

## ANCIENT ROCK-AVALANCHES AS MICROREFUGIA FOR RELICT CONIFERS: A GEOECOLOGICAL STUDY IN THE AKAISHI MOUNTAINS, CENTRAL JAPAN

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With 5 figures and 5 tables

Received 08 March 2026 · Accepted 21 September 2026

**Summary:** Large-scale landslides are fundamental drivers of landscape dynamics that generate distinct abiotic legacies; however, few studies have explicitly linked geomorphological history to long-term ecological processes. This study investigates the geoeological role of a rock-avalanche deposit formed approximately 1100 years ago in the Akaishi Mountains (central Japan). It aims to elucidate how such geomorphic legacies contribute to the persistence of forests dominated by relict conifers. Detailed field surveys revealed a clear differentiation of site conditions within the landslide deposit, distinguishing with-matrix (WM) from no-matrix (NM) boulder slopes. At WM sites, fine-grained material infilling inter-boulder voids has promoted soil development over the past millennium, thereby supporting a closed-canopy mixed forest structurally comparable to the zonal vegetation on adjacent undisturbed slopes. In contrast, NM sites lack fine sediment. These severe edaphic conditions act as a spatial filter, limiting the establishment of competitively dominant broad-leaved species and thereby maintaining an edaphic climax community. NM sites harbor a distinctive assemblage of stress-tolerant relict taxa belonging to lineages that originated in the Tertiary (e.g., *Chamaecyparis pisifera*), as well as disturbance-dependent species with glacial histories. The latter group includes the glacial relict *Picea alcoquiana* and the cold-adapted pioneer *Larix kaempferi*, whose contemporary distributions are largely confined to unstable substrates. Our findings demonstrate that the ancient rock avalanche creates competitor-reduced rocky habitats that replicate the historical niches of these diverse lineages. Furthermore, given the region's ongoing tectonic activity, we propose that spatially dispersed landslide scars form a dynamic habitat network. This network likely facilitates the regional persistence of relict populations through metapopulation dynamics. We conclude that ancient landslide scars are not merely sites of destruction but are critical geoeological structures that enhance landscape heterogeneity and contribute to the conservation of regional floristic diversity.

**Keywords:** Geobotany, geodiversity, geomorphic legacy, landslide, microrefugia, relict species

### 1 Introduction

Landslides are a dominant geomorphological process in mountainous regions and are among the most pronounced disturbance factors affecting mountain vegetation. Landslides create vegetation of different successional stages as well as various habitats, thereby promoting the development of diverse vegetation (GEERTSEMA & POJAR 2007, ALEXANDROWICZ & MARGIELEWSKI 2010, WALKER & SHIELS 2012). Numerous studies have investigated vegetation succession on landslide sites, particularly focusing on recovery processes. The time required for vegetation to return to a pre-landslide state is estimated to range from decades to centuries, depending on factors such as slope stability, biological legacies, and surrounding vegetation (WALKER & SHIELS 2012). Although empirical studies examining the immediate aftermath of landslides are essential, many investigations based on field observations or monitoring data are limited to timescales of only several years to a decade. The use of historical aerial

photographs has substantially extended the temporal scope of landslide research, allowing analyses over multidecadal periods. Nevertheless, even these valuable studies generally cover less than 100 years (GUARIGUATA 1990, FRANCESCATO et al. 2001, LOPES et al. 2020, CHEN et al. 2022, HOTTA et al. 2024). Considering that the recovery of species composition following major disturbances often requires centuries in tropical (GUARIGUATA & OSTERTAG 2001, CHAZDON 2003), temperate (NAKASHIZUKA 1987), and boreal forests (ANYOMI et al. 2022), extending the research to longer-term successional processes is necessary to fully understand the role of landslides in generating vegetation diversity.

Another critical reason to adopt a long-term perspective is that landslides do more than reset vegetation succession to early stages; they also generate abiotic legacies, including depressions, ponds, wetlands, rocky slopes, and scarps, which persist locally and influence vegetation establishment over extended periods. These abiotic disturbance legacies, shaped by landform and soil properties, can leave long-lasting



imprints on the landscape for millennia (HEWITT et al. 2008). Such sites have functioned as microrefugia during past climatic fluctuations, and landslide-affected areas can serve as habitats for rare or relict species (ALEXANDROWICZ & MARGIELEWSKI 2010). In East Asia, for instance, forests dominated by relict species, commonly referred to as relict forests, are concentrated on specific landforms, including scree, steep slopes, cliffs, and rocky terrain (TANG et al. 2018), many of which are products of landslides. Indeed, the presence of Tertiary relict species on landslide sites has been frequently documented in this region (TANG & OHSAWA 2002, TANG et al. 2015, HE et al. 2015, SHANG et al. 2020).

To understand the role of landslide sites as microrefugia, it is necessary not only to study early successional processes but also to elucidate the long-term history of vegetation development within these habitats. Paleoecological approaches are particularly effective for evaluating the historical influence of landslides on vegetation over timescales spanning centuries to millennia and beyond. Analyses of pollen, plant macrofossils, and testate amoebae have demonstrated that landslides create diverse landforms that provide refugia for plants during Holocene climatic fluctuations (ŠÍMOVÁ et al. 2019).

However, few empirical studies have clarified which specific physical environments within landslide sites function as refugia, based on the relationship between landforms and present-day vegetation. To address this gap, vegetation studies should consider the evolutionary history of landforms, as exemplified by TAKAOKA and KARIYA (2020), who examined the relationship between current vegetation and microlandforms formed by a landslide approximately 350 years ago. By elucidating vegetation development in areas where the origin and age of landforms are well established, researchers can better understand the spatial patterns and historical context of current vegetation, including relict and rare species. This knowledge enhances our understanding of vegetation history associated with climate change since the Last Glacial Maximum (LGM) and informs biodiversity conservation strategies grounded in geodiversity (GRAY 2013).

The present study aims to elucidate how landslide sites function as refugia by examining the relationships between landforms and the mechanisms that maintain the forests established on them. We focus on an old, large-scale landslide site for which the history of landform evolution has been well documented (KARIYA 2012, KIMURA et al. 2018, YAMADA et al. 2018). Specifically, we investigate forests char-

acterized by *Chamaecyparis pisifera* and *Thuja standishii*. These taxa represent relict lineages of Cupressaceae with Tertiary origins; while their ancestors were once widespread across the Northern Hemisphere, they endured Quaternary climatic extremes and subsequent competitive exclusion, now persisting in restricted, fragmented habitats such as edaphically harsh rocky landforms. We also examine species with distinct glacial histories, which originated in high-latitude forests of the Paleogene–Neogene Northern Hemisphere: *Picea alcoquiana*, a glacial relict with a narrow and fragmented distribution, and *Larix kaempferi*, a cold-adapted pioneer. During post-glacial warming, the ranges of both species shifted to higher altitudes; however, while *P. alcoquiana* is now more restricted to specialized niches as a relict, *L. kaempferi* maintains its presence by colonizing disturbed habitats such as volcanoes and landslides. By examining these key taxa – each representing unique evolutionary and migratory responses to past climate changes – we aim to clarify the relationship between landslide landforms and forest composition and structure.

## 2 Study area

The study area is located in the Komu River basin in the northern Akaishi Mountains, reaching a maximum elevation of 2780 m (Fig. 1). The western part of the basin is underlain by Middle Miocene granodiorite, whereas the eastern part is dominated by Late Miocene mudstone, alternating mudstone and sandstone beds, and Late Miocene basalt-andesite pyroclastic rocks and lavas. Rock-avalanche deposits fill the valley of the Dondokosawa River, a tributary of the Komu River (KARIYA 2012) (Fig. 1c). These deposits originated from the eastern slope of Mount Jizogatake (35°42'43.39" N, 138°17'55.69" E) and are estimated to have formed around AD 887, based on dendrochronological analysis of the oxygen isotopic composition ( $^{18}\text{O}/^{16}\text{O}$ ) of cellulose from buried wood (YAMADA et al. 2018).

Within the depositional area, microlandforms such as scarps, ridges, lobes, and flat surfaces are present (KIMURA et al. 2018). The deposits consist of granitic boulders ranging in diameter from several meters to over 10 m. Interstitial spaces are filled with fine-grained material in some locations but lack a matrix in others (Fig. 1d). Despite these variations, all sites are currently forested, and matrix-free slopes support mature conifer-dominated forests, including *Chamaecyparis pisifera* (Fig. 2a).

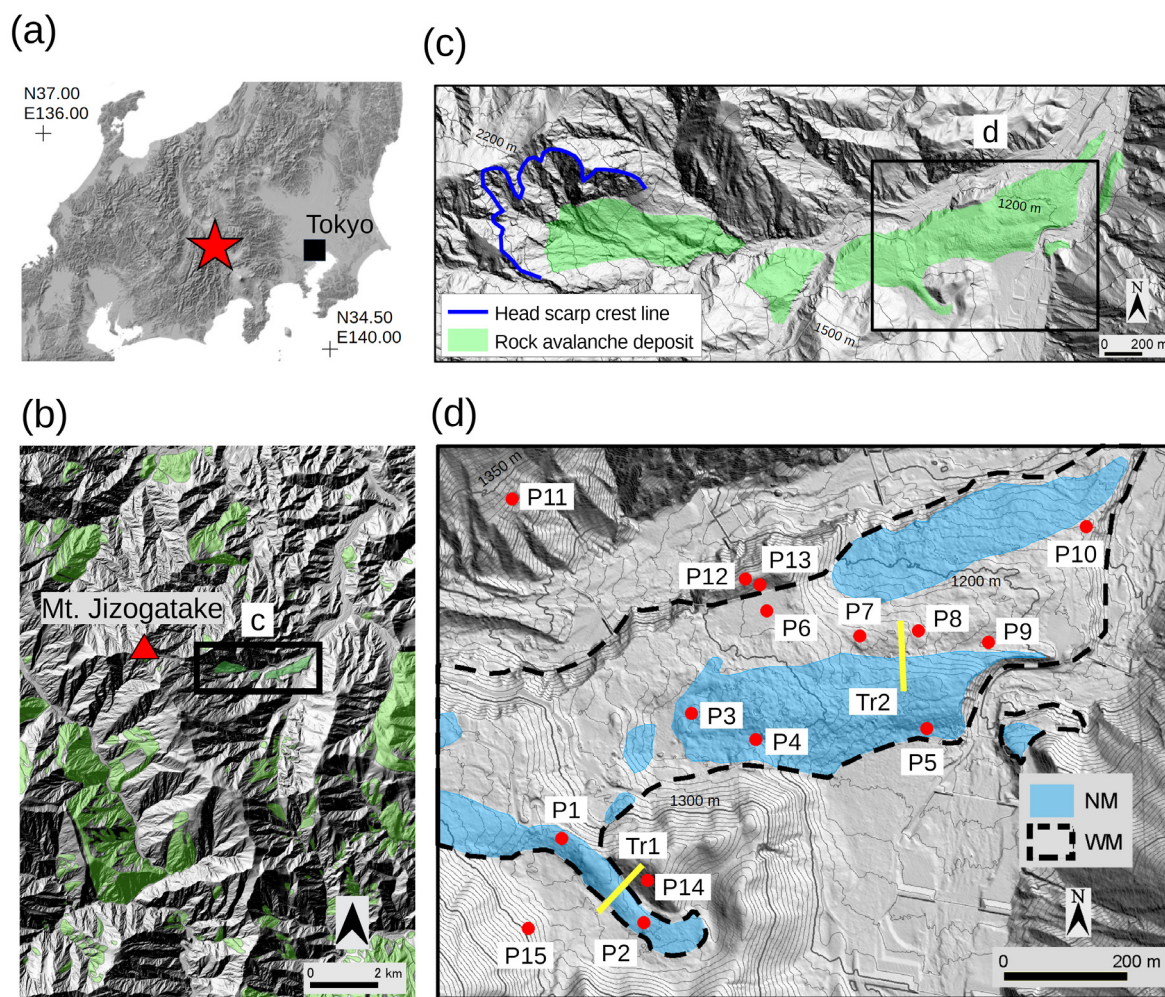


Fig. 1: Study area. Shaded relief maps for panels (a) and (b) are based on the digital elevation model provided by the Geospatial Information Authority of Japan, while those for panels (c) and (d) are based on the digital elevation model from the Fujikawa River Basin SABO Office, Ministry of Land, Infrastructure, Transport and Tourism. The mass-movement domain (landslide bodies, collapse deposits, and deep-seated gravitational slope deformation areas) shown in panel (b) is derived from the landslide map published by the National Research Institute for Earth Science and Disaster Resilience. The distribution of rock-avalanche deposits shown in panels (c) and (d) was created with reference to Kariya (2012). In panel (d), P1–P15 indicate the vegetation survey sites, and Tr1 and Tr2 indicate the transect baselines. NM denotes a matrix-free boulder slope, whereas WM denotes a matrix-supported slope.

Based on vegetation maps at a 1:25,000 scale (BIODIVERSITY CENTER OF JAPAN 2010) and field observations, the natural forests within the basin are distributed as follows. Up to an elevation of approximately 1700 m, deciduous broad-leaved forests are dominated by *Fagus crenata* and *Quercus crispula* var. *crispula*; also present are mixed forests containing these broad-leaved trees and conifers, such as *Abies homolepis* and *Tsuga sieboldii*. Above 1700 m, subalpine forests composed of *Abies veitchii*, *Abies mariesii*, *Tsuga diversifolia*, and *Betula ermanii* occur. Elevations above 2600 m exhibit an alpine landscape dominated by *Pinus pumila* scrub.

According to climatological normals (1991–2020) from the nearest meteorological station in Nirasaki (341 m a.s.l.), the mean annual precipitation is 1212.9 mm, and mean temperatures for the warmest month (August) and the coldest month (January) are 25.5°C and 2.0°C, respectively. Using a temperature lapse rate of 0.6°C per 100 m, temperatures at the median elevation of the investigated forest are estimated at 19.4°C in August and −4.1°C in January. Except at high elevations, snow accumulation is not abundant around Mount Jizogatake. Snow is generally low. Snow cover estimates derived from Landsat-7 satellite data acquired between March and



Fig. 2: Stand structure and root micro-environment on the matrix-free boulder slope (NM site). (a) General view of the *Chamaecyparis pisifera*-dominated forest established on the boulder deposit. (b) Root system directly wrapping around exposed, matrix-free boulders, illustrating the absence of fine-earth soil matrix and the presence of large void spaces beneath the root collar.

August (2009–2011) indicate that snow was present in some areas above approximately 1500 m in March, whereas snow from April onward was confined to elevations above approximately 2000 m (SUGITA 2013).

### 3 Methods

The study focused on forests at elevations of 1150–1350 m within the rock-avalanche depositional area. To elucidate the relationships among microtopography, substrate conditions, and tree distribution, we conducted topographic surveys along representative transects crossing the rock-avalanche deposits. Cross-sectional topography was measured using a tape measure and a clinometer. Along these transects, the positions of canopy-forming species taller than 2 m were recorded and projected onto profile diagrams to visualize the stand structure relative to microlandforms.

Fifteen plots, ranging from 0.5 to 0.75 ha, were established as study sites on slopes covered with rock-avalanche deposits (hereafter RA) and on adjacent stable slopes unaffected by the rock-avalanche (hereafter NRA) (Fig. 1d). Within these plots, diameter at breast height (DBH) and tree height were measured for all woody species taller than 1.5 m.

Plots 1–5 were located on slopes where accumulated boulders lacked fine-grained interstitial material (no-matrix type; hereafter NM). Among these, Plots 1 and 2 were situated on a narrow ridge, Plot 3 on a broad ridge, Plot 4 in a shallow depression, and Plot 5 at the base of the slope. Plots 6–10 are characterized by boulders largely embedded in a matrix of silt, sand, and gravel (with-matrix type; hereafter WM). Specifically, Plot 6 was located on a flat surface, Plots 7, 8 and 10 on broad ridge slopes, and Plot 9 at the bottom of a valley without constant flow. Finally, Plots 11–15 were situated on NRA slopes. Plot 11 was located on the mid-slope of the left bank of the Dondokosawa River. Plot 12 was situated on a narrow ridge, Plot 13 on the adjacent upper slope, Plot 14 on the mid-slope of another ridge, and Plot 15 on a lower slope.

Species composition was analyzed using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarities calculated from Hellinger-transformed tree basal area. Differences in community composition between site types were evaluated using pairwise permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. Homogeneity of multivariate dispersion was assessed using permutational analysis of multivariate dispersions (PERMDISP). Indicator species analysis (IndVal) was performed to identify species significantly associated with each vegetation type. All statistical analyses were performed in R version 4.5.2 (R Core Team 2025) using the *vegan* package (OKSANEN et al. 2026) and the *indicspecies* package (DE CÁCERES & LEGENDRE 2009). To evaluate local regeneration dynamics specific to the matrix-free boulder environment, two 5 m × 5 m quadrats per plot were established in NM plots (except Plot 2) to count woody plants shorter than 1.5 m. A cross-site quantitative comparison of understory vegetation was not conducted because heavy browsing pressure by sika deer (*Cervus nippon*) at the WM and NRA sites had resulted in a near-total absence of woody species (except transient current-year seedlings), making quantitative quadrat surveys uninformative at those two sites.

Soil profiles were described using test pits excavated in selected plots: 6, 8, and 9 from the WM areas, and 13 and 14 from the NRA areas. For each soil

horizon, soil color, texture, consistency (field rupture resistance in a moist state), and rock fragment content were recorded according to the guidelines of JAHN et al. (2006). Soil consistency was qualitatively evaluated in the field by manually applying force to moist soil aggregates following the FAO criteria.

Soil profiles could not be excavated in NM plots because these sites consist of open-work, matrix-free boulder deposits devoid of fine-grained earth matrix. The complete absence of matrix fine sediment physically precluded standard soil profile descriptions, bulk density measurements, or void space quantification (Fig. 2b).

## 4 Results

### 4.1 Species composition of forest stands

In Plots 1–5 within the matrix-free NM area, conifers such as *Chamaecyparis pisifera*, *Tsuga sieboldii*, and *Abies homolepis* exhibited high RBA, whereas the RBA of deciduous broad-leaved trees was low (ranging from 3.7% to 16.1% for broad-leaved species; Tab. 1). The pioneer species *Betula grossa* accounted for most of the broad-leaved component. Regarding conifers, *C. pisifera* showed high dominance in Plots 3–5 but was scarcely present in Plots 1 and 2, which were situated on narrow ridges. In addition, *Larix kaempferi* (Plots 3 and 4), *Picea alcoquiana* (Plots 1 and 2), and *Thuja standishii* (Plot 2) appeared as solitary individuals, although their abundance was low.

In Plots 6–8 and 10 within the matrix-supported WM area, *Abies homolepis* was dominant, yet a diverse range of deciduous broad-leaved trees was also present. Deciduous broad-leaved species characteristic of the montane zone, such as *Quercus crispula* var. *crispula*, *Fagus crenata*, *Castanea crenata*, and *Acer* spp., accounted for a substantial proportion of the basal area (total deciduous broad-leaved RBA ranged from 24.9% to 89.5%). In Plot 9, located on the valley floor, *Pterocarya rhoifolia* exhibited the highest RBA, followed by *Cercidiphyllum japonicum*. Across Plots 6–10, the RBA of *Chamaecyparis pisifera* was low (0.0%–4.7%), and *Larix kaempferi*, *Picea alcoquiana*, and *Thuja standishii* were absent.

In Plots 11–15 within the NRA reference area, evergreen conifers, including *Tsuga sieboldii* and *Abies homolepis*, exhibited high RBA values. In particular, in Plot 12, which was located on a narrow ridge, the RBA of *T. sieboldii* reached 81.6%. At the same time, these plots supported a diverse assemblage of broad-leaved trees, including *Quercus crispula* var. *crispula*,

*Fagus crenata*, *Castanea crenata*, and *Acer* spp. The RBA of deciduous broad-leaved trees ranged from 9.3% in Plot 12 to 74.7% in Plot 13. *Chamaecyparis pisifera*, *Larix kaempferi*, *Picea alcoquiana*, and *Thuja standishii* were absent.

Broad-leaved trees were classified into three groups: Group A, primarily present in the NM plots; Group B, mainly in the WM and NRA plots; and Group C, occurring across all plots (NM, WM, and NRA). Of the 20 species in Group B, 16 were shared between the WM and NRA plots.

The NMDS ordination showed differences in species composition among the three site types (Fig. 3). NM sites formed a distinct cluster, whereas WM sites largely overlapped with NRA sites. Pairwise PERMANOVA supported these patterns (Tab. 2). Species composition differed significantly between NM and NRA sites ( $Pseudo-F = 5.768$ ,  $R^2 = 0.419$ ,  $p = 0.008$ ) and between NM and WM sites ( $Pseudo-F = 5.539$ ,  $R^2 = 0.409$ ,  $p = 0.010$ ), whereas no significant difference was detected between WM and NRA sites ( $Pseudo-F = 1.499$ ,  $R^2 = 0.158$ ,  $p = 0.158$ ). Multivariate dispersion did not differ significantly among vegetation types (PERMDISP,  $p = 0.609$ ). Indicator species analysis identified three indicator species for NM sites (*Betula grossa*, *Fraxinus lanuginosa*, and *Chamaecyparis pisifera*) and one for NRA sites (*Fagus crenata*). No indicator species were identified for WM sites.

### 4.2 Vertical structure of forest stands

Cumulative height-stratum distributions differed markedly among coniferous species and between NM and WM plots (Tab. 3). In NM plots, *Abies homolepis* and *Tsuga sieboldii* showed broad vertical distributions, with individuals occurring from the lower strata ( $\leq H_{25}$ ) to the upper canopy ( $\leq H_{95}$ ). In contrast, *Larix kaempferi* was rare ( $n = 2$ ) and did not occur in any of the defined height strata, indicating its restriction to the uppermost canopy. Species such as *Picea alcoquiana* and *Thuja standishii* were absent from the lower strata and occurred mainly in the middle to upper strata, although total numbers were small.

In WM plots, *Abies homolepis*, *Tsuga sieboldii*, and *Chamaecyparis pisifera* were more frequently observed in the lower and middle strata than in NM plots. In contrast, *Larix kaempferi*, *Picea alcoquiana*, and *Thuja standishii* were not recorded.

In quadrats established within Plots 1 and 3–5 to describe the shrub and herb layers, large boulders with diameters of approximately 2 m, occasionally exceed-

Tab. 1: Relative basal area in each plot

| Plot number                                                    | NM   |      |      |      |      | WM   |      |      |      |      | NRA  |      |      |      |      |
|----------------------------------------------------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
|                                                                | P1   | P2   | P3   | P4   | P5   | P6   | P7   | P8   | P9   | P10  | P11  | P12  | P13  | P14  | P15  |
| <b>Conifer total</b>                                           | 91.9 | 91.0 | 92.6 | 83.9 | 96.3 | 53.0 | 75.1 | 61.2 | 10.5 | 49.9 | 60.3 | 90.7 | 25.3 | 76.5 | 33.6 |
| <b>Broadleaf total</b>                                         | 8.1  | 9.0  | 7.4  | 16.1 | 3.7  | 47.0 | 24.9 | 38.8 | 89.5 | 50.1 | 39.7 | 9.3  | 74.7 | 23.5 | 66.4 |
| <b>Conifer</b>                                                 |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| <i>Abies homolepis</i>                                         | 40.2 | 69.2 | 19.4 | 4.3  | 3.0  | 53.0 | 68.0 | 53.4 | 5.9  | 31.3 | 16.6 | 9.1  | 8.8  | 45.0 | 33.6 |
| <i>Tsuga sieboldii</i>                                         | 47.3 | 7.8  | 12.2 | 7.1  | 24.1 |      | 6.9  | 7.1  |      | 18.6 | 43.7 | 81.6 | 16.5 | 31.5 |      |
| <i>Chamaecyparis pisifera</i>                                  |      | 7.3  | 42.4 | 65.8 | 69.2 | 0.0  | 0.1  | 0.7  | 4.7  |      |      |      |      |      |      |
| <i>Larix kaempferi</i>                                         |      |      | 10.1 | 6.7  |      |      |      |      |      |      |      |      |      |      |      |
| <i>Picea alcoquiana</i>                                        | 4.3  |      | 8.6  |      |      |      |      |      |      |      |      |      |      |      |      |
| <i>Thuja standishii</i>                                        |      | 6.6  |      |      |      |      |      |      |      |      |      |      |      |      |      |
| <b>Broadleaf A</b>                                             |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| <i>Betula grossa</i>                                           | 5.4  | 5.1  | 6.0  | 15.2 | 0.7  |      |      |      |      |      |      |      | 0.9  |      |      |
| <i>Fraxinus lanuginosa</i>                                     | 0.0  | 2.3  | 0.3  | 0.6  | 1.0  |      |      |      |      |      |      |      |      |      |      |
| <i>Acer micranthum</i>                                         | 1.0  | 0.0  | 0.1  | 0.1  | 0.0  |      |      |      |      |      |      | 2.0  |      |      |      |
| <i>Acer capillipes</i>                                         | 0.1  |      |      |      | 1.2  |      |      |      |      |      |      |      |      |      |      |
| <b>Broadleaf B</b>                                             |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| <i>Quercus crispula</i>                                        |      |      |      |      |      | 16.1 | 1.5  | 18.1 |      |      | 10.5 |      | 34.5 |      |      |
| var. <i>crispula</i>                                           |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| <i>Pterocarya rhoifolia</i>                                    |      |      |      |      |      |      | 6.6  |      | 64.3 |      |      |      |      |      | 11.1 |
| <i>Castanea crenata</i>                                        |      |      |      |      |      |      |      | 8.0  |      | 11.4 | 13.8 | 0.7  | 2.7  | 9.2  |      |
| <i>Acer pictum</i> subsp. <i>dissectum</i>                     |      |      |      |      |      | 6.1  | 0.1  |      | 8.3  |      | 1.1  | 0.0  | 10.0 |      |      |
| <i>Kalopanax septemlobus</i>                                   |      |      |      |      |      |      | 12.0 | 3.3  |      | 5.1  |      |      |      | 2.2  | 1.1  |
| <i>Cercidiphyllum japonicum</i>                                |      |      |      |      |      |      |      |      | 12.5 |      |      |      |      |      | 5.7  |
| <i>Fagus crenata</i>                                           |      |      |      |      |      |      |      | 2.5  |      |      | 0.4  | 2.1  | 4.1  | 4.6  | 9.0  |
| <i>Acer diabolicum</i>                                         |      |      |      |      |      | 6.7  |      |      | 1.4  |      | 1.5  | 0.6  |      | 0.0  | 3.5  |
| <i>Ilex macropoda</i>                                          |      |      | 0.0  |      |      | 0.6  | 0.5  | 0.7  | 0.0  | 1.0  |      | 3.8  | 1.6  | 2.7  | 2.0  |
| <i>Fagus japonica</i>                                          |      |      |      |      |      |      |      |      |      | 15.2 |      |      | 9.1  |      | 8.8  |
| <i>Carpinus cordata</i> var. <i>cordata</i>                    |      |      |      |      |      | 2.3  | 1.2  | 1.0  | 1.0  | 1.5  | 0.5  |      | 2.3  |      | 3.5  |
| <i>Padus grayana</i>                                           |      |      |      |      |      | 7.0  |      | 0.6  |      | 4.6  |      |      |      | 0.0  |      |
| <i>Acer amoenum</i> var. <i>amoenum</i>                        |      |      |      |      |      |      |      | 0.1  |      | 7.8  | 2.5  |      | 4.3  |      | 1.2  |
| <i>Zelkova serrata</i>                                         |      |      |      |      |      |      |      |      |      |      | 6.7  |      |      |      |      |
| <i>Acer distylum</i>                                           |      |      |      |      |      | 1.0  | 1.7  |      | 0.5  | 1.0  |      |      |      | 0.9  | 3.5  |
| <i>Acer pictum</i> subsp. <i>dissectum</i> f. <i>dissectum</i> |      |      |      |      |      |      |      | 1.8  | 0.3  |      | 0.5  |      | 1.1  |      |      |
| <i>Carpinus tschonoskii</i>                                    |      |      |      |      |      |      |      |      |      |      | 1.6  |      |      |      |      |
| <i>Alnus hirsuta</i>                                           |      |      |      |      |      |      |      |      |      |      |      |      | 1.6  |      |      |
| <i>Styrax obassia</i>                                          |      |      |      |      |      | 1.0  | 0.0  |      |      |      |      |      | 0.1  |      |      |
| <i>Fraxinus spaethiana</i>                                     |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 13.2 |
| <b>Broadleaf C</b>                                             |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
| <i>Acer sieboldianum</i>                                       | 0.6  | 0.4  | 0.5  |      | 0.4  | 6.1  | 1.3  | 2.2  | 0.5  | 1.3  | 0.6  |      | 1.8  | 2.8  | 1.8  |
| <i>Clethra barbinervis</i>                                     | 0.0  | 1.1  | 0.2  |      | 0.2  |      |      | 0.3  |      |      |      | 0.1  | 0.2  | 1.0  |      |

NM, matrix-free site; WM, matrix-supported site; NRA, non-rock-avalanche site.

Only species with a relative basal area (RBA) of 1% in at least one plot are shown.

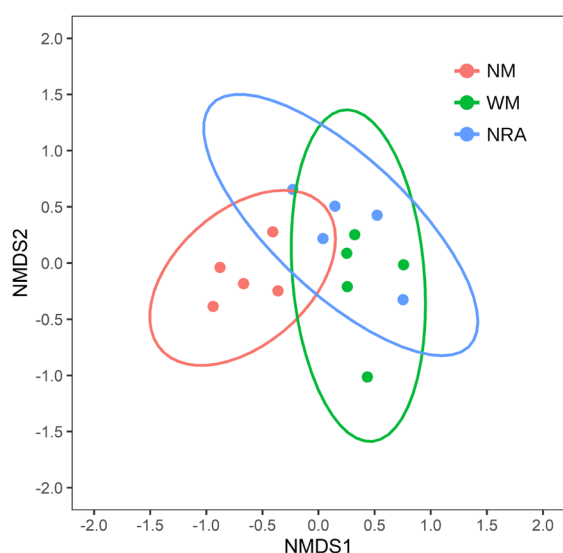


Fig. 3: Non-metric multidimensional scaling (NMDS) ordination of forest stands based on Bray–Curtis dissimilarities calculated from tree basal area. Ellipses represent the 95% confidence intervals of matrix-free boulder slopes (NM), matrix-supported boulder slopes (WM), and adjacent undisturbed slopes (NRA). Most WM plots overlapped with NRA plots, except for one valley-bottom plot dominated by *Pterocarya rhoifolia*, whereas NM plots were clearly separated from both WM and NRA plots. Final stress = 0.103.

ing 5 m, had accumulated without interstitial material. The surfaces of these boulders were covered with bryophytes and served as germination beds for tree species (Tab. 4). In these quadrats, saplings and seedlings of *Chamaecyparis pisifera* were observed in Plots 3–5, where the canopy and subcanopy layers were dominated by *C. pisifera*. All *C. pisifera* individuals exhibited a creeping growth form. Saplings and seedlings of *Abies homolepis* were present in all plots, although their abundance was low. Additionally, many broad-leaved species occurred,

Tab. 2: Results of pairwise PERMANOVA based on Bray–Curtis dissimilarities calculated from Hellinger-transformed tree basal area

| Comparison | Pseudo- <i>F</i> | <i>R</i> <sup>2</sup> | <i>p</i> |
|------------|------------------|-----------------------|----------|
| NM vs. NRA | 5.768            | 0.419                 | 0.008    |
| NM vs. WM  | 5.539            | 0.409                 | 0.010    |
| WM vs. NRA | 1.499            | 0.158                 | 0.158    |

*P*-values were obtained using 999 permutations.

Differences in multivariate dispersion were not significant (PERMDISP, *p* = 0.609).

including *Rhododendron benhallii*, *Fraxinus lanuginosa* f. *ser-rata*, *Clethra barbinervis*, *Acer micranthum*, and *Rhododendron wadanum*. Signs of animal browsing were noted on the foliage of some plants.

#### 4.3 Spatial distribution of canopy trees along topographic transects

Transect 1, established to examine the spatial arrangement of topography and vegetation, traversed the NRA and RA slopes. The NRA slope supported a mixed forest of conifers (*Abies homolepis* and *Tsuga sieboldii*) and deciduous broad-leaved trees (e.g., *Acer sieboldianum*) (Fig. 4a). The RA slope was predominantly coniferous, with *A. homolepis* and *Chamaecyparis pisifera* dominating; this slope included a small WM section, while the remainder corresponded to NM. In the NM section of the RA slope, *Thuja standishii* occurred only rarely. A single broad-leaved canopy tree at the center of the RA slope was *Betula grossa*.

Transect 2 extended from the WM slope to the NM slope within the RA area (Fig. 4b). In the WM

Tab. 3: Cumulative occurrence (%) of coniferous species across relative height strata

|                               | NM plots |      |       |          | WM plots |      |       |          |
|-------------------------------|----------|------|-------|----------|----------|------|-------|----------|
|                               | ≤H25     | ≤H75 | ≤H95  | <i>n</i> | ≤H25     | ≤H75 | ≤H95  | <i>n</i> |
| <i>Abies homolepis</i>        | 24.5     | 49.1 | 94.3  | 53       | 23.4     | 63.6 | 96.1  | 77       |
| <i>Tsuga sieboldii</i>        | 7.2      | 74.7 | 98.8  | 83       | 23.1     | 57.7 | 100.0 | 26       |
| <i>Chamaecyparis pisifera</i> | 7.9      | 52.5 | 97.0  | 101      | 57.1     | 85.7 | 100.0 | 7        |
| <i>Larix kaempferi</i>        | 0.0      | 0.0  | 0.0   | 2        | -        | -    | -     | 0        |
| <i>Picea alcoquiana</i>       | 0.0      | 20.0 | 60.0  | 5        | -        | -    | -     | 0        |
| <i>Thuja standishii</i>       | 0.0      | 50.0 | 100.0 | 2        | -        | -    | -     | 0        |

Height strata were defined using plot-level height percentiles (H25, H75, and H95) calculated from all trees within each plot. Values represent the cumulative percentage of plots in which at least one individual of each species occurred at or below a given stratum. Only coniferous species are presented.

*n* denotes the total number of individuals recorded for each species.

Tab. 4: Number of woody individuals recorded in the shrub layer and the herb plus moss layer

| Plot                                                | 1   |     | 3  |    | 4   |    | 5  |    | Total |
|-----------------------------------------------------|-----|-----|----|----|-----|----|----|----|-------|
| Quadrat                                             | a   | b   | a  | b  | a   | b  | a  | b  |       |
| <b>Shrub layer (0.5–1.5 m)</b>                      |     |     |    |    |     |    |    |    |       |
| Shrub cover (%)                                     | 10  | 20  | 40 | 50 | 55  | 35 | 55 | 70 |       |
| <i>Rhododendron benhallii</i>                       | 8   | 7   | 27 | 12 | 16  | 9  | 9  | 17 | 105   |
| <i>Fraxinus lanuginosa</i> f. <i>serrata</i>        | -   | -   | 1  | 1  | 1   | 2  | 3  | 13 | 21    |
| <i>Chamaecyparis pisifera</i>                       | -   | -   | -  | 1  | 4   | 5  | 5  | 5  | 20    |
| <i>Clethra barbinervis</i>                          | -   | 2   | 2  | 2  | 2   | 1  | -  | 4  | 13    |
| <i>Abies homolepis</i>                              | -   | -   | -  | -  | 1   | -  | -  | 4  | 5     |
| <i>Rhododendron wadanum</i>                         | -   | 1   | -  | 3  | -   | 1  | -  | -  | 5     |
| <i>Cerasus nipponica</i>                            | -   | -   | -  | 2  | -   | -  | 1  | 1  | 4     |
| <i>Acer micranthum</i>                              | -   | -   | -  | -  | -   | 1  | 1  | -  | 2     |
| <i>Acer pictum</i> subsp. <i>dissectum</i>          | -   | -   | -  | -  | -   | -  | -  | 1  | 1     |
| <i>Viburnum dilatatum</i>                           | -   | -   | -  | -  | 1   | -  | -  | -  | 1     |
| <i>Acer sieboldianum</i>                            | -   | -   | -  | -  | -   | 1  | -  | -  | 1     |
| <b>Herb and moss layer (&lt;0.5 m)</b>              |     |     |    |    |     |    |    |    |       |
| Vasc. plant cover (%)                               | 10  | 10  | 20 | 40 | 60  | 35 | 15 | 40 |       |
| Moss cover (%)                                      | 90  | 90  | 95 | 85 | 70  | 95 | 95 | 70 |       |
| <i>Rhododendron benhallii</i>                       | 45  | 105 | -  | 68 | 124 | 26 | 36 | 34 | 438   |
| <i>Acer micranthum</i>                              | 175 | -   | 28 | 64 | 52  | 44 | 44 | 26 | 433   |
| <i>Clethra barbinervis</i>                          | -   | 7   | 7  | 21 | 24  | 12 | -  | 22 | 93    |
| <i>Chamaecyparis pisifera</i>                       | -   | -   | -  | 5  | 11  | 5  | 14 | 6  | 41    |
| <i>Rhododendron wadanum</i>                         | 8   | 3   | 1  | 7  | 2   | 2  | -  | -  | 23    |
| <i>Fraxinus lanuginosa</i> f. <i>serrata</i>        | -   | 4   | 1  | 1  | 3   | 6  | 1  | 6  | 22    |
| <i>Acer nipponicum</i>                              | -   | 1   | 2  | 6  | 7   | 2  | -  | 1  | 19    |
| <i>Abies homolepis</i>                              | 6   | 2   | 1  | 1  | 2   | -  | -  | -  | 12    |
| <i>Acer palmatum</i>                                | -   | -   | 1  | 1  | 3   | -  | 8  | -  | 12    |
| <i>Rhododendron kaempferi</i> var. <i>kaempferi</i> | -   | -   | -  | -  | -   | -  | -  | 3  | 3     |
| <i>Cerasus nipponica</i>                            | -   | -   | 1  | -  | 1   | -  | 1  | -  | 3     |
| <i>Acer pictum</i> subsp. <i>dissectum</i>          | -   | -   | 1  | -  | 1   | -  | -  | -  | 2     |

section, the canopy was composed of *A. homolepis*, *T. sieboldii*, *Pterocarya rhoifolia*, and *Acer pictum*, with only a single sapling of *C. pisifera*. By contrast, the NM section was conifer-dominated, with *C. pisifera*, *A. homolepis*, and *T. sieboldii* forming the canopy. *Picea alcockiana* and *Larix kaempferi* were each represented by a single tall individual and were not encountered elsewhere in the adjacent forest.

#### 4.4 Soil and substrate characteristics

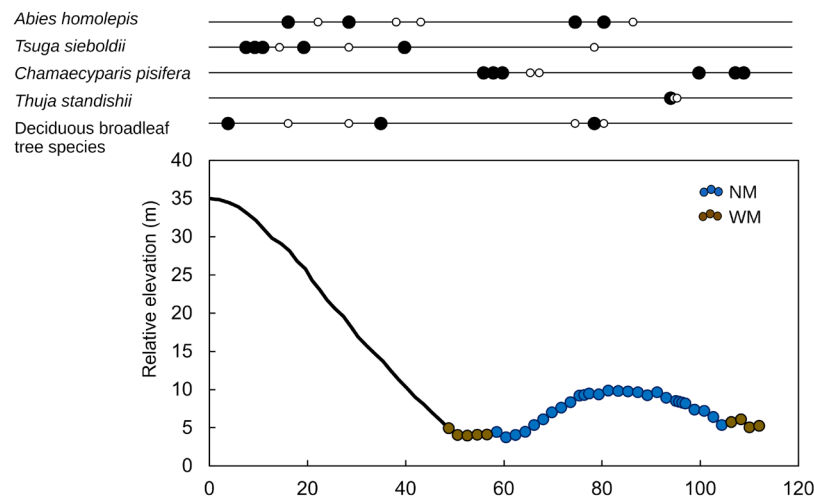
Soil profile in Plots 13 and 14, located in the NRA area, generally exhibited characteristics of brown forest soils (KUBO 1982), which are widely developed

in the cool-temperate mountains of Japan (Tab. 5). However, Plot 13, situated near a ridge, and Plot 14, on a steep 35° slope, had Ah horizons slightly thinner than those typical of brown forest soils.

In contrast, Plots 6, 8, and 9 within the WM area exhibited developed Ah horizons with some characteristics of brown forest soils; however, the overall profiles were gravelly, with a matrix containing abundant fine gravel and sand. Angular and sub-angular clasts with long axes of 5–25 cm occurred in the Ah and AB horizons, while lower layers were rich in cobbles and boulders.

Observations at a roadcut exposure along the forest road traversing the WM slope revealed that the root system of *Abies homolepis* was predominantly confined

## (a) Transect 1



## (b) Transect 2

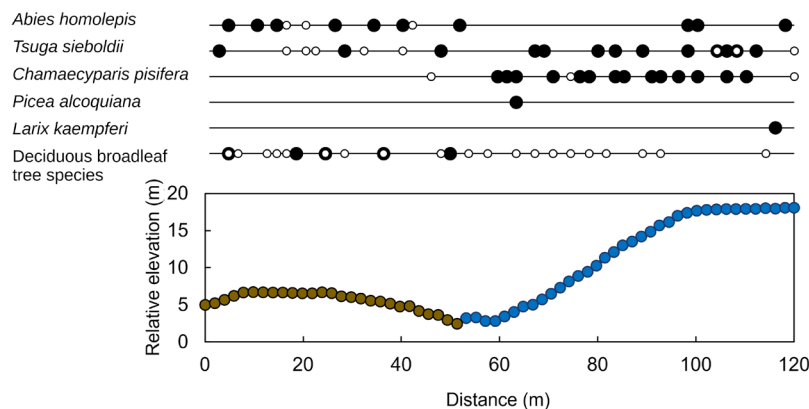


Fig. 4: Spatial distribution of canopy trees along topographic transects. Locations of transects are shown in Fig. 1d. Symbols indicating plant distribution use filled circles for individuals taller than 20 m and open circles for individuals shorter than 20 m.

to the upper 50 cm of the profile (Fig. 5). Below this depth, roots were scarce; however, in some locations, coarse roots (diameter > 1 cm) extended to approximately 120 cm beneath the ground surface.

## 5 Discussion

### 5.1 Vegetation differentiation and stand dynamics

The rock-avalanche deposit comprises two contrasting geomorphic units: matrix-free (NM) sites and matrix-supported (WM) sites. These units differ fundamentally in substrate structure and the degree of soil development—ranging from continuous

brown forest soils in WM (Tab. 5) to a complete absence of fine-earth soil matrix in NM, where trees establish on moss-covered boulders with extensive subterranean air spaces (Fig. 2b) - resulting in distinct forest communities (Tab. 1).

On the WM sites, although *Abies homolepis* remains dominant in some stands, *Chamaecyparis pisifera* exhibits negligible dominance. Instead, the canopy is composed considerably of broad-leaved tree species common to the surrounding non-landslide area (NRA), yielding an overlap of plots between WM and NRA in the ordination space (Fig. 3). The composition of Plots 6-8 and 10 resembles the *Rhododendron wadanum*–*Abies homolepis* community described in regional studies (NAGAOKA & OKUDA 1999). Moreover,

Tab. 5: Morphological properties of the soils

| Site | Plot    | Horizon | Depth (cm) | Munsell Color (moist) | Texture | Consistency (moist) | Rock fragments |
|------|---------|---------|------------|-----------------------|---------|---------------------|----------------|
| WM   | Plot 6  | Ah      | 0-2        | 5YR2/2                | SL      | SHA                 | C              |
|      |         | AB      | 2-14       | 5TR3/2                | SL      | SHA                 | C              |
|      |         | Bw1     | 14-22      | 7.5YR4/2              | LS      | HA                  | M              |
|      |         | Bw2     | 22-60+     | 7.5YR4/3              | LS      | HA                  | A              |
|      | Plot 8  | Ah      | 0-12       | 5YR2/2                | L       | SO                  | C              |
|      |         | Bw      | 12-28      | 7.5YR2/3              | SL      | SHA                 | M              |
|      |         | BC      | 28-45+     | 7.5YR3/3              | LS      | HA                  | A              |
|      | Plot 9  | Ah      | 0-7        | 5YR2/2                | SL      | SHA                 | M              |
|      |         | AB      | 7-21       | 5YR3/2                | LS      | SHA                 | A              |
|      |         | BW      | 21-40+     | 7.5YR3/3              | LS      | SHA                 | D              |
|      | Plot 13 | Ah      | 0-5        | 5YR2/1                | L       | SO                  | F              |
|      |         | AB      | 5-24       | 5YR3/2                | SiL     | SO                  | C              |
|      |         | Bw      | 24-50      | 7.5YR4/3              | SL      | SHA                 | M              |
|      |         | BC      | 50-75+     | 7.5YR4/3              | SL      | SHA                 | A              |
|      | Plot 14 | Ah      | 0-8        | 5YR2/2                | SiL     | SO                  | F              |
|      |         | AB      | 8-24       | 7.5YR4/4              | SiL     | SHA                 | M              |
|      |         | Bw      | 24-40      | 7.5YR4/6              | SL      | SHA                 | A              |
|      |         | BC      | 40-55+     | 7.5YR4/6              | SL      | SAH                 | D              |

Texture: LS, loamy sand; SiL, silt loam; SL, sandy loam; L, loam

Consistence: SO, soft; SHA, slightly hard; HA, hard

Rock fragments: F, few; C, common; M, many; A, abundant; D, dominant

Plot 9, located on the valley floor within the WM unit, is dominated by *Pterocarya rhoifolia*, a characteristic riparian species in the montane zone (MIYAWAKI 1985).

These findings indicate that, despite the gravelly nature of the substrate, the presence of a fine matrix in the WM sites has facilitated pedogenesis over the last millennium. As a result, our comparison suggests that vegetation succession over the last millennium has progressed to a stage that is structurally and compositionally convergent with the regional zonal vegetation. This interpretation is further supported by soil profiles exhibiting characteristics of brown forest soils (Tab. 5).

In sharp contrast, the NM sites are characterized by closed-canopy coniferous forests established on block slopes. Here, severe edaphic constraints, particularly the absence of fine sediment, act as strong environmental filters, limiting the establishment of competitive climax broad-leaved species. Consequently, the vegetation is dominated by conifers adapted to rocky substrates, including shallow-rooted species such as *Tsuga sieboldii* and *Chamaecyparis pisifera* (KARIZUMI 2010), as well as *Abies homolepis*, which is known to occur on poorly developed soils (NAGAOKA & OKUDA 1999, 2000, BESSHO et al. 2009).



Fig. 5: Exposed root system of *Abies homolepis* at a roadcut along the WM slope

Forests dominated by *C. pisifera* are typically found on moist lower slopes where large boulders accumulate (HAYASHI 1960, SAKIO 2017). Our results indicate that, even within the NM unit, this species is absent or shows low dominance on narrow, relatively dry ridges (Tab. 1; Fig. 4). This distribution pattern is consistent with previous reports regarding the species' moisture requirements.

The persistence of *C. pisifera* in the NM area appears to be supported by its regeneration strategies. Previous studies have reported that *C. pisifera* can maintain populations through clonal propagation, even on immature soils (YAMAMOTO & MORIYAMA 1997). In the NM plots, *C. pisifera* was abundant in the subcanopy and lower layers (Tab. 3), and saplings - many of which exhibited creeping growth forms indicative of clonal/vegetative propagation - were frequently observed on the forest floor (Tab. 4). These observations indicate that the conifer-dominated community is stably maintained as an edaphic climax. Although seedlings of broad-leaved canopy species were occasionally present, their successful recruitment into the canopy layer is likely constrained by the physical limitations imposed by the substrate.

*Larix kaempferi* and *Picea alcoquiana* were also present in the NM plots, albeit at low densities. These individuals were almost exclusively confined to the canopy layer (Tab. 3), with a complete absence of seedlings or saplings (Tab. 4). Given the low shade tolerance of these species, small-scale gap dynamics are insufficient to promote their regeneration. Particularly, *L. kaempferi* typically requires large-scale disturbances that expose open mineral soil to facilitate cohort establishment (TATEWAKI et al. 1965, BABA 1989).

The NM area, characterized by an open-work boulder substrate with subterranean air spaces rather than a continuous soil matrix (Fig. 2b), is prone to secondary disturbances such as windthrow; indeed, uprooted patches of *C. pisifera* and *A. homolepis* were observed during the survey. This suggests that the scattered canopy individuals of *L. kaempferi* and *P. alcoquiana* may represent a senescent cohort that established following past large-scale disturbance events within the landslide deposit.

## 5.2 The rock-avalanche deposit as a microrefugium

Although the rock-avalanche occurred approximately 1100 years ago, the NM sites remain characterized by blocky slopes, poorly developed soils, and a conspicuous absence of fine-grained matrix material. Whether this matrix-free condition resulted from initial material segregation during the flow (e.g., FRODELLA et al. 2014, PIERRE et al. 2020) or from subsequent post-depositional washout processes, the ecological consequence is the same: the development of a distinct edaphic climax community.

The complete absence of a fine soil matrix forces establishing seedlings to rely almost entirely on thin surface moss layers for initial moisture retention, while mature canopy trees must extend their roots deep through interstitial boulder voids to access subterranean moisture (Fig. 2b). These structural constraints impose severe physiological filters during early regeneration, effectively precluding the recruitment and dominance of zonal broad-leaved species found in the surrounding NRA. Consequently, competitive pressure from broad-leaved trees is presumably minimal, permitting only scattered pioneer individuals of *Betula grossa* to persist. This inhibition of succession toward the regional zonal mixed forest has created a stable habitat for stress-tolerant conifers, effectively functioning as a microrefugium within the matrix of the cool-temperate broad-leaved forest zone.

The dominance of *Chamaecyparis pisifera* on these block slopes underscores the geocological significance of the landslide deposit for preserving ancient lineages. The genus *Chamaecyparis* has a deep evolutionary history, originating in the mid-Paleogene and once widely distributed throughout the Northern Hemisphere (WANG et al. 2022). Although its range contracted substantially during Neogene and Quaternary cooling, the extant species in East Asia and North America represent disjunct remnants of this Tertiary lineage. These taxa are thought to

have persisted within specific topographic refugia that buffered them from climatic extremes and competitive exclusion.

Previous studies indicate that *Chamaecyparis* species frequently occupy edaphically harsh environments, such as rocky boulder fields and wetlands, where interspecific competition is reduced (ANTOS & ZOBEL 1986, YAMAMOTO & MORIYAMA 1997, LI et al. 2015). Our findings strongly indicate that the large-scale rock-avalanche created a persistent habitat analogous to these ecological safe sites. It is therefore highly probable that many montane *C. pisifera* forests described in the literature as occurring on boulder slopes are, in fact, established on ancient mass-movement deposits similar to the present study area.

*Thuja standishii*, which like *Chamaecyparis pisifera* represents a Cupressaceae lineage with Tertiary origins at the genus level, was also recorded at the NM sites (Tab. 1; Fig. 4), but it did not attain the high dominance observed for *C. pisifera*. Although *T. standishii* exhibits an affinity for rocky substrates (WORTH 2019), its lower abundance in the present study area may reflect the influence of macroclimatic filters operating above microtopographic conditions. The core distribution of *T. standishii* is centered in heavy snow regions of the Sea of Japan side, where it relies on vegetative regeneration (layering) under snow cover. The study area, located on the Pacific side, lacks deep snow accumulation, which likely limits the competitive advantage of *T. standishii* relative to *C. pisifera* and *Abies homolepis*, despite the availability of suitable rocky substrate.

*Picea alcoquiana* is regarded as a glacial relict species; however, fossil evidence from the Last Glacial Maximum (LGM) typically identifies spruce remains only to the sectional level rather than to the species level. These records indicate that members of the *Picea* sect. *Picea* were more widely distributed in lowland regions during the LGM. Similarly, *Larix kaempferi* is a cold-adapted pioneer species that currently persists primarily on harsh, rocky substrates. It is therefore plausible that both taxa, or closely related lineages within the same clades, had broader lowland distributions during the LGM and subsequently retreated to higher elevations or specific rocky habitats in response to post-glacial warming (NOTE et al. 1998, AIZAWA et al. 2008, OKITSU et al. 2016, TOMARU et al. 2022).

In contrast to the shade-tolerant *C. pisifera*, both *L. kaempferi* and *P. alcoquiana* are light-demanding species confined to the canopy layer in the study area. *Larix kaempferi* is a typical pioneer species requiring bright, open environments (TATEWAKI et al. 1965), whereas *P. alcoquiana* possesses intermediate

shade tolerance and typically relies on disturbances for successful regeneration. Neither species is likely to regenerate successfully within small canopy gaps, underscoring their dependence on larger-scale disturbance events, particularly for *L. kaempferi*. Their continued coexistence suggests that localized windthrow events on the matrix-free boulder substrate generate recurrent disturbances sufficient to maintain these light-demanding taxa.

In summary, the rock-avalanche deposit functions as a multifaceted refugium. It excludes competitive broad-leaved trees through edaphic filtering, thereby preserving stress-tolerant conifers of Tertiary lineage (*Chamaecyparis*). Simultaneously, it maintains disturbance-dependent species of glacial origin (*Larix*, *Picea*) through localized geomorphic instability. Thus, this landform acts as a geo-historical archive, conserving phylogenetically and ecologically distinct lineages from different geological epochs within a single geomorphic unit.

### 5.3 Regional persistence of relict species via landslide networks

Because the rock-avalanche examined in this study occurred relatively recently (approximately 1100 years ago), it could not have served as a continuous habitat throughout the entire post-glacial period since the LGM (~20,000 BP). However, numerous large-scale landslides, including rock-avalanches, are distributed in the vicinity of the study area (Fig. 1). It is therefore plausible that the four focal species, all of which possess wind-dispersed seeds, have maintained their populations across the mountain range through dispersal among multiple landslide sites.

For example, a *Chamaecyparis pisifera*-dominated forest persists on the rocky slope of Mt. Kogarasu, located approximately 30 km east of the study site, which was formed by a landslide dated to approximately 6300 <sup>14</sup>C BP (KARIYA & SAIGUSA 1993, SAIGUSA & KARIYA 1994). This example highlights both the multi-millennial stability of boulder substrates as refugia and the presence of landslides of diverse ages across the region. In the mountainous regions of Japan, located within a tectonically active, high precipitation zone, numerous landslides have occurred since the LGM. Although individual landslide sites functioning as microrefugia are temporally limited, the refugial function is likely sustained at the landscape scale. In other words, these spatially dispersed landslide scars collectively form a dynamic habitat network that functions as a microrefugium. Rather

than representing static habitat patches, they constitute recurrent habitats generated and maintained by ongoing geomorphological processes.

*Abies homolepis* and *Tsuga sieboldii* were inferred to have been distributed at lower elevations in relatively warm regions of western Japan during the LGM, based on pollen fossil evidence and species distribution modeling (Ooi 2016, UCHIYAMA et al. 2023). During post-glacial warming, these species migrated upslope to higher elevations, where they not only persisted but also expanded their distributions relatively readily. This pattern is likely attributed to their high shade tolerance, which enables regeneration beneath closed forest canopies. In contrast, *Picea alcoquiana* and *Larix kaempferi*, being light-demanding and disturbance-dependent species, likely persisted only in spatially restricted patches where canopy-opening disturbances occurred.

## 6 Conclusion

This study elucidated the geoecological role of large-scale landslide scars in sustaining vegetation diversity and conserving relict lineages, focusing on a rock-avalanche deposit approximately 1100 years old in the Akaishi Mountains. The results demonstrate that the deposit comprises two distinct habitat types governed by substrate conditions: NM fields and WM slopes. In the WM sites, vegetation succession over the past 1100 years has promoted the development of mixed conifer-broadleaf forests that increasingly resemble the zonal vegetation of adjacent stable slopes. In contrast, the NM sites impose severe edaphic constraints due to the absence of fine soil, thereby limiting the establishment of highly competitive broad-leaved tree species. Consequently, an edaphic climax community dominated by stress-tolerant conifers, such as *Chamaecyparis pisifera*, *Abies homolepis*, and *Tsuga sieboldii*, has been maintained.

Notably, the NM sites support a distinctive assemblage of relicts of Tertiary lineages (e.g., *C. pisifera* and *Thuja standishii*) as well as species with glacial history (e.g., the glacial relict *P. alcoquiana* and the cold-adapted *L. kaempferi*). These taxa, having been displaced from their primary distributional ranges by past climatic shifts and interspecific competition, persist in rocky habitats limited by competitors. Our findings suggest that the geomorphic legacy of the ancient rock-avalanche can function as a vital microrefugium by suppressing competitively dominant species through edaphic filtering while simultaneously providing disturbance-mediated niche opportunities. Furthermore,

the results indicate that scattered landslide scars across the mountain range collectively form a dynamic habitat network. This network may facilitate the regional persistence of relict populations through metapopulation dynamics, thereby compensating for the transient nature of individual landslide sites.

Combining precise chronological dating with detailed geomorphological characterization has provided a key framework for drawing these conclusions from a long-term perspective. Nevertheless, the specific trajectory of vegetation development and geomorphic stabilization during the 1100 years following the disturbance remains unresolved. Given the presence of wetlands and ponds within the rock-avalanche deposit, future research should reconstruct long-term ecological succession by analyzing plant macrofossils preserved in sedimentary sequences from these depressions. Such paleoecological investigations will further refine our understanding of the temporal dynamics of landslides as microrefugia.

## Acknowledgments

This work was supported by JSPS KAKENHI Grant Number JP23K25424. The authors sincerely thank Associate Professor Takashi Kimura of Ehime University, Dr. Ryuji Yamada of the National Research Institute for Earth Science and Disaster Resilience, Japan, and Dr. Shoji Doshida of National Research Institute of Fire and Disaster for their valuable discussions on geology and landforms. The authors also express their appreciation to Dr. Kimio Inoue of the Sabo Frontier Foundation for his insightful comments and generous support.

## References

- AIZAWA M, YOSHIMARU H, KATSUKI T, KAJI M (2008) Imprint of post-glacial history in a narrowly distributed endemic spruce, *Picea alcoquiana*, in central Japan observed in nuclear microsatellites and organelle DNA markers. *Journal of Biogeography* 35: 1295–1307. <https://doi.org/10.1111/j.1365-2699.2008.01880.x>
- ALEXANDROWICZ Z, MARGIELEWSKI W (2010) Impact of mass movements on geo- and biodiversity in the polish outer (Flysch) Carpathians. *Geomorphology* 123: 290–304. <https://doi.org/10.1016/j.geomorph.2010.07.020>
- ANTOS JA, ZOBEL DB (1986) Habitat relationships of *Chamaecyparis nootkatensis* in southern Washington, Oregon, and California. *Canadian Journal of Botany* 64: 1898–1909. <https://doi.org/10.1139/b86-253>

- ANYOMI KA, NEARY B, CHEN J, MAYOR SJ (2022) A critical review of successional dynamics in boreal forests of North America. *Environmental Reviews* 30: 563–594. <https://doi.org/10.1139/er-2021-0106>
- BABA T (1989) A study of the relation between stability of gravel and succeeding vegetation of *Larix kaempferi* at Kumaanazawa of Mt. Nokogiri in the Southern Alps. *Bulletin of the Shinshu University Forests* 26: 31–56.
- BESHO N, KAMIJO T, OGAWA M, TSUYAMA I (2009) Causes of varying regeneration dynamics of *Abies homolepis* among topographically distinct stands. *Vegetation Science* 26: 89–102. <https://doi.org/10.15031/vegsci.26.89>
- BIODIVERSITY CENTER OF JAPAN (2010) Existing vegetation map 1:25,000. (in Japanese). <http://gis.biodic.go.jp/webgis/>
- CHAZDON RL (2003) Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6: 51–71. <https://doi.org/10.1078/1433-8319-00042>
- CHEN CF, LI CF, HUANG CM, LIN HY, ZELÉNY D (2022) Secondary succession on landslides in submontane forests of central Taiwan: Environmental drivers and restoration strategies. *Applied Vegetation Science* 25: e12635. <https://doi.org/10.1111/avsc.12635>
- DE CÁCERES M, LEGENDRE P (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology* 90: 3566–3574. <https://doi.org/10.1890/08-1823.1>
- FRANCESCATO V, SCOTTON M, ZARIN DJ, INNES JC, BRYANT DM (2001) Fifty years of natural revegetation on a landslide in Franconia Notch, New Hampshire, USA. *Canadian Journal of Botany* 79: 1477–1485. <https://doi.org/10.1139/b01-121>
- FRODELLA W, MORELLI S, FIDOLINI F, PAZZI V, FANTI R (2014) Geomorphology of the Rotolon landslide (Veneto region, Italy). *Journal of Maps* 10: 394–401. <https://doi.org/10.1080/17445647.2013.869666>
- GEERTSEMA M, POJAR JJ (2007) Influence of landslides on biophysical diversity - a perspective from British Columbia. *Geomorphology* 89: 55–69. <https://doi.org/10.1016/j.geomorph.2006.07.019>
- GRAY M (2013) Geodiversity: Valuing and conserving abiotic nature. Chichester.
- GUARIGUATA MR (1990) Landslide disturbance and forest regeneration in the upper Luquillo Mountains of Puerto Rico. *The Journal of Ecology* 78: 814–832. <https://doi.org/10.2307/2260901>
- GUARIGUATA MR, OSTERTAG R (2001) Neotropical secondary forest succession: Changes in structural and functional characteristics. *Forest Ecology and Management* 148: 185–206. [https://doi.org/10.1016/S0378-1127\(00\)00535-1](https://doi.org/10.1016/S0378-1127(00)00535-1)
- HAYASHI Y (1960) Taxonomy and distribution of Japanese conifers. Tokyo. (in Japanese).
- HE LY, TANG CQ, WU ZL, WANG HC, OHSAWA M, YAN K (2015) Forest structure and regeneration of the Tertiary relict *Taivania cryptomerioides* in the Gaoligong Mountains, Yunnan, southwestern China. *Phytocoenologia* 45: 135–156. <https://doi.org/10.1127/phyto/2015/0038>
- HEWITT K, CLAGUE JJ, ORWIN JF (2008) Legacies of catastrophic rock slope failures in mountain landscapes. *Earth-Science Reviews* 87: 1–38. <https://doi.org/10.1016/j.earscirev.2007.10.002>
- 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. <https://doi.org/10.1016/j.catena.2023.107578>
- JAHN R, BLUME H, ASIO V, SPAARGAREN O, SCHAD P (2006) Guidelines for soil description. Rome.
- KARIYA Y, SAIGUSA S (1993) The origin of block streams in and around Mt. Kogarasu, Yamanashi Prefecture, Central Japan. *Quarterly Journal of Geography* 45: 254–265. (in Japanese with English abstract). <https://doi.org/10.5190/tga.45.254>
- KARIYA Y (2012) Debris avalanche features of the Nara-Heian period in the east of Mount Jizo, the Akaishi Range of central Japan. *Chikei (Transactions of the Japanese Geomorphological Union)* 33: 297–313. (in Japanese with English abstract).
- KARIZUMI N (2010) The latest illustrations of tree roots. Tokyo. (in Japanese).
- KIMURA T, YAMADA R, KARIYA Y, INOUE K (2018) Revisiting geomorphic changes caused by the Dondokosawa rock avalanche in the Akaishi Mountains, central Japan. *Journal of the Japan Landslide Society* 55: 42–52. <https://doi.org/10.3313/jls.55.42>
- KUBO T (1982) Classification of forest soils in Japan. *Japan Agricultural Research Quarterly* 16: 212–217.
- LI CF, ZELÉNY D, CHYTRÝ M, CHEN MY, CHEN TY, CHIOU CR, HSIA YJ, LIU HY, YANG SZ, YEH CL, WANG JC, YU CF, LAI YJ, GUO K, HSIEH CF (2015). *Chamaecyparis* montane cloud forest in Taiwan: ecology and vegetation classification. *Ecological Research*, 30: 771–791. <https://doi.org/10.1007/s11284-015-1284-0>
- LOPES LF, OLIVEIRA SC, NETO C, ZÉZERE JL (2020) Vegetation evolution by ecological succession as a potential bioindicator of landslides relative age in Southwestern Mediterranean region. *Natural Hazards* 103: 599–622. <https://doi.org/10.1007/s11069-020-04002-y>
- MİYAWAKI A (ed) (1985) Vegetation of Japan, Vol. 6: Chubu. Tokyo. (in Japanese).
- NAGAOKA F, OKUDA S (1999) Species composition and environmental factors of *Abies homolepis* forest around Mt. Yatsugatake. *Actinia* 12: 11–22. (in Japanese with English abstract).
- NAGAOKA S, OKUDA S (2000) Species composition of *Abies homolepis* forests in relation to landforms along the Azusa

- River around Kamikochi, Central Japan. *Vegetation Science* 17: 55–72. (in Japanese with English abstract). <https://doi.org/10.15031/vegsci.17.55>
- NAKASHIZUKA T (1987) Regeneration dynamics of beech forests in Japan. *Vegetatio* 69: 169–175. <https://doi.org/10.1007/BF00038698>
- NOTE H, OKITSU S, MOMOHARA A (1998) Present distribution of *Picea* sect. *Picea* Farjon and distribution changes since the Last Glacial Age in Japan. *Japanese Journal of Historical Botany* 6: 3–13. (in Japanese with English abstract). [https://doi.org/10.34596/hisbot.6.1\\_3](https://doi.org/10.34596/hisbot.6.1_3)
- OKITSU S, KRESTOV PV, MOMOHARA A, NAKAMURA Y (2016) The distribution of a *Picea koraiensis*–*Pinus koraiensis*: Deciduous broadleaved mixed forest along a soil moisture in the southern—most Primorie, the Russian Far East and its significant for the vegetation history in mountainous areas of central Japan. *Vegetation Science* 33: 33–43. (in Japanese with English abstract). <https://doi.org/10.15031/vegsci.33.3>
- OXSANEN, J., SIMPSON, G., BLANCHET, F., KINDT, R., LEGENDRE, P., MINCHIN, P., O'HARA, R., SOLYMOS, P., STEVENS, M., SZOEC, E., WAGNER, H., BARBOUR, M., BEDWARD, M., BOLKER, B., BORCARD, D., BORMAN, T., CARVALHO, G., CHIRICO, M., DE CACERES, M., DURAND, S., EVANGELISTA, H., FITZJOHN, R., FRIENDLY, M., FURNEAUX, B., HANNIGAN, G., HILL, M., LAHTI, L., MARTINO, C., MCGLINN, D., OUELLETTE, M., RIBEIRO CUNHA, E., SMITH, T., STIER, A., TER BRAAK, C. AND WEEDON, J. (2026) Vegan: Community Ecology Package. R package version 2.7-3. URL: <https://CRAN.R-project.org/package=vegan> (accessed 25/07/2026).
- OOI N (2016) Vegetation history of Japan since the last glacial based on palynological data. *Japanese Journal of Historical Botany* 25: 1–101. [https://doi.org/10.34596/hisbot.25.1-2\\_1](https://doi.org/10.34596/hisbot.25.1-2_1)
- PIERRE F, MILLARD TH, MITCHELL A, ALLSTADT KE, BRIAN M, MARTEN G, CLAGUE JJ (2020) Observations on the May 2019 Joffe Peak landslides, British Columbia. *Landslides* 17: 913–930. <https://doi.org/10.1007/s10346-019-01332-2>
- R CORE TEAM (2025) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL: <https://www.R-project.org/> (accessed 25/07/2026).
- SAIGUSA S, KARIYA Y (1994) Radiocarbon age of charcoal wood from the forming material of block stream in Mount Kogarasu, Yamanashi Prefecture. *Quarterly Journal of Geography* 46: 173–175. (in Japanese with English abstract). <https://doi.org/10.5190/tga.46.173>
- SAKIO H (2017) A natural history of trees in riparian forests. Tokyo. (in Japanese).
- SHANG KK, CHEN B, ZHANG XJ, DA LJ (2020) Topographic influences on the population persistence of a tertiary relict deciduous tree *Emmenopterys henryi* Oliv. on Mt. Tianmu, Eastern China. *Applied Ecology & Environmental Research* 18: 6053–6067.
- ŠÍMOVÁ A, PÁNEK T, GÁLKA M, ZERNITSKAYA V, HÁJKOVÁ P, BRODSKÁ H, SVITAVSKÁ-SVOBODOVÁ H, HORTON BP, TSYGANOV AN, MAZEI YA, HÁJEK M (2019) Landslides increased Holocene habitat diversity on a flysch bedrock in the Western Carpathians. *Quaternary Science Reviews* 219: 68–83. <https://doi.org/10.1016/j.quascirev.2019.07.009>
- SUGITA M (2013) Snow-covered area extraction around Mount Kita using satellite data. *Y-CROST Research Report* 8: 13–17. (in Japanese with English abstract).
- TAKAOKA S, KARIYA Y (2020) History of landform–vegetation relationships in the upper Azusa River basin, central Japan: Effects of landform evolution on vegetation structures. *Japanese Journal of Historical Botany* 28: 47–58. (in Japanese with English abstract). [https://doi.org/10.34596/hisbot.28.2\\_47](https://doi.org/10.34596/hisbot.28.2_47)
- TANG CQ, OHSAWA M (2002) Tertiary relict deciduous forests on a humid subtropical mountain, Mt. Emei, Sichuan, China. *Folia Geobotanica* 37: 93–106. <https://doi.org/10.1007/BF02803193>
- TANG CQ, YANG Y, OHSAWA M, MOMOHARA A, YI SR, ROBERTSON K, SONG K, ZHANG SQ, HE LY (2015) Community structure and survival of tertiary relict *Thuja sutchuenensis* (Cupressaceae) in the subtropical Daba Mountains, southwestern China. *PLoS One* 10: e0125307. <https://doi.org/10.1371/journal.pone.0125307>
- TANG CQ, MATSUI T, OHASHI H, DONG YF, MOMOHARA A, HERRANDO-MORAIRA S, QIAN S, YANG Y, OHSAWA M, LUU HT, GROTE PJ, KRESTOV PV, LEPAGE B, WERGER M, ROBERTSON K, HOBOM C, WANG CY, PENG MC, CHEN X, WANG HC, SU WH, ZHOU R, LI S, HE LY, YAN K, ZHU MY, HU J, YANG RH, LI WJ, TOMITA M, WU ZL, YAN HZ, ZHANG GF, HE H, YI SR, GONG H, SONG K, SONG D, LI XS, ZHANG ZY, HAN PB, SHEN LQ, HUANG DS, LUO K, LÓPEZ-PUJOL J (2018) Identifying long-term stable refugia for relict plant species in East Asia. *Nature Communications* 9: 4488. <https://doi.org/10.1038/s41467-018-06837-3>
- TATEWAKI M, ITO K, TOHYAMA M (1965) Phytosociological study of the forests of Japanese Larch (*Larix leptolepis* Gordon). *Research Bulletins of the College Experiment Forests Hokkaido University* 24: 1–176. (in Japanese with English abstract).
- TOMARU N, UCHIYAMA K, TAMAKI I, SAKAGUCHI S (2022) Genetic diversity and population genetic structure of forest tree species in Japan. Japanese Society of Forest Genetics and Tree Breeding, Hitachi. (in Japanese).
- UCHIYAMA K, FUJII S, TSUYAMA I, TANAKA N, SETSUKO S, KIMURA MK, NAKAO K, MATSUI T, TSUMURA Y (2023) Range shift and introgression of three Japanese *Abies* species: insights from population genetic data and species distribution modeling. *Tree Genetics & Genomes* 19: 41. <https://doi.org/10.1007/s11295-023-01617-7>

- WALKER LR, SHIELS AB (2012) Landslide ecology. Cambridge. <https://doi.org/10.1017/CBO9780511978685>
- WANG Y, RUHSAM M, MILNE R, GRAHAM SW, LI J, TAO T, KNOWLES LL, MAO K (2022) Incomplete lineage sorting and local extinction shaped the complex evolutionary history of the Paleogene relict conifer genus, *Chamaecyparis* (Cupressaceae). *Molecular Phylogenetics and Evolution* 172: 107485. <https://doi.org/10.1016/j.ympev.2022.107485>
- WORTH JR (2019) Current distribution and climatic range of the Japanese endemic conifer *Thuja standishii* (Cupressaceae). *Bulletin of the Forestry and Forest Products Research Institute* 18: 275–288. [https://doi.org/10.20756/ffpri.18.3\\_275](https://doi.org/10.20756/ffpri.18.3_275)
- YAMADA R, KARIYA Y, KIMURA T, SANO M, LI Z, NAKATSUKA T (2018) Age determination on a catastrophic rock avalanche using tree-ring oxygen isotope ratios—the scar of a historical gigantic earthquake in the Southern Alps, central Japan. *Quaternary Geochronology* 44: 47–54. <https://doi.org/10.1016/j.quageo.2017.12.004>
- YAMAMOTO S, MORIYAMA M (1997) Stand structure and the regeneration of *Chamaecyparis pisifera* (Sieb. et Zucc.) Endl. on sites with different soil development in an old-growth coniferous forest, central Japan. *Journal of Forest Research* 2: 133–140. <https://doi.org/10.1007/BF02348210>

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