recoveries of forest ecosystem components. *Catena*, 234, 107578. doi:10.1016/j.catena.2023.107578

Hu, S., Jiao, J. Y., García-Fayos, P., Kou, M., Chen, Y. X., Wang, W. Z. (2018). Telling a different story: plant recolonization after landslides under a semi-arid climate. *Plant and Soil*, 426, 163-178. doi:10.1007/s11104-018-3612-y

Hu, S., Jiao, J. Y., Li, Y. J., Deng, N., Wu, D. Y., Zhang, Y. F. (2020). Seedling and ramet recruitment at the community level on recent landslide scars on the hilly and gullied Loess Plateau, China. *Land Degradation & Development*, 31, 168-180. doi:10.1002/ldr.3437

Husain Jaafry, S. W., Li, D., Ouyang, Y., Liu, L., Li, L., Yang, T., Wei, X., Zhu, Y., Sun, Y., Ren, Z., Kong, R. (2020). Interactions among individuals of *Setaria Italica* at different levels of genetic relatedness under different nutrient and planting density conditions. *Acta Oecologica*, 105, 103549. doi:10.1016/j.actao.2020.103549

Ihrmark, K., Bödeker, I. T. M., Cruz-Martinez, K., Friberg, H., Kubartova, A., Schenck, J., Strid, Y., Stenlid, J., Brandström-Durling, M., Clemmensen, K. E., Lindahl, B. D. (2012). New primers to amplify the fungal ITS2 region – evaluation by 454-sequencing of artificial and natural communities. *FEMS Microbiology Ecology*, 82, 666-677. doi:10.1111/j.1574-6941.2012.01437.x

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W. S., Reich, P. B., Scherer-Lorenzen, M., Schmid, B., Tilman, D., Van Ruijven, J. (2011). High plant diversity is needed to maintain ecosystem services. *Nature*, 477, 199-202. doi:10.1038/nature10282

Islam, W., Saqib, H. S. A., Adnan, M., Wang, Z., Tayyab, M., Huang, Z., Chen, H. Y. H. (2022). Differential response of soil microbial and animal communities along the chronosequence of *Cunninghamia lanceolata* at different soil depth levels in subtropical forest ecosystem. *Journal of Advanced Research*, 38, 41-54. doi:10.1016/j.jare.2021.08.005

Ito, Y., Yamazaki, S., Kurahashi, T. (2021). Geological features of landslides caused by the 2018 Hokkaido Eastern Iburi Earthquake in Japan. doi:10.1144/SP501-2019-122

Jiang, L., Pu, Z., Nemergut, D. R. (2008). On the importance of the negative selection effect for the relationship between biodiversity and ecosystem functioning. *Oikos*, 117, 488-493. doi:10.1111/j.0030-1299.2008.16401.x

Jiang, L., Wan, S., Li, L. (2009). Species diversity and productivity: why do results of diversity-manipulation experiments differ from natural patterns? *Journal of Ecology*, 97, 603-608. doi:10.1111/j.1365-2745.2009.01503.x

Jombart, T., Devillard, S., Balloux, F. (2010). Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics*, 11, 1-15. doi:10.1186/1471-2156-11-94

Jones, C. G., Lawton, J. H., Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373-386. doi:10.2307/3545850

Kagiya, S., Utsumi, S. (2020). Spatial heterogeneity in genetic diversity and composition of bacterial symbionts in a single host species population. *Plant and Soil*, 452, 513-527. doi:10.1007/s11104-020-04583-4

Kéfi, S., Holmgren, M., Scheffer, M. (2016). When can positive interactions cause alternative stable states in ecosystems? *Functional Ecology*, 30, 88-97. doi:10.1111/1365-2435.12601

Kempel, A., Brandl, R., Schädler, M. (2009). Symbiotic soil microorganisms as players in aboveground plant–herbivore interactions – the role of rhizobia. *Oikos*, 118, 634-640. doi:10.1111/j.1600-0706.2009.17418.x

Köhl, M., Lasco, R., Cifuentes, M., Jonsson, Ö., Korhonen, K. T., Mundhenk, P., de Jesus Navar, J., Stinson, G. (2015). Changes in forest production, biomass and carbon: results from the 2015 UN FAO Global Forest Resource Assessment. *Forest Ecology and Management*, 352, 21-34. doi:10.1016/j.foreco.2015.05.036

Kunz, M., Fichtner, A., Härdtle, W., Raumonen, P., Bruelheide, H., von Oheimb, G. (2019). Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. *Ecology Letters*, 22, 2130-2140. doi:10.1111/ele.13400

Lara-Romero, C., de la Cruz, M., Escribano-Avila, G., García-Fernández, A., Iriondo, J. M. (2016). What causes conspecific plant aggregation? Disentangling the role of dispersal, habitat heterogeneity and plant-plant interactions. *Oikos*, 125, 1304-1313. doi:10.1111/oik.03099

Larsen, M. C., Torres-Sánchez, A. J., Concepción, I. M. (1999). Slopewash, surface runoff and fine-litter transport in forest and landslide scars in humid-tropical steeplands, Luquillo Experimental Forest, Puerto Rico. *Earth Surface Processes and Landforms*, 24, 481-502. doi:10.1002/(SICI)1096-9837(199906)24:6<481::AID-ESP967>3.0.CO;2-G

Lavahun, M. F. E., Joergensen, R. G., Meyer, B. (1996). Activity and biomass of soil microorganisms at different depths. *Biology and Fertility of Soils*, 23, 38-42. doi:10.1007/BF00335816

Lehouck, V., Spanhove, T., Colson, L., Adringa-Davis, A., Cordeiro, N. J., Lens, L. (2009). Habitat disturbance reduces seed dispersal of a forest interior tree in a fragmented African cloud forest. *Oikos*, 118, 1023-1034. doi:10.1111/j.1600-0706.2009.17300.x

Li, L., Huang, Z. L., Ye, W. H., Cao, H. L., Wei, S. G., Wang, Z. G., Lian, J. Y., Sun, I. F., Ma, K. P., He, F. L. (2009). Spatial distributions of tree species in a subtropical forest of China. *Oikos*, 118, 495-502. doi:10.1111/j.1600-0706.2009.16753.x

Lian, C., Goto, S., Kubo, T., Takahashi, Y., Nakagawa, M., Hogetsu, T. (2008). Nuclear and chloroplast microsatellite analysis of Abies sachalinensis regeneration on fallen logs in a subboreal forest in Hokkaido, Japan. *Molecular Ecology*, 17, 2948-2962. doi:10.1111/j.1365-294X.2008.03802.x

Liang, M. X., Shi, L. Q., Burslem, D., Johnson, D., Fang, M., Zhang, X. Y., Yu, S. X. (2021). Soil fungal networks moderate density-dependent survival and growth of seedlings. *New Phytologist*, 230, 2061-2071. doi:10.1111/nph.17237

Lin, Y. C., Chang, L. W., Yang, K. C., Wang, H. H., Sun, I. F. (2011). Point patterns of tree distribution determined by habitat heterogeneity and dispersal limitation. *Oecologia*, 165, 175-184. doi:10.1007/s00442-010-1718-x

Lincoln, D. E., Mooney, H. A. (1984). Herbivory on *Diplacus aurantiacus* shrubs in sun and shade. *Oecologia*, 64, 173-176. doi:10.1007/BF00376867

Lind, B. M., Menon, M., Bolte, C. E., Faske, T. M., Eckert, A. J. (2018). The genomics of local adaptation in trees: are we out of the woods yet? *Tree Genetics & Genomes*, 14, 29. doi:10.1007/s11295-017-1224-y

Litrico, I., Ronfort, J., Verlaque, R., Thompson, J. D. (2005). Spatial structure of genetic variation and primary succession in the pioneer tree species *Antirhea borbonica* on La Réunion. *Molecular Ecology*, 14, 1575-1584. doi:10.1111/j.1365-294X.2005.02502.x

Liu, Q., Jian, W., Nie, W. (2021). Rainstorm-induced landslides early warning system in mountainous cities based on groundwater level change fast prediction. *Sustainable Cities and Society*, 69, 102817. doi:10.1016/j.scs.2021.102817

Lladó, S., López-Mondéjar, R., Baldrian, P. (2017). Forest soil bacteria: diversity, involvement in ecosystem processes, and response to global change. *Microbiology and Molecular Biology Reviews*, 81, 10-1128. doi:10.1128/mmbr.00063-16

Lobo, N. (2014). Conifer seed predation by terrestrial small mammals: a review of the patterns, implications, and limitations of top-down and bottom-up interactions. *Forest Ecology and Management*, 328, 45-54. doi:10.1016/j.foreco.2014.05.019

Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91, 3-17. doi:10.1034/j.1600-0706.2000.910101.x

Loreau, M., Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72-76. doi:10.1038/35083573

Luo, S., De Deyn, G. B., Jiang, B., Yu, S. (2017). Soil biota suppress positive plant diversity effects on productivity at high but not low soil fertility. *Journal of Ecology*, 105, 1766-1774. doi:10.1111/1365-2745.12773

Major, E. I., Höhn, M., Avanzi, C., Fady, B., Heer, K., Opgenoorth, L., Piotti, A., Popescu, F., Postolache, D., Vendramin, G. G., Csilléry, K. (2021). Fine-scale spatial genetic structure across the species range reflects recent colonization of high elevation habitats in silver fir (*Abies alba* Mill.). *Molecular Ecology*, 30, 5247-5265. doi:10.1111/mec.16107

Makoto, K., Utsumi, S., Zeng, R., Mamiya, W., Miyazaki, T., Okuyama, T., Tanaka, F., Yamada, T., Yoshida, T. (2024). Which native legume or non-legume nitrogen-fixing tree is more efficient in restoring post-landslide forests along an environmental gradient? *Forest Ecology and Management*, 554, 121672. doi:10.1016/j.foreco.2023.121672

Masaki, T., Nakashizuka, T., Niiyama, K., Tanaka, H., Iida, S., Bullock, J. M., Naoe, S. (2019). Impact of the spatial uncertainty of seed dispersal on tree colonization dynamics in a temperate forest. *Oikos*, 128, 1816-1828. doi:10.1111/oik.06236

Materechera, S. A., Dexter, A. R., Alston, A. M. (1992). Formation of aggregates by plant-roots in homogenized soils. *Plant and Soil*, 142, 69-79. doi:10.1007/BF00010176

Mazal, L., Corenblit, D., Barsoum, N., Steiger, J., Skot, L., Fumanal, B., Till-Bottraud, I. (2021). Fine-scale spatial genetic structure and intra-specific interactions of *Populus nigra* within a natural river corridor along the lower Allier River (France). *Flora*, 275, 151763. doi:10.1016/j.flora.2021.151763

Mejstřík, M., Svátek, M., Pollastrini, M., Šrámek, M., Matula, R. (2024). Differential roles of seed and sprout regeneration in forest diversity and productivity after disturbance. *Forest Ecosystems*, 11, 100198. doi:10.1016/j.fecs.2024.100198

Metz, M. R., Wright, S. J., Zimmerman, J. K., Hernandéz, A., Smith, S. M., Swenson, N. G., Umaña, M. N., Valencia, L. R., Waring-Enriquez, I., Wordell, M., Zambrano, M., Garwood, N. C. (2023). Functional traits of young seedlings predict trade-offs in seedling performance in three neotropical forests. *Journal of Ecology*, 111, 2568-2582. doi:10.1111/1365-2745.14195

Montesinos, D. (2015). Plant-plant interactions: from competition to facilitation. *Web Ecology*, 15, 1-2. doi:10.5194/we-15-1-2015

Morin, X., Fahse, L., Scherer-Lorenzen, M., Bugmann, H. (2011). Tree species richness promotes productivity in temperate forests through strong complementarity between species. *Ecology Letters*, 14, 1211-1219. doi:10.1111/j.1461-0248.2011.01691.x

Murali, A., Bhargava, A., Wright, E.S. (2018). IDTAXA: a novel approach for accurate taxonomic classification of microbiome sequences. *Microbiome*, 6, 140. doi:10.1186/s40168-018-0521-5

Naeem, S., Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390, 507-509. doi:10.1038/37348

Nakagawa, M., Kurahashi, A., Hogetsu, T. (2003). The regeneration characteristics of Picea jezoensis and Abies sachalinensis on cut stumps in the sub-boreal forests of Hokkaido Tokyo University Forest. *Forest Ecology and Management*, 180, 353-359. doi:10.1016/S0378-1127(02)00654-0

Nazareno, A. G., Knowles, L. L., Dick, C. W., Lohmann, L. G. (2021). By animal, water, or wind: can dispersal mode predict genetic connectivity in riverine plant species? *Front Plant Sci*, 12, 626405. doi:10.3389/fpls.2021.626405

Obase, K., Yamanaka, S., Yamanaka, T., Ozaki, K. (2022). Short-term effects of retention forestry on the diversity of root-associated ectomycorrhizal fungi in Sakhalin fir plantations, Hokkaido, Japan. *Forest Ecology and Management*, 523, 120501. doi:10.1016/j.foreco.2022.120501

Ohwaki, A., Ishikawa, T., Morita, S., Okatsu, Y., Nakano, Y., Sakio, H. (2023). The effects of heterogeneity created by treefall, landslide, and stream on ground beetle assemblages in a primary beech forest. *Forest Ecology and Management*, 547, 121394. doi:10.1016/j.foreco.2023.121394.

Ou, X., Hu, Y., Li, X., Guo, S., Liu, B. (2021). Advancements and challenges in rill formation, morphology, measurement and modeling. *CATENA*, 196, 104932. doi:10.1016/j.catena.2020.104932

Ozturk, U., Bozzolan, E., Holcombe, E. A., Shukla, R., Pianosi, F., Wagener, T. (2022). How climate change and unplanned urban sprawl bring more landslides. *Nature*, 608, 262-265.

Pacheco Quevedo, R., Velastegui-Montoya, A., Montalván-Burbano, N., Morante-Carballo, F., Korup, O., Daleles Rennó, C. (2023). Land use and land cover as a conditioning factor in landslide susceptibility: a literature review. *Landslides*, 20, 967-982. doi:10.1007/s10346-022-02020-4

Pan, Y., Birdsey, R. A., Phillips, O. L., Houghton, R. A., Fang, J., Kauppi, P. E., Keith, H., Kurz, W. A., Ito, A., Lewis, S. L., Nabuurs, G.-J., Shvidenko, A., Hashimoto, S., Lerink, B., Schepaschenko, D., Castanho, A., Murdiyarso, D. (2024). The enduring world forest carbon sink. *Nature*, 631, 563-569. doi:10.1038/s41586-024-07602-x

Pang, C. C., Ma, X. K. K., Lo, J. P. L., Hung, T. T. H., Hau, B. C. H. (2018). Vegetation succession on landslides in Hong Kong: Plant regeneration, survivorship and constraints to restoration. *Global Ecology and Conservation*, 15, e00428. doi:10.1016/j.gecco.2018.e00428

Patiño, J., Werner, O., González-Mancebo, J. M. (2010). The impact of forest disturbance on the genetic diversity and population structure of a late-successional moss. *Journal of Bryology*, 32, 220-231. doi:10.1179/037366810X12735734836133

Peakall, R., Smouse, P. E. (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics*, 28, 2537-2539. doi:10.1093/bioinformatics/bts460

Pedersen, N. K., Schmidt, I. K., Kepfer-Rojas, S. (2023). Drivers of tree colonization, species richness, and structural variation during the initial three decades of natural forest colonization in abandoned agricultural soils. *Forest Ecology and Management*, 543, 121138. doi:10.1016/j.foreco.2023.121138

Poirier, V., Roumet, C., Munson, A. D. (2018). The root of the matter: linking root traits and soil organic matter stabilization processes. *Soil Biology & Biochemistry*, 120, 246-259. doi:10.1016/j.soilbio.2018.02.016

Policelli, N., Bruns, T. D., Vilgalys, R., Nuñez, M. A. (2019). Suilloid fungi as global drivers of pine invasions. *New Phytologist*, 222, 714-725. doi:10.1111/nph.15660

Quevedo, R. P., Velastegui-Montoya, A., Montalván-Burbano, N., Morante-Carballo, F., Korup, O., Rennó, C. D. (2023). Land use and land cover as a conditioning factor in landslide susceptibility: a literature review. *Landslides*, 20, 967-982. doi:10.1007/s10346-022-02020-4

Rashid, M. I., Mujawar, L. H., Shahzad, T., Almeelbi, T., Ismail, I. M. I., Oves, M. (2016). Bacteria and fungi can contribute to nutrients bioavailability and aggregate formation in degraded soils. *Microbiological Research*, 183, 26-41. doi:10.1016/j.micres.2015.11.007

Raynaud, T., Pivato, B., Siol, M., Spor, A., Blouin, M. (2021). Soil microbes drive the effect of plant species and genotypic diversity interaction on productivity. *Plant and Soil*, 467, 165-180. doi:10.1007/s11104-021-05071-z

Reid, J. L., Holl, K. D., Zahawi, R. A. (2015). Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications*, 25, 1072-1082. doi:10.1890/14-1399.1

Reiss, E. R., Drinkwater, L. E. (2018). Cultivar mixtures: a meta-analysis of the effect of intraspecific diversity on crop yield. *Ecological Applications*, 28, 62-77. doi:10.1002/eap.1629

Ren, X., Huang, C., Zhu, Z., Wang, L., Wang, N., Mu, X., Luo, D., Zhang, J., Xiang, L., Huang, X. (2024). Anthropogenic forest degradation and its impact on soil erosion in the mountainous region of northern China. *CATENA*, 243, 108217. doi:10.1016/j.catena.2024.108217

Restrepo, C., Walker, L. R., Shiels, A. B., Bussmann, R., Claessens, L., Fisch, S., Lozano, P., Negi, G., Paolini, L., Poveda, G., Ramos-Scharrón, C., Richter, M., Velázquez, E. (2009). Landsliding and its multiscale influence on mountainscapes. *Bioscience*, 59, 685-698. doi:10.1525/bio.2009.59.8.10

Sala, O. E., Vivanco, L., Flombaum, P. (2017). Grassland Communities and Ecosystems. In: Roitberg, B. D. (Ed), *Reference Module in Life Sciences*. Oxford, United Kingdom: Elsevier, 1-9.

Sánchez, J., Curt, M. D., Robert, N., Fernández, J. (2019). Biomass resources. In: Lago, C., Caldés, N, Lechón, Y. (Eds.), *The Role of Bioenergy in the Bioeconomy*. London, United Kindom: Academic Press, 25-111.

Sandhu, H. S., Shi, P., Yang, Q. (2013). Intraspecific spatial niche differentiation: evidence from *Phyllostachys edulis*. *Acta Ecologica Sinica*, 33, 287-292. doi:10.1016/j.chnaes.2013.07.009

Sato, Y., Wuest, S. E. (2024). The genetics of plant–plant interactions and their cascading effects on agroecosystems—from model plants to applications. *Plant and Cell Physiology,* pcae092. doi:10.1093/pcp/pcae092

Scheidl, C., Heiser, M., Kamper, S., Thaler, T., Klebinder, K., Nagl, F., Lechner, V., Markart, G., Rammer, W., Seidl, R. (2020). The influence of climate change and canopy disturbances on landslide susceptibility in headwater catchments. *Science of The Total Environment*, 742, 140588. doi:10.1016/j.scitotenv.2020.140588

Schuster, R. L., Highland, L. M. (2003). *Impact of landslides and innovative landslide-mitigation measures on the natural environment.* Paper presented at the International conference on slope engineering, Hong Kong, China.

Schöb, C., Armas, C., Guler, M., Prieto, I., Pugnaire, F. I. (2013). Variability in functional traits mediates plant interactions along stress gradients. *Journal of Ecology*, 101, 753-762. doi:10.1111/1365-2745.12062

Schweitzer, J. A., Fischer, D. G., Rehill, B. J., Wooley, S. C., Woolbright, S. A., Lindroth, R. L., Whitham, T. G., Zak, D. R., Hart, S. C. (2011). Forest gene diversity is correlated with the composition and function of soil microbial communities. *Population Ecology*, 53, 35-46. doi:10.1007/s10144-010-0252-3

Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M. J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T. A., Reyer, C. P. O. (2017). Forest disturbances under climate change. *Nature Climate Change*, 7, 395-402. doi:10.1038/nclimate3303

Soliveres, S., Maestre, F. T. (2014). Plant-plant interactions, environmental gradients and plant diversity: a global synthesis of community-level studies. *Perspectives in Plant Ecology Evolution and Systematics*, 16, 154-163. doi:10.1016/j.ppees.2014.04.001

Stoll, P., Weiner, J. (2000). A neighborhood view of interactions among individual plants. In: Dieckmann, U., Law, R., Metz, J. A. J. (Eds.), *The Geometry of Ecological Interactions: Simplifying Spatial Complexity*. Cambridge, United Kingdom: Cambridge University Press, 11-27.

Suárez, D., Arribas, P., Jiménez-García, E., Emerson, B. C. (2022). Dispersal ability and its consequences for population genetic differentiation and diversification. *Proceedings of the Royal Society B: Biological Sciences*, 289, 20220489. doi:10.1098/rspb.2022.0489

Subrahmaniam, H. J., Roby, D., Roux, F. (2021). Toward unifying evolutionary ecology and genomics to understand positive plant–plant interactions within wild species. *Frontiers in Plant Science*, 12, 683373. doi:10.3389/fpls.2021.683373

Sukumar Chakraborty, S. C., Luck, J., Hollaway, G., Freeman, A., Norton, R., Garrett, K., Percy, K., Hopkins, A., Davis, C., Karnosky, D. (2008). Impacts of global change on diseases of agricultural crops and forest trees. *CABI Reviews*, 1–15. doi:10.1079/pavsnnr20083054

Suyama, Y., Matsuki, Y. (2015). MIG-seq: an effective PCR-based method for genome-wide single-nucleotide polymorphism genotyping using the next-generation sequencing platform. *Scientific Reports*, 5, 16963. doi:10.1038/srep16963

Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., Lindenmayer, D. B., Swanson, F. J. (2011). The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, 9, 117-125. doi:10.1890/090157

Tabata, H. (1966). A Contribution to the Biology of Japanese Birches. *Memoirs of the College of Science, University of Kyoto. Series B*, 32, 239-271.

Takaoka, S. (2019). Regional variations in vegetation patterns on landslides in the snowy mountains of central Japan. *Mountain Research and Development*, 39, R33-R41. doi:10.1659/MRD-JOURNAL-D-19-00028.1

Tanaka, H. (1995). Seed demography of three co-occurring Acer species in a Japanese temperate deciduous forest. *Journal of Vegetation Science*, 6, 887-896. doi:10.2307/3236403

Tang, B. Z., Jiao, J. Y., Chen, Y. X., Liang, Y. (2024). Rill investigation on landslide scar highlights the shortcomings of current knowledge on erosion of shallow landslides. *Land Degradation & Development*, 35, 1495-1510. doi:10.1002/ldr.5001

Thijs, K. W., Aerts, R., Musila, W., Siljander, M., Matthysen, E., Lens, L., Pellikka, P., Gulinck, H., Muys, B. (2014). Potential tree species extinction, colonization and recruitment in Afromontane forest relicts. *Basic and Applied Ecology*, 15, 288-296. doi:10.1016/j.baae.2014.05.004

Thom, D., Rammer, W., Seidl, R. (2017). The impact of future forest dynamics on climate: interactive effects of changing vegetation and disturbance regimes. *Ecological Monographs*, 87, 665-684. doi:10.1002/ecm.1272

Tilman, D. (2001). An evolutionary approach to ecosystem functioning. *Proceedings of the National Academy of Sciences, 98*, 10979-10980. doi:10.1073/pnas.211430798

Tobner, C. M., Paquette, A., Gravel, D., Reich, P. B., Williams, L. J., Messier, C. (2016). Functional identity is the main driver of diversity effects in young tree communities. *Ecology Letters*, 19, 638-647. doi:10.1111/ele.12600

Tomiolo, S., Thomas, C., Jespersen, M. K., Damgaard, C. F., Ehlers, B. K. (2021). Intraspecific interactions in the annual legume *Medicago minima* are shaped by both genetic variation for competitive ability and reduced competition among kin. *Basic and Applied Ecology*, 53, 49-61. doi:10.1016/j.baae.2021.03.003

Tooker, J. F., Frank, S. D. (2012). Genotypically diverse cultivar mixtures for insect pest management and increased crop yields. *Journal of Applied Ecology*, 49, 974-985. doi:10.1111/j.1365-2664.2012.02173.x

Trivedi, P., Singh, B. P., Singh, B. K. (2018). Soil carbon: introduction, importance, status, threat, and mitigation. In: Singh, B. K. (Ed.), *Soil Carbon Storage*. London, United Kindom: Academic Press, 1-28.

Trogisch, S., Liu, X., Rutten, G., Xue, K., Bauhus, J., Brose, U., Bu, W., Cesarz, S., Chesters, D., Connolly, J., Cui, X., Eisenhauer, N., Guo, L., Haider, S., Härdtle, W., Kunz, M., Liu, L., Ma, Z., Neumann, S., Sang, W., Schuldt, A., Tang, Z., van Dam, N. M., von Oheimb, G., Wang, M.-Q., Wang, S., Weinhold, A., Wirth, C., Wubet, T., Xu, X., Yang, B., Zhang, N., Zhu, C.-D., Ma, K., Wang, Y., Bruelheide, H. (2021). The significance of tree-tree interactions for forest ecosystem functioning. *Basic and Applied Ecology*, 55, 33-52. doi:10.1016/j.baae.2021.02.003

Utsumi, S., Ando, Y., Roininen, H., Takahashi, J., Ohgushi, T. (2013). Herbivore community promotes trait evolution in a leaf beetle via induced plant response. *Ecology Letters*, 16, 362-370. doi:10.1111/ele.12051

van der Plas, F., Manning, P., Allan, E., Scherer-Lorenzen, M., Verheyen, K., Wirth, C., Zavala, M. A., Hector, A., Ampoorter, E., Baeten, L., Barbaro, L., Bauhus, J., Benavides, R., Benneter, A., Berthold, F., Bonal, D., Bouriaud, O., Bruelheide, H., Bussotti, F., Carnol, M., Castagneyrol, B., Charbonnier, Y., Coomes, D., Coppi, A., Bastias, C. C., Muhie Dawud, S., De Wandeler, H., Domisch, T., Finér, L., Gessler, A., Granier, A., Grossiord, C., Guyot, V., Hättenschwiler, S., Jactel, H., Jaroszewicz, B., Joly, F.-X., Jucker, T., Koricheva, J., Milligan, H., Müller, S., Muys, B., Nguyen, D., Pollastrini, M., Raulund-Rasmussen, K., Selvi, F., Stenlid, J., Valladares, F., Vesterdal, L., Zielínski, D., Fischer, M. (2016). Jack-of-all-trades effects drive biodiversity–ecosystem multifunctionality relationships in European forests. *Nature Communications*, 7, 11109. doi:10.1038/ncomms11109

van Schrojenstein Lantman, I. M., Hertzog, L. R., Vandegehuchte, M. L., Martel, A., Verheyen, K., Lens, L., Bonte, D. (2018). Leaf herbivory is more impacted by forest composition than by tree diversity or edge effects. *Basic and Applied Ecology*, 29, 79-88. doi:10.1016/j.baae.2018.03.006

van Westen, C. J., Rengers, N., Soeters, R. (2003). Use of Geomorphological Information in Indirect Landslide Susceptibility Assessment. *Natural Hazards*, 30, 399-419. doi:10.1023/B:NHAZ.0000007097.42735.9e

Vandepitte, K., Gristina, A. S., De Hert, K., Meekers, T., Roldan-Ruiz, I., Honnay, O. (2012). Recolonization after habitat restoration leads to decreased genetic variation in populations of a terrestrial orchid. *Molecular Ecology*, 21, 4206-4215. doi:10.1111/j.1365-294X.2012.05698.x

Vander Wall, S. B., Kuhn, K. M., Beck, M. J. (2005). Seed Removal, seed predation, and secondary dispersal. *Ecology*, 86, 801-806. doi:10.1890/04-0847

Velázquez, E., De la Cruz, M., Gómez-Sal, A. (2014). Changes in spatial point patterns of pioneer woody plants across a large tropical landslide. *Acta Oecologica-International Journal of Ecology*, 61, 9-18. doi:10.1016/j.actao.2014.09.001

Velázquez, E., Gómez-Sal, A. (2008). Landslide early succession in a neotropical dry forest. *Plant Ecology*, 199, 295-308. doi:10.1007/s11258-008-9433-y

Wahab, A., Muhammad, M., Munir, A., Abdi, G., Zaman, W., Ayaz, A., Khizar, C., Reddy, S. P. (2023). Role of arbuscular mycorrhizal fungi in regulating growth, enhancing productivity, and potentially influencing ecosystems under abiotic and biotic stresses. *Plants*, 12, 3102. doi:10.3390/plants12173102

Walker, L. R., Shiels, A. B. (2008). Post-disturbance erosion impacts carbon fluxes and plant succession on recent tropical landslides. *Plant and Soil*, 313, 205-216. doi:10.1007/s11104-008-9692-3

Walker, L. R., Shiels, A. B. (2012). *Landslide Ecology*. Cambridge, United Kingdom: Cambridge University Press.

Walker, L. R., Shiels, A. B., Bellingham, P. J., Sparrow, A. D., Fetcher, N., Landau, F. H., Lodge, D. J. (2013). Changes in abiotic influences on seed plants and ferns during 18 years of primary succession on Puerto Rican landslides. *Journal of Ecology*, 101, 650-661. doi:10.1111/1365-2745.12071

Wan, N.-F., Fu, L., Dainese, M., Hu, Y.-Q., Pødenphant Kiær, L., Isbell, F., Scherber, C. (2022). Plant genetic diversity affects multiple trophic levels and trophic interactions. *Nature Communications*, 13, 7312. doi:10.1038/s41467-022-35087-7

Wang, D., Qiao, J., Zhang, Y., Wu, T., Li, J., Wang, D., Zhao, X., Shen, H., Zou, J. (2022). Effects of erosion micro-topographies on plant colonization on weathered gangue dumps in northeast China. *Sustainability*, 14, 8468. doi:10.3390/su14148468

Wang, N., Jiao, J. Y., Lei, D., Chen, Y., Wang, D. L. (2014). Effect of rainfall erosion: seedling damage and establishment problems. *Land Degradation & Development*, 25, 565-572. doi:10.1002/ldr.2183

Watanabe, T., Fukuzawa, K., Shibata, H. (2016). Short-term response of Sasa dwarf bamboo to a change of soil nitrogen fertility in a forest ecosystem in northern Hokkaido, Japan. *Plants*, 5, 19. doi:10.3390/plants5020019

Wehenkel, C., Bergmann, F., Gregorius, H.-R. (2006). Is there a trade-off between species diversity and genetic diversity in forest tree communities? *Plant Ecology*, 185, 151-161. doi:10.1007/s11258-005-9091-2

Yamanaka, T., Taniguchi, T., Ogawa, Y., Imaya, A., Kaneko, S., Daimaru, H. (2022). Distribution of *Frankia* and ectomycorrhizal fungi in a denuded volcanic soil exposed by a landslide during heavy rainfall caused by typhoon No. 26 (Wipha) in 2013. *Journal of Forest Research*, 27, 133-139. doi:10.1080/13416979.2022.2026558

Yang, J. H., Chang, L. W., Hsu, K. C., Fan, C. C., Doley, D., Song, G. Z. M. (2023). The nurse-plant effect under the dislodgement stress of landslides. *Iforest-Biogeosciences and Forestry*, 16, 78-85. 10.3832/ifor4017-015

Yoshida, M., Tamai, Y., Miyamoto, T., Yajima, T. (2011). The study on mycorrhizal status of current-year *acer mono* seedlings. *Eurasian Journal of Forest Research*, 14, 39-41.

Zarin, D. J., Johnson, A. H. (1995). Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. *Soil Science Society of America Journal*, 59, 1444-1452. doi:10.2136/sssaj1995.03615995005900050034x

Zélé, F., Magalhães, S., Kéfi, S., Duncan, A. B. (2018). Ecology and evolution of facilitation among symbionts. *Nature Communications*, 9, 4869. doi:10.1038/s41467-018-06779-w

Zeng, R. Q., Makoto, K. (2023). Is the fine root tensile strength predictable from structural and morphological traits across mycorrhizal types in cool-temperate woody species? *Forests*, 14, 11. doi:10.3390/f14081542

Zhang, H. Y., Lü, X. T., Knapp, A. K., Hartmann, H., Bai, E., Wang, X. B., Wang, Z. W., Wang, X. G., Yu, Q., Han, X. G. (2018). Facilitation by leguminous shrubs increases along a precipitation gradient. *Functional Ecology*, 32, 203-213. doi:10.1111/1365-2435.12941

Zhang, Z. H., Hu, G., Zhu, J. D., Ni, J. (2013). Aggregated spatial distributions of species in a subtropical karst forest, southwestern China. *Journal of Plant Ecology*, 6, 131-140. doi:10.1093/jpe/rts027

Zheng, F., Gao, X. (2003). Research progresses in hillslope soil erosion processes. *Scientia Geographica Sinica*, 23, 230-235. doi:10.13249/j.cnki.sgs.2003.02.230

Zong, G. (2018). Spatial pattrens and interspecific spatial associations of tree seedlings in a secondary forest in montane region of Eastern Liaoning Province, China. [Master's dissertation, Shengyang Agricultural University].

Zou, C. B., Barnes, P. W., Archer, S., McMurtry, C. R. (2005). Soil moisture redistribution as a mechanism of facilitation in savanna tree–shrub clusters. *Oecologia*, 145, 32-40. doi:10.1007/s00442-005-0110-8

Zou, L., Xie, Z., Li, Q., Zhao, C., Li, C. (2007). Spatial and temporal pattern of seed rain of *Abies fargesii* in Shennongjia Nature Reserve, Hubei. *Biodiversity Science*, 15, 500-509. doi:10.1360/biodiv.060234