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Identifying characteristics of post-landslide habitats and potential native herbaceous species for revegetation after landslides across Taiwan

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ABSTRACT: In Taiwan, using exotic plants for landslide revegetation has sparked concerns over biological invasion. This study focuses on identifying native herbaceous species suitable for landslide revegetation across Taiwan. We analyzed environmental factors of post-landslide habitats (PLHs) island-wide and developed a classification system with 20 habitat types, which were organized by elevation (0–3,100 m) and aspect. A preliminary list of 319 species with potential for landslide revegetation was established with three sources: revegetation guidebooks, field studies, and expert questionnaires. These species were refined to 42 native species by excluding exotics and less-mentioned or -abundant species. Many of these native species were characterized by traits of long-distance dispersal, heat, and drought tolerance, which can promote plant establishment and survival in PLHs. To determine species suitable for the 20 identified PLHs, we used GIS to segment Taiwan into these habitat categories and assessed the presence frequency of the 42 species across them. The analysis indicated that the number of suitable species decreases with elevation, with a shift towards temperate species at higher altitudes, while the aspect had minimal impact on species suitability. This suggests that elevation is a key determinant in selecting appropriate species for revegetation. Our study developed a systematic method for compiling a native species list for Taiwan's varied PLHs, highlighting the importance of native plant diversity in sustainable landslide recovery and ecosystem restoration, while reducing the risks of biological invasions by minimizing the use of exotic species.

KEY WORDS: Environmental stress, herbaceous plants, landslide, native plants, revegetation, restoration.

INTRODUCTION

The increasing frequency of rain-induced landslides, driven by climate change, has intensified not only the loss of life and economic damage but also the destruction of ecosystems and habitats (Huggel *et al.*, 2012; Rianna *et al.*, 2016; Sangelantoni *et al.*, 2018; Niculiţă, 2020; Picarelli *et al.*, 2021). Vegetation is essential for stabilizing slopes, controlling erosion, and mitigating sediment-related disasters (Walker *et al.*, 1996; Burri *et al.*, 2009). Fast-growing, adaptable herbaceous ground covers are particularly effective for landslide revegetation, reducing erosion and surface runoff (Gray and Sotir, 1996; Adekalu *et al.*, 2007; Hou *et al.*, 2020). Consequently, countries like Japan, the United States, and New Zealand often use exotic herbaceous species to speed up vegetation recovery (Basher, 2013; Morgan *et al.*, 2014; Kondo *et al.*, 2016).

However, the widespread use of exotic species poses risks to native ecosystems (Hale *et al.*, 2016). Due to their higher seed vitality and density, exotic species can become invasive, negatively affecting soil properties, carbon storage, and biological cycles (Ehrenfeld, 2003; Tamura and Tharayil, 2014; Aerts *et al.*, 2017). In regions like the western United States, Hawaii, and Brazil, exotic species invasions have increased wildfire frequency and intensity, worsening climate change (Hoffmann *et al.*, 2004; Bradley *et al.*, 2006; Litton *et al.*, 2008). Climate change further promotes invasive traits, raising competition for native species (Seager *et al.*, 2007; Hellmann *et al.*, 2008).

Although native plants may not be as effective as some exotics in revegetation, they pose fewer economic and ecological risks (Schmitz and Simberloff, 1997; Cardinale *et al.*, 2012; Palmgren *et al.*, 2015). Native species integrate more smoothly with local ecosystems, reducing the need for fertilizers and pest management, and exhibit long-term resilience in harsh post-landslide conditions (Hawkes *et al.*, 2007; Scotton and Andreatta, 2021; Balestrini *et al.*, 2024). Furthermore, using native species can lower the carbon footprint of revegetation efforts (Shelef *et al.*, 2017; Acevedo *et al.*, 2021). Due to the high price, low availability, and slow growth of native herbaceous species, along with limited research, exotic species have been widely used for landslide revegetation in Taiwan. Consequently, current plant lists are often based on subjective observations (Landis *et al.*, 2005; Bischoff *et al.*, 2010; Ladouceur *et al.*, 2018).

This study presents a comprehensive meta-analysis of vegetation habitat characteristics related to landslides across Taiwan, utilizing available data to understand the environmental stresses of landslides and categorize post-landslide habitats (PLHs). A list of native herbaceous species suitable for revegetation (NHS_{LR}) was compiled

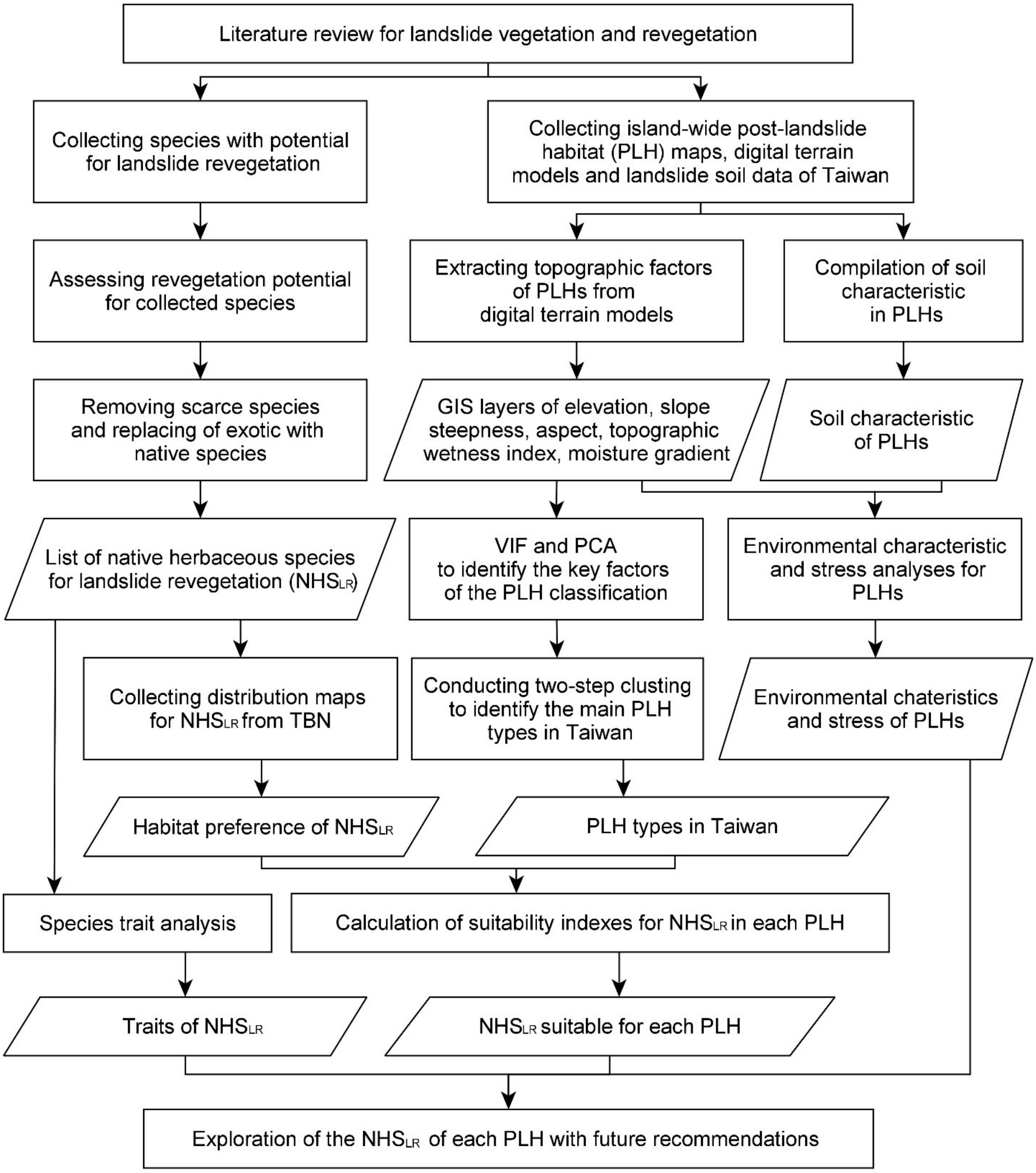


Fig. 1. Flowchart of the research process for native herbaceous species for landslide revegetation. The flowchart outlines the key stages in analyzing native herbaceous species for landslide revegetation.

from plant guidebooks, vegetation from landslide site surveys, and expert questionnaire surveys (Fig. 1). These species' characteristics and suitability across different PLHs were evaluated to offer valuable references for vegetation management in Taiwan.

MATERIAL AND METHODS

Study area

The study area is located in Taiwan, on the western side of East Asia, within the transition zone from tropical to subtropical climates (Fig. 2). It has an average annual

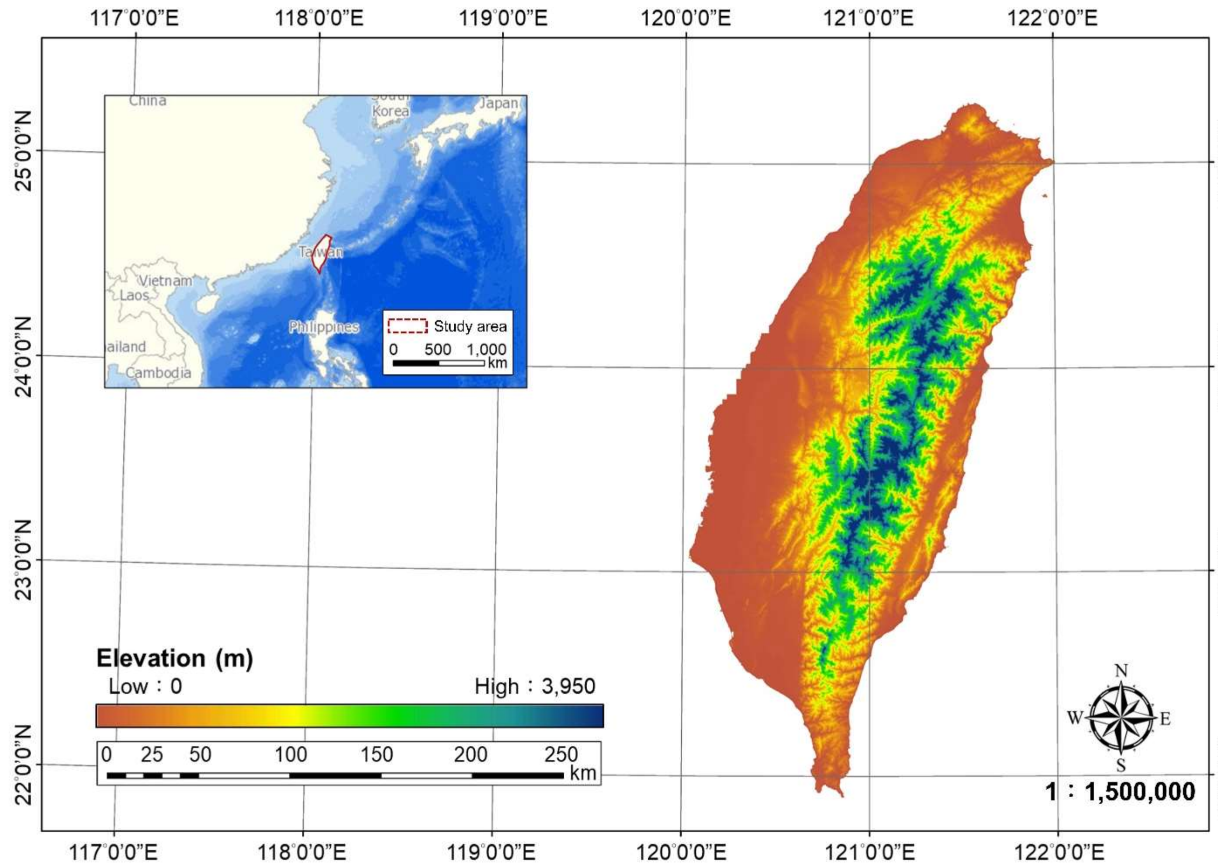


Fig. 2. The study site of this study, Taiwan, located in the western Pacific between 21.89 °N– 25.29 °N latitude and 120.0 °E–121.9 °E longitude, is in the transition zone between tropical and subtropical climates. The elevation ranges from sea level to 3,950 m.

temperature of 24.1°C and annual precipitation of 2,244.6 mm (2022 Meteorological Bureau data). The region is affected by yearly typhoons, with heavy rainfall being a primary cause of landslides. Additionally, Taiwan's position along the Pacific Ring of Fire results in frequent seismic activity, leading to rough, steep terrain with elevations ranging from sea level to 3,950 m, contributing to frequent landslides (Lee, 2017).

Classification of PLHs in Taiwan

In this study, the term "post-landslide habitat" (PLH) refers to the environmental factors influencing plant growth in the post-landslide habitat. To classify Taiwan's PLHs by environmental characteristics, we reviewed the literature and applied principal component analysis (PCA) (Dunteman, 1989) and two-stage cluster analysis (Milligan and Sokol, 1980). Environmental factors affecting plant growth were categorized as topographical and soil-related (Gairola *et al.*, 2011; Zeng *et al.*, 2014; Yanyan *et al.*, 2017). Plant growth and survival in landslides are mainly influenced by microclimate rather than regional climate (McClean *et al.*, 2005; Pinto *et al.*, 2020; De Frenne *et al.*, 2021). Consequently, factors in our analyses only included topography factors (elevation, slope steepness, aspect, terrain wetness index (TWI), and soil factors (soil thickness, texture, pH, organic matter, hardness).

Topographical data for PLHs was obtained by overlaying six years of landslide maps (2007, 2009, 2011, 2013, 2015, 2017) (Liu *et al.*, 2019) with 20-meter grid digital terrain models (DTMs) provided by Taiwan's Ministry of the Interior (MOI, Taiwan, 2024). Soil data, including texture, pH, organic matter, and hardness, were compiled from studies at 100 landslide sites (Table 1). Soil factors were excluded from PLH classification because prior research indicates that topographical factors related to temperature and moisture have a stronger influence on plant composition (Jiang *et al.*, 1994; Yang, 1997). Additionally, soil data were excluded from the PLH classification due to their low spatial autocorrelation and the impracticality of site-specific sampling (Yang, 1997; Yang and Lee, 2005).

To avoid multicollinearity among factors, we conducted a variance inflation factor (VIF) analysis, which confirmed no collinearity among the five topographic factors. This allowed us to proceed with PCA to identify the primary environmental factors distinguishing landslide habitats. Subsequently, we applied a two-stage clustering analysis to pinpoint additional key factors and further classify PLHs.

Table 1. Post-landslide habitat (PLH) environmental factors analyzed in the study.

Type of factor	Environmental factors	Analysis and extraction	Method references
Topography factors	Elevation Slope steepness Aspect	Overlay existing landslide areas with DTM data for extraction.	ESRI ArcGIS (1999)
	Terrain wetness index (TWI)	Analysis based on slope steepness factor.	Wilson and Gallant (2000)
	Moisture gradient	Analysis based on aspect factor.	Day and Monk (1974)
Soil factors	Thickness	Analysis based on slope steepness factor.	Wang *et al.* (2009)
	Texture	Compilation of information from soil investigations in 100 landslides documented in the literature.	Shirazi and Boersma (1984)
	pH value		Schofield and Taylor (1955)
	Organic matter		Schnitzer and Khan (1975)
	Hardness		Yamanaka and Matsuo (1962)

*The topographic factors "elevation," "slope steepness," and "aspect" were derived from the 2007, 2009, 2011, 2013, 2015, and 2017 landslide maps provided by Liu *et al.* (2019), combined with the Ministry of the Interior's DTM analysis.

Developing a list of native herbaceous species for landslide revegetation (NHS_{LR})

We compiled a list of 319 herbaceous species with potential for landslide revegetation from three main sources: 11 plant guidebooks, vegetation data from 186 landslide sites surveyed over less than five years, and suggestions from a questionnaire involving 52 experts (Table S1). We developed two indices: "adduce frequency," representing the number of sources recording each species, and "adduce accumulated value," which scores species based on guidebook frequency, field dominance, and expert recommendations to assess the significance of each data source. These scores were normalized, summed, and averaged. Species with an adduce frequency ≥ 2 and adduce accumulated value ≥ 25% were considered high potential for revegetation. To integrate both indices, we created the application potential index (API). Since each index represents a different meaning, they were each given a weight of 50% in the API calculation. The exotic species were replaced with the same genus species native to the list of 319 or removed, resulting in the final list of native herbaceous species for landslide revegetation (NHS_{LR}).

Trait analyses for species in the NHS_{LR} list

We summarized the traits of NHS_{LR} by gathering species-specific data from various sources, including previous studies, websites, and plant specimen databases. This data encompassed factors such as climate zone, family, photosynthetic pathways, life span, drought tolerance, soil nutrient tolerance, seed type, primary seed dispersal mode, and the number of seed dispersal modes.

By laying the presence records of every NHS_{LR} in the Taiwan Biodiversity Network (TBN) on the GIS environmental layer of annual average temperature provided by the Taiwan Climate Change Projection Information and Adaptation Knowledge Platform (TCCIP), the annual mean temperature for every presence record was obtained. With such data, the temperature niche and Species Temperature Index (STI) for each NHS_{LR} were identified (Sparrius *et al.*, 2018; de Azevedo *et al.*, 2023). Furthermore, we used the 10^{th} and 90^{th} percentiles of temperatures as the upper and lower limits for the survival of each NHS_{LR} (Jezkova and Wiens, 2016).

Identifying native species for revegetating specific PLH ($NHS_{1\text{-}20}$)

To assess the suitability of NHS_{LR} for different PLHs, we used a "suitability index" that quantifies the effectiveness of each NHS_{LR} species within each PLH based on presence records. We extracted NHS_{LR} distribution data from the TBN database and associated these records with island-wide GIS layers for key environmental factors, as identified in Section 2.2 of the study. Presence records for each NHS_{LR} were categorized by PLH type, creating a matrix that shows occurrences of each NHS_{LR} across different PLHs. This matrix was normalized by dividing each value by the maximum value and converting it to a 0–100% scale.

To account for habitat size bias, where smaller habitats may have fewer records, each suitability index value was further adjusted by dividing it by the area percentage of the corresponding habitat in Taiwan. This adjustment ensures that the suitability index accurately reflects habitat suitability regardless of habitat size. Each $PLH_{1\text{-}20}$ in this study corresponds to NHS_{LR} species denoted as $NHS_{1\text{-}20}$.

$$Suitability\ index_{ij} = \frac{Number\ of\ presence\ records\ of\ species_i\ in\ PLH_j}{The\ maximum\ number\ of\ presence\ records\ in\ the\ PLH-by-species\ matrix} \times \frac{The\ area\ of\ the\ PLH_j}{The\ total\ area\ of\ all\ PLHs} \times 100\%$$

All suitability index values in the matrix were pooled and sorted in ascending order. Using the six value ranges of the Braun-Blanquet (1932) classification system, the suitability index values were classified as follows: extremely suitable (> 99^{th}), highly suitable ($99-95^{th}$), very suitable ($95-75^{th}$), suitable ($75-50^{th}$), potentially suitable ($50-25^{th}$), and ever recorded for landslide revegetation (< 25^{th}).

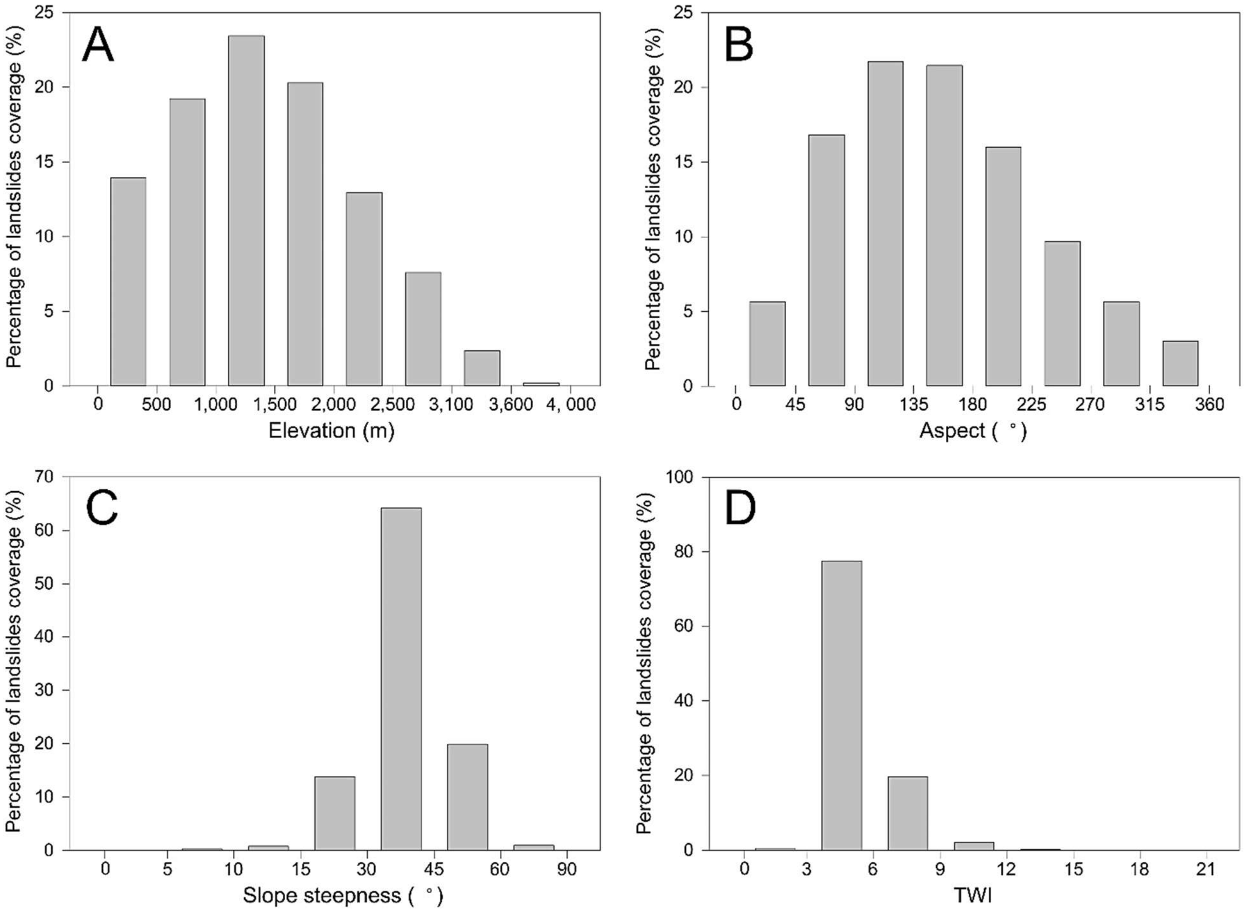


Fig. 3. PLH frequency across different topography factors categories in Taiwan. **A.** Elevation. **B.** Aspect. **C.** Slope steepness. **D.** TWI.

Exploration of NHS$_{1–20}$ with future recommendations

After determining the suitability levels for each NHS$_{1–20}$ and analyzing NHS$_{LR}$ traits, findings will be presented with heat maps (Wilkinson and Friendly, 2009) to visually show suitability variations across different PLHs for each NHS$_{LR}$. Additionally, the Bray-Curtis dissimilarity index (Bray and Curtis, 1957) will be used to assess species composition similarity among PLHs with different environmental characteristics, focusing on NHS$_{LR}$ species rated as "suitable" or above.

Finally, recommendations for the practical application of native herbaceous species in landslide vegetation management and climate change adaptation will be provided, offering guidance for future landslide management and research.

RESULTS

Environmental factors of PLHs

GIS analyses of topographic features show that about 80% of PLHs occur below 2,000 m, with the highest proportion in the 1,000–1,500 m range (≈25%), followed by 500–1,000 m and 1,500–2,000 m. PLHs above 3,100 m are rare (≈2.5%). Landslide occurrence increases with elevation, peaking around 1,500 m before declining, indicating that most PLHs in Taiwan are found between 500–2,000 m. The aspect of PLHs predominantly fell within the east-to-south direction. The moisture gradient was roughly in the range of 5, 7, 9, and 11 (≈ 60%) (Fig. 3B, 4). Slope steepness most frequently ranged between 15–60°, with 30–45° being the most common (≈ 65%) (Fig. 3C). The Terrain Wetness Index (TWI) derived mostly ranged from 3–6 (Fig. 3D), reflecting generally dry environments of PLHs. Moreover, due to steep slopes, PLHs often have shallow soils, averaging around 0.5 meters in depth.

Soil analysis from 100 landslide sites showed that 55% of soils in PLHs were sandy loam, slightly acidic with pH values of 5.5 to 7.0. Organic matter varied widely (SD=10.92), averaging under 20%, indicating low organic content. PLHs also had loose surface soil with a hardness of about 10–15 mm.

Classification of PLHs in Taiwan

The PCA biplot (Fig. 5A) and scree plot (Fig. S1) indicate that the PLH principal components can be grouped into three categories: elevation, aspect, and slope-related factors. The eigenvalue and loadings of PC1

Table 2. Environmental factors differentiating PLHs in Taiwan.

PLH type	Elevation classification (m)	*Average temperature (˚C)	Aspect classification (˚)	*Moisture gradient
Type 1	< 500	> 23	175–250	1–4
Type 2			100–175	5–8
Type 3			250–355	9–12
Type 4			355–100	13–16
Type 5	500–1,000	20–23	175–250	1–4
Type 6			100–175	5–8
Type 7			250–355	9–12
Type 8			355–100	13–16
Type 9	1,000–1,500	17–20	175–250	1–4
Type 10			100–175	5–8
Type 11			250–355	9–12
Type 12			355–100	13–16
Type 13	1,500–2,000	14–17	175–250	1–4
Type 14			100–175	5–8
Type 15			250–355	9–12
Type 16			355–100	13–16
Type 17	2,000–3,100	8–14	175–250	1–4
Type 18			100–175	5–8
Type 19			250–355	9–12
Type 20			355–100	13–16

*Based on the two-stage cluster analysis, Taiwan's PLH can be classified by combining elevation and aspect, according to Su's (1984) and Day and Monk's (1974) criteria.

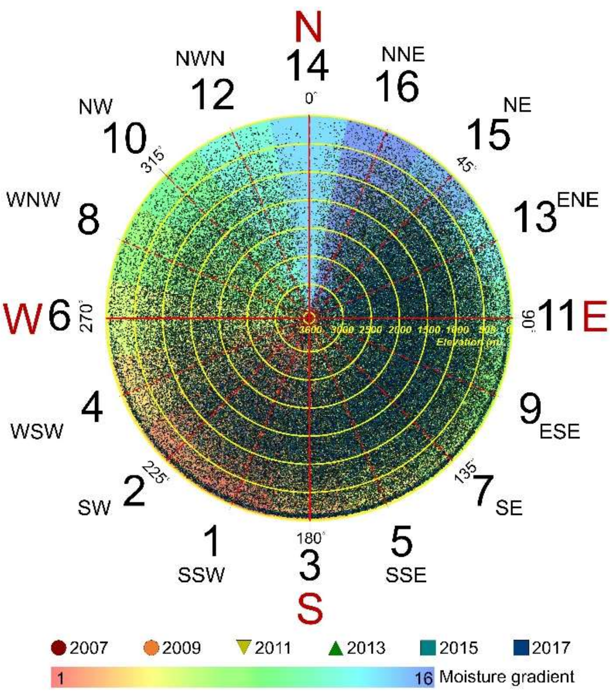


Fig. 4. Distribution of PLH in Taiwan along the gradients of elevation and moisture gradient. The yellow circles represent elevations, while the red lines represent moisture gradients.

emphasize elevation as the most significant factor (Table S2). Based on these results, we first applied clustering to landslide samples by elevation, resulting in five elevation groups (Table S3). These groups align closely with Su's (1984) vegetation zone classification, so we adopted Su's 500 m intervals to define five elevation categories: 0–500 m, 500–1,000 m, 1,000–1,500 m, 1,500–2,000 m, and 2,000–3,100 m.

To ensure elevation did not overshadow other variables, we further refined the classification and conducted PCA for each elevation range to better understand the contributions of slope steepness, aspect, moisture gradient, and TWI (Fig. 5B). The results indicate that below 1,000 m, slope steepness and TWI are the most influential factors, though their impact decreases with elevation. In contrast, aspect and moisture gradient have minimal influence at lower elevations but become significantly more impactful as elevation rises, particularly around 1,000 m. The second clustering stage within each elevation group identified four aspect-based subgroups, ranging from dry to wet: 175–250° (extremely dry), 100–175° (moderately dry), 250–355° (dry), and 355–100° (wet). Therefore, by combining these five elevation and four aspect groups, Taiwan's PLHs were divided into 20 distinct types (Table 2).

The NHS$_{LR}$ list in Taiwan

A list of 319 species was obtained with three data sources. After excluding species with adduce frequency < 2 and adduce accumulated value < 25%, 69 species (58 genera, 17 families) with high potential for landslide revegetation were identified, including 38 native species and 31 exotic species. Four of these exotic species (*Chloris gayana*, *Conyza canadensis*, *Bidens pilosa* var. *pilosa*, and *Zoysia japonica*) were replaced with native species (*Chloris barbata*, *Conyza japonica*, *Bidens pilosa*

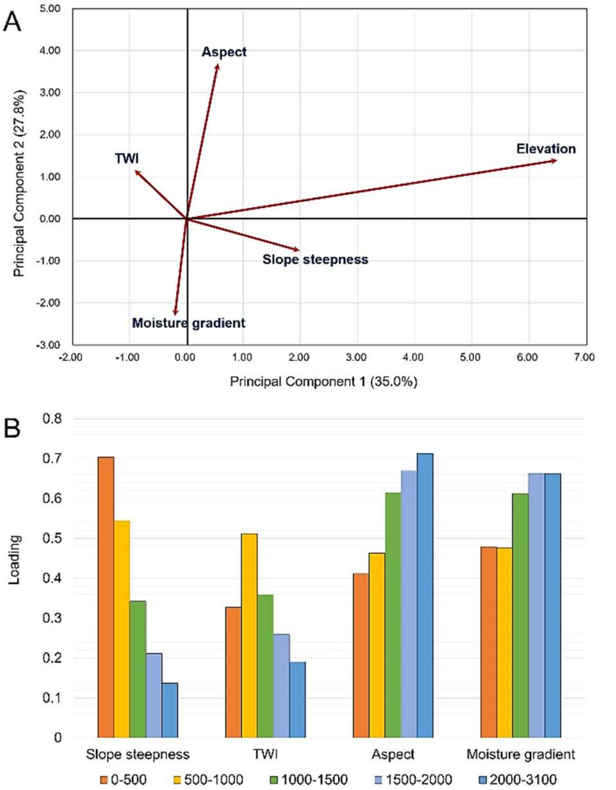


Fig. 5. PCA of PLH topographic factors: The biplot shows that elevation strongly influences PC 1, explaining 35.0% of the variance. Aspect mainly contributes to PC 2, explaining 27.8% of the variance. The PCA1 absolute loadings in PLH elevation groups show the trend of the other topographic factors. **A.** PCA biplot for PLH topographic factors (PC 1 vs. PC 2). **B.** PCA1 absolute loadings in PLHs of elevation groupings.

var. *minor*, and *Zoysia matrella*) respectively (Table S4). Ultimately there were 42 species (41 genera, 17 families) in the NHS_{LR} list (Table 3).

Species composition and species traits of NHS_{LR}

The NHS_{LR} is dominated by Poaceae (43%), followed by Asteraceae, Polygonaceae, Cyperaceae, and Commelinaceae (Fig. 6A). Tropical species make up the largest portion of NHS_{LR} (48%), with 31% originating from dry tropical regions (Fig. 6B). C4 plants represent nearly half (45%) of NHS_{LR} (Fig. 6C), and herbaceous perennials (71%) are the main life form, adapted to the harsh PLH conditions. Most NHS_{LR} species show drought tolerance (79%) and resistance to nutrient deficiency (76%) (Fig. 6D, E, F). Dispersal is primarily through caryopses and achenes, allowing for animal and wind dispersal, with 50% of species using multiple methods to increase reproductive success (Fig. 6G, H, I).

The temperature adaptability of NHS_{LR} is primarily within the 20–24 °C range, with limits of 18 and 25 °C (Fig. 7). C3 species display broader temperature adaptability, while C4 species are better suited to high temperatures. Temperate herbaceous species generally have a wider adaptability range, but subtropical species like *Arundo formosana* and *Nephrolepis cordifolia* show higher API and adaptability. Moreover, C4 species with high API, such as *Miscanthus floridulus* and *Arundo formosana*, have broader temperature adaptability, making them suitable for various PLH types.

Evaluation of NHS_{LR} suitability and species composition across different PLHs

The suitability of NHS_{LR} species across different PLH types shows significant variability. A total of 697 suitability indices were computed based on the distribution records of 42 NHS_{LR} species in the TBN, following islandwide classification standards for PLHs. The highest suitability index was observed for *Eleusine indica* in PLH_3 and the lowest for *Miscanthus transmorrisonensis* in PLH_4. These indices were normalized and classified using Braun-Blanquet's percentage method, with cumulative percentages of 99%, 95%, 75%, 50%, and 25% corresponding to indices of 51.96, 27.47, 10.60, 3.04, and 0.84. These six suitability indices were used for classifying suitability and generating heatmaps (Table 3 & S6).

In the line graphs and bar charts of NHS_{LR} species rated as "suitable" or above for each PLH type, the suitability and numbers of NHS_{LR} decrease with increasing elevation (Fig. 8A), while aspect has no significant effect. Bray-Curtis analysis reveals marked differences in species composition across elevations (similarity < 0.7), particularly between low ($NHS_{1–4}$) and high ($NHS_{17–20}$) elevations (similarity < 0.4), while mid-elevations ($NHS_{5–12}$) show greater similarity (similarity > 0.6). Among PLHs within the same elevation but different aspects, species similarity is high (similarity > 0.8), indicating that aspect does not significantly influence species suitability.

NHS_{LR} classification based on Su's (1984) vegetation zones highlights elevation's importance in species suitability. While suitable NHS_{LR} species and STI vary significantly with elevation, aspect exhibits minimal variation (Fig. 8). Simultaneously, the suitable NHS_{LR} for PLHs in Taiwan can be broadly categorized into four types: (1) Dry tropical zones below 500 m ($PLH_{1–4}$), dominated by heat- and drought-tolerant C4 species; (2) Subtropical zones from 500–1,500 m ($PLH_{5–12}$), featuring adaptable species from subtropical and tropical regions; (3) Warm temperate zones from 1,500–2,000 m ($PLH_{13–16}$), with species adapted to warm summer and cold winters; and (4) Cool temperate zones above 2,000–3,100 m ($PLH_{17–20}$), characterized by species adapted to consistently low temperatures.

DISCUSSION

Environmental characteristics and stresses of PLHs

Environmental stresses in PLHs, such as extreme temperature, soil moisture, and nutrient levels, are strongly

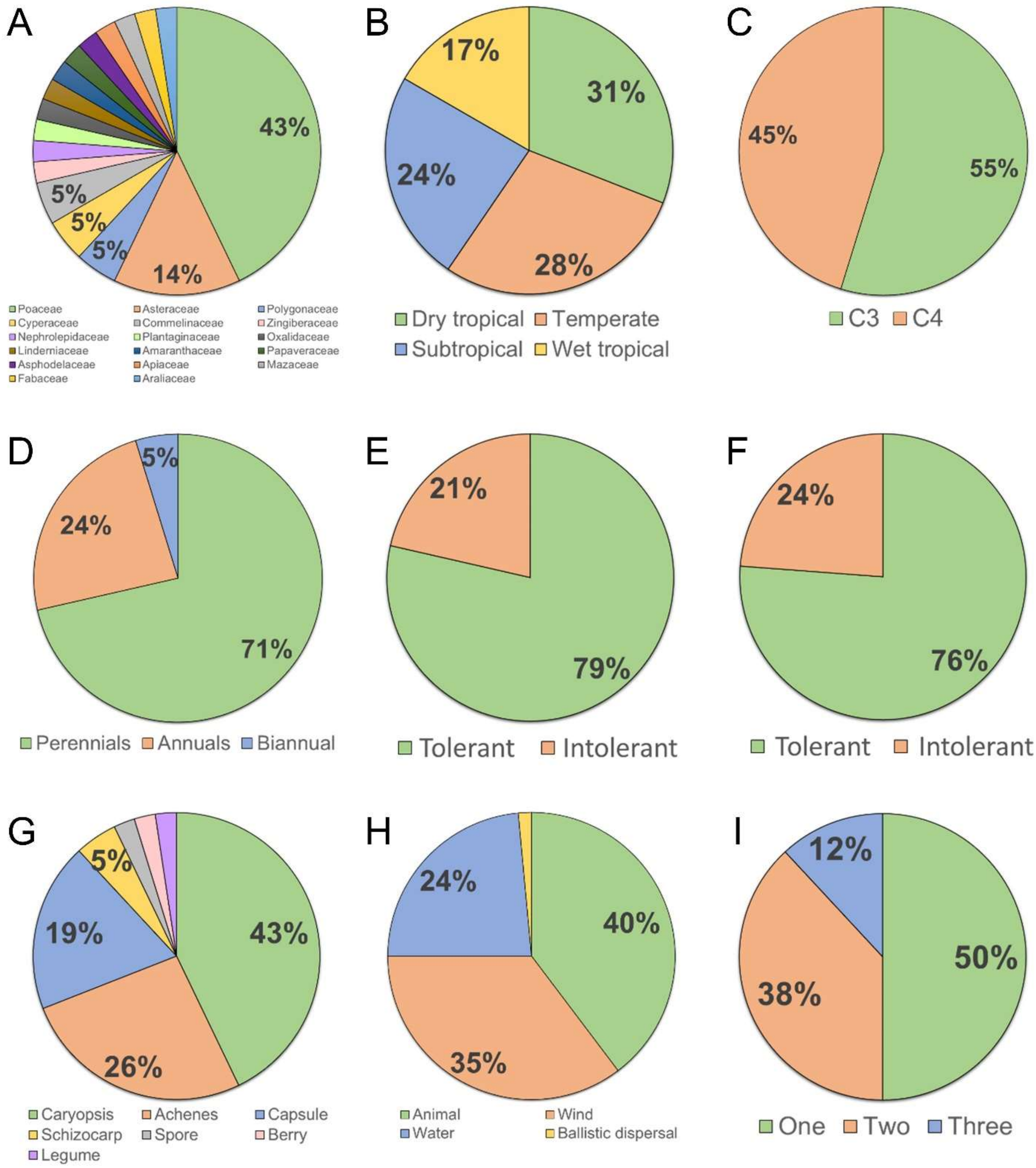
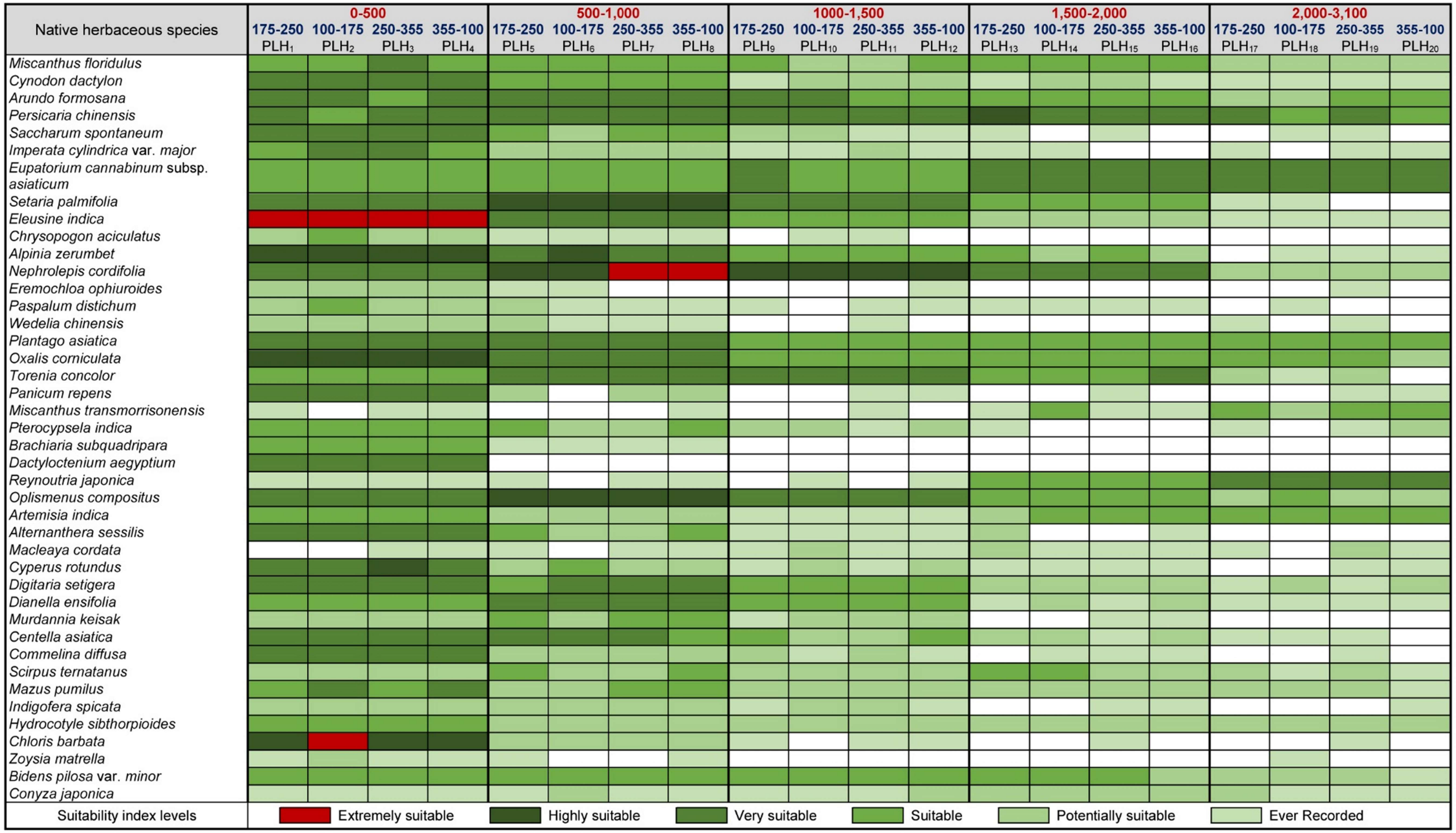


Fig. 6. Species composition and traits of NHS_{LR}. Panel A is based on data obtained from TaiCOL (https://taicol.tw/zh-hant/api). Panel B utilizes data sourced from Kew's Plants of the World Online database (https://powo.science.kew.org/). Panel C draws on data provided by Sage (2017). Panels D, G, H, and I are informed by data from relevant books and botanical websites. Panels E and F are derived from data published in peer-reviewed papers and reputable websites. **A.** Family. **B.** Climate zone. **C.** C3 or C4 plant. **D.** Life cycle. **E.** Drought tolerance. **F.** Tolerance to low soil nutrients. **G.** Fruit type. **H.** Dispersal method. **I.** Number of dispersal method

Table 3. Heatmap of NHS_{LR} for each PLH.



*The empty cell indicates that there is no record in the TBN database. The table shows that NHS_{LR} suitability varies across PLHs, with some adapting to multiple PLHs and others concentrated in specific ones. For the complete raw data of the heat map, please refer to Table S6.

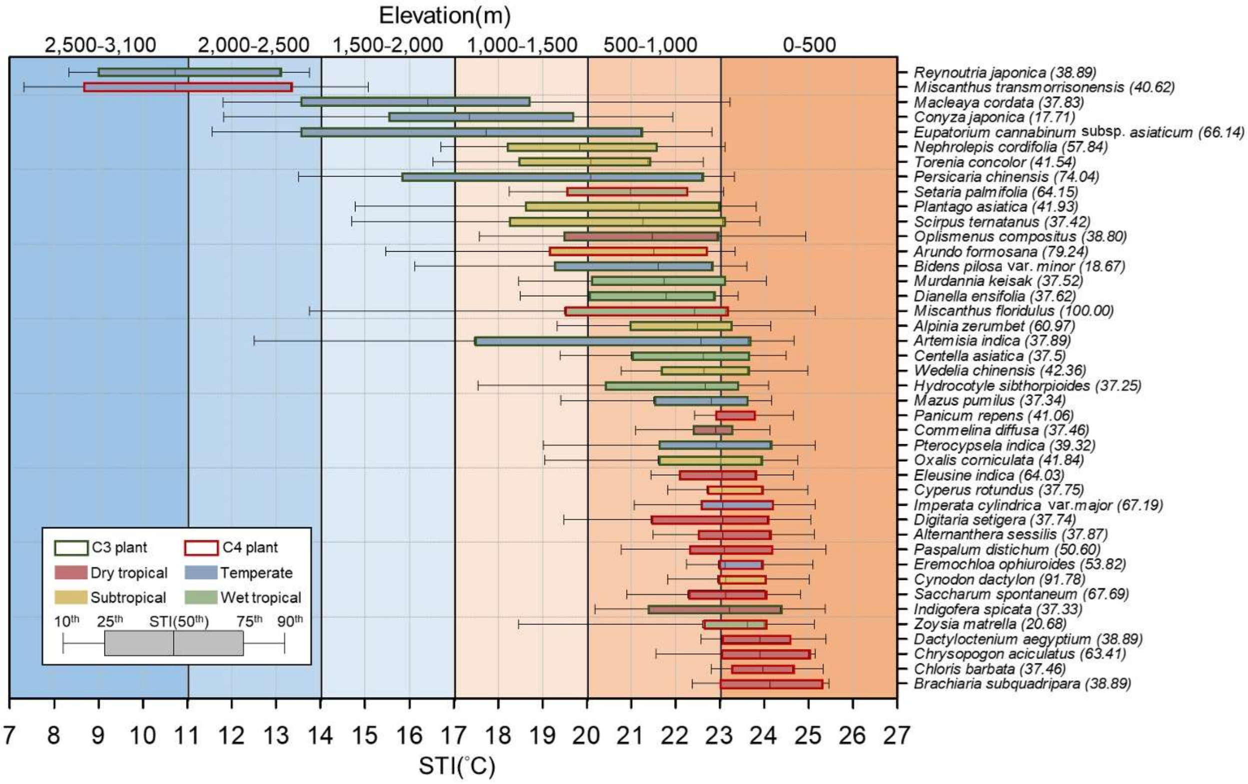


Fig. 7. Temperature niche and STI of NHS_{LR}. The 10th, 25th, median, 75th, and 90th percentiles represent the minimum survival temperature, suitable low temperature, suitable temperature (STI), suitable high temperature, and maximum survival temperature for species growth. The numbers in parentheses after each species represent the API.

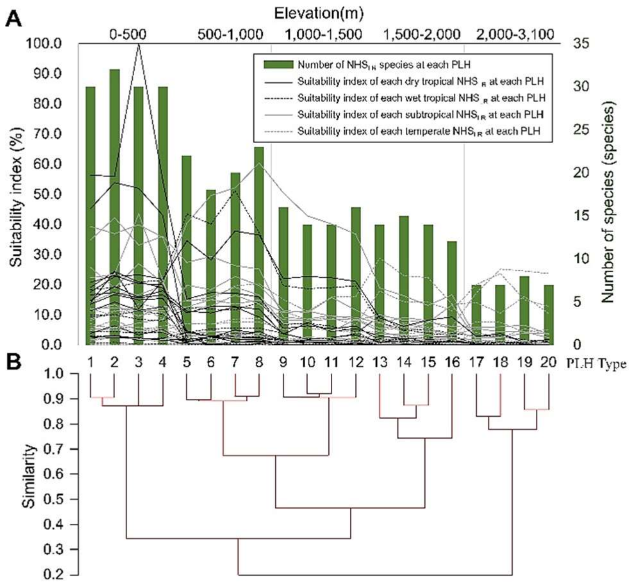


Fig. 8. Species number, suitability index and species composition similarity of native herbaceous species suitable for revegetating specific PLHs. Bars indicate the number of herbaceous species in each PLH whose API level reaches "suitable." The lines represent the suitability index of 42 NHS_{LR} for different PLHs. **A.** Number and suitability index of each NHS_{LR} at each PLH. **B.** The compositional similarity of suitable NHS_{LR} within each PLH.

influenced by topography and geomorphology (Dalling and Tanner, 1995; Fetcher *et al.*, 1996; Yang *et al.*, 2023). These factors interact, creating complex stresses for plants (Wang *et al.*, 2003; Harfouche *et al.*, 2014). Among these, temperature and moisture are crucial for plant growth and survival in landslide habitats (Hodges, 1991; Akıncı and Lösel, 2012; Hatfield and Prueger, 2015).

Environmental stresses in PLHs, such as extreme temperature, soil moisture, and nutrient levels, are strongly influenced by topography and geomorphology (Dalling and Tanner, 1995; Fetcher *et al.*, 1996; Yang *et al.*, 2023). These factors interact to create complex stresses for plants (Wang *et al.*, 2003; Harfouche *et al.*, 2014). Among these, temperature and moisture are crucial for plant growth and survival in landslide habitats (Hodges, 1991; Akıncı and Lösel, 2012; Hatfield and Prueger, 2015). Elevation indirectly influences plant distribution and growth by altering temperature, light exposure, and atmospheric pressure (Körner, 2007; Habibi and Ajory, 2015; Wani *et al.*, 2023). As elevation increases, temperatures drop, causing significant diurnal temperature and humidity changes (Ohmura, 2012). Elevation also affects solar radiation, evapotranspiration, and humidity. Mid-to-high elevations, despite cloud forests, face water stress due to lower overall humidity (Hsieh *et al.*, 2007; Duane *et al.*, 2008; Gheyret *et al.*, 2020). Since 62.96% of Taiwan's landslides occur between 500 to 2,000 m, the associated temperature drops and humidity fluctuations at these elevations impose significant stress on plant growth and survival.

While aspect does not directly influence plant growth, it affects vegetation through sunlight exposure and evaporation on slopes (Mohammad, 2008; Huang *et al.*, 2015; Yang *et al.*, 2020). In the northern hemisphere, south-facing slopes experience more sunlight, higher temperatures, and faster evaporation, reducing soil moisture and affecting soil microorganisms, nutrients, and texture (Mohammad, 2008; Huang *et al.*, 2015; Yang *et al.*, 2020). Fig. 4 shows that PLHs fall into a relatively dry moisture gradient, leading to water stress for plants.

Slope steepness influences plant growth by affecting soil stability and moisture. In Taiwan, slopes of common landslide materials (e.g. sandy loam, gravel) range from 28.7–44.7°, with PLHs averaging 38 ± 8.86° (Wang *et al.*, 2013). Slopes below 30° are conducive to plant establishment, while slopes between 35–65° often require human intervention for successful growth. Slopes over 60° make plant growth challenging, even with aid (Wang *et al.*, 2020). Steep slopes lead to soil erosion, nutrient loss, and restricted root systems, indirectly stressing plant growth (Pimentel and Kounang, 1998; Mishra *et al.*, 2022). Soils lacking vegetation cover result in the loss of organic matter and structural degradation, consequently leading to loose and unstable soil (Chang *et al.*, 2014; Chalise *et al.*, 2019). Steep slopes also hinder rainwater retention, exacerbate moisture deficiency, and contribute to the extremely dry TWI (Meles *et al.*, 2020).

Influence of variables in elevation-based classifications on PLH

The influence (PCA loading) of other topographical factors on PLHs varies significantly across elevation groups. Slope steepness is a key factor at lower elevations, while aspect becomes more important at higher elevations. At lower elevations, slopes are gentler but steepen with increasing elevation, enhancing their influence (Montgomery, 2001). However, beyond a certain elevation, slope steepness no longer increases, reducing its impact. As shown in Fig. S2, PLHs below 500 m have a slope steepness range of 20–35°, resulting in greater variation and stronger influence. In contrast, PLHs above 1,000 m show less variation, with slope steepness between 30–45°, reducing their effect. Since TWI is derived from slope, it follows a similar pattern, peaking between 500–1,000 m due to the nonlinear conversion process.

Aspect, while less significant at lower elevations, becomes more influential above 1,000 m. At lower elevations, PLHs cover larger areas with minimal aspect variation (Stage and Salas, 2007). As elevation increases, aspect variation grows, amplifying its impact. According to Fig. S2, PLHs below 500 m mostly face southwest (120–220°), but at higher elevations, PLHs are distributed across more aspects. Since the moisture gradient is based on aspect, it closely follows its trends. These findings suggest that in low-elevation PLHs, slope steepness variation should be considered for plant selection (Chiatante *et al.*, 2002), while in mid-to-high-elevation, it is necessary to include the influence of aspects (Burnett *et al.*, 2008; Moeslund *et al.*, 2013).

Species composition and traits of NHS_{LR}

Poaceae is the most dominant plant family in PLHs, comprising 43% of the NHS_{LR} (Fig. 6A), due to its adaptation to dry and arid conditions. Although individual Poaceae species may have narrow STI adaptation ranges (Fig. 7), the family is globally distributed, from deserts to polar regions (Ziegler *et al.*, 1981; Tzvelev, 1989; Gallaher *et al.*, 2022). Seventeen of 18 Poaceae species in NHS_{LR} are C4 plants, accounting for 40% of the total species (Table S5). C4 photosynthesis in Poaceae enhances CO_2 utilization, allowing survival in arid environments (Zhang and Kirkham, 1995; Wand *et al.*, 1999; Rangan *et al.*, 2022). Asteraceae, the second-largest family of angiosperms, is evolutionarily advanced and mainly found in subtropical and temperate regions (Abraham and Thomas, 2016; Mitra and Mukherjee, 2017; Xu *et al.*, 2017). Some Asteraceae species modify their tissues and cells to minimize water loss, adapting to arid environments (Martorell and Martínez-López, 2014; Ferraro and Scremin-Dias, 2017; Cowie *et al.*, 2020). As shown in Table 3, species like *Eupatorium cannabinum* subsp. *asiaticum*, *Wedelia chinensis*, and *Pterocypsela indica* thrive in low-elevation PLHs. Fabaceae, the third most dominant family, copes with infertile soils through nitrogen fixation (EL Sabagh *et al.*, 2020; Girmay *et al.*, 2020; Ramos *et al.*, 2020). Due to these traits, Poaceae, Asteraceae, and Fabaceae dominate secondary succession areas globally, including landslides, burnt areas, and clearcut regions, playing key roles in revegetation and habitat restoration (Calle *et al.*, 2013; de Moraes *et al.*, 2016; Neto *et al.*, 2017; Chen *et al.*, 2022). Other families like Polygonaceae, Amaranthaceae, and Cyperaceae also dominate landslides and barren lands, indicating their revegetation potential (Figueiredo-Ribeiro, 1986; Kalapos *et al.*, 1997; Wang *et al.*, 2022).

Perennial species dominate NHS_{LR} due to their ability to reproduce asexually and survive unfavorable seasons (Fig. 6D). They spread effectively through vegetative organs like rhizomes, tubers, and roots, aiding colonization in landslide areas (Ito, 1992; Roumet *et al.*, 2006; Ringselle *et al.*, 2021). At the same time, NHS_{LR} demonstrates strong drought resistance and tolerance to nutrient-poor conditions (Fig. 6E, F) (Volaire, 2003; Toker *et al.*, 2007; Vaughn *et al.*, 2011), making them suitable for revegetating harsh habitats (Wagle, 1981; Velázquez and Gómez-Sal, 2007; Saito *et al.*, 2022).

NHS_{LR} seeds are primarily hard and dry caryopsis

(43%), achenes (26%), and capsules (19%) (Fig. 6G). Seed size, morphology, and dispersal methods are influenced by different habitats (Hernandez *et al.*, 2023). Caryopsis seeds are protected by lemmas and paleas, making them resistant to external disturbances, and facilitate wind dispersal (Thomasson, 1985; Gossen *et al.*, 1998; Benvenuti, 2007). Achenes, with protective bracts and seed coats, can thrive in harsh environments, and enhance wind dispersal efficiency (Andersen, 1992; Gutterman and Ginott, 1994; Mandel *et al.*, 2019). Capsules disperse seeds using the twisting force of drying seed coats or rain splashing, allowing them to colonize remote habitats (Beattie and Lyons, 1975; Nakanishi, 2002; Fukano *et al.*, 2023). Due to the aridness of PLHs, animal dispersal is limited, making wind the primary seed dispersal method (35%) (Fig. 6H) (Lehouck *et al.*, 2009; Swemmer *et al.*, 2018). Nevertheless, due to caryopsis and achenes small size, can still disperse and spread even without animal-mediated dispersal (Hensen and Muller, 1997).

Based on NHS_{LR}'s STI (Fig. 7) and the suitability index for each PLH (Table 3), NHS_{LR} species exhibit varying degrees of specialization and generalization in response to different PLHs. Ecologically, species are categorized as specialists with narrower niches, or generalists with broader ecological tolerances (Levins, 1968). Specialists have stronger environmental resistance in specific regions but are less adaptable to change and less capable of dispersing across diverse habitats (Brouat *et al.*, 2004; Boulangeat *et al.*, 2012). Generalists, while less suited to extreme environments, thrive in diverse habitats, showing strong competitiveness and population expansion under common conditions (Southwood, 1988; Slatyer *et al.*, 2013; Denelle *et al.*, 2020).

Elevation is the primary factor influencing NHS_{LR} adaptability in PLHs (Fig. 5A). Certain specialists like *Imperata cylindrica* var. *major*, *Eleusine indica*, and *Dactyloctenium aegyptium* exhibit high suitability at specific elevations but have limited adaptability (Table 3 & S6). In contrast, generalists like *Miscanthus floridulus*, *Arundo formosana*, *Persicaria chinensis*, and *Eupatorium cannabinum* subsp. *asiaticum* have broader STI and higher suitability indices. Therefore, species with broader ecological niches and generalist traits are more suitable for landslide revegetation (Richmond *et al.*, 2005; Büchi and Vuilleumier, 2014; Gya *et al.*, 2023).

NHS_{LR} in different PLHs types

According to the environmental filtering hypothesis, species without traits to survive under certain environmental stresses might be eliminated from local habitats (Kraft *et al.*, 2015). In the extreme conditions of landslides, NHS_{LR} often shows resistance to dryness and barren soils (Alonso-Amelot, 2008; Rathore *et al.*, 2022). A decrease in the suitability index, species count, and herbaceous species diversity as elevation increases (Fig. 8A), consistent with previous studies (Tranquillini, 1964; Rahbek, 1995; Dierig *et al.*, 2006). Lower temperatures at higher elevations limit plant growth, with most physiological processes occurring optimally between 15–30°C (Went, 1953). Data from TCCIP show that at elevations above 1,500 m, the annual average temperature is 13.8 ± 3.4°C. Consequently, NHS_{LR} suitability at elevations above 1,500 m is less than half that of low elevations (Fig. 8A). On the other hand, although aspect influences solar radiation and evapotranspiration, species composition and suitability did not significantly vary by aspect within the same elevation zones (Fig. 8B). Thus, while Fig. S2 illustrates that slope and aspect may vary with elevation, their influence on the suitability of NHS_{LR} remains insignificant.

In Taiwan's low-elevation PLHs (0–500 m), tropical herbaceous species dominate, especially those adapted to dry tropical conditions (Fig. S3). Additionally, the species numbers in $NHS_{1–4}$ are significantly higher than in $NHS_{5–20}$. Tropical climate zones are divided into dry and humid tropics based on rainfall distribution and seasonality (Murphy and Bowman, 2012). Dry tropical regions, with limited and unpredictable rainfall, support sparse tree canopies and continuous herb layers (Beard, 1955; Pfadenhauer *et al.*, 2020), while humid tropical regions have dense vegetation due to consistent rainfall (Ratnam *et al.*, 2011). Although Taiwan is in the subtropical zone, low-elevation PLHs are quite arid, creating hot and dry habitats (Chiang, 2004). As a result, $NHS_{1–4}$ mainly consists of heat-resistant and drought-tolerant species, such as *Eleusine indica* and *Chloris barbata* (Singh and Singh, 1967; Rojas-Sandoval, 2018) (Table 3). These species are restricted to habitats with temperatures above 21°C, explaining the low similarity (<0.4) between $NHS_{1–4}$ and $NHS_{5–20}$ (Fig. 8B).

With an increase in elevation to 500–1,500 m, NHS_{LR} gradually transitions from tropical to subtropical herbaceous species (Fig. S3). Subtropical climates experience pronounced seasonal variations, greater temperature fluctuations, and are influenced by monsoons and high atmospheric pressure (Corlett, 2013). Plants in these regions have stronger environmental resilience, such as broader temperature tolerance, enabling them to adapt to various habitats (Campbell *et al.*, 1996; Schuldt *et al.*, 2012). Consequently, the STI ranges of many subtropical herbaceous species span 500–1,500 m ($PLH_{5–12}$) (Fig. 7), explaining the high species composition similarity (>0.6) among NHS_{LR} in these PLHs (Fig. 8B). This also aligns with Su's (1984) classification of the 500–1,500 m elevation range as a single vegetation zone.

As elevation continues to rise to 1,500–2,000 m, PLHs transition from a subtropical to a warm temperate climate. Compared to temperate regions, this climate zone features warmer summers with longer growing seasons and colder, drier winters, limiting plant growth (Kira, 1945; Box and Fujiwara, 2015). In Taiwan, habitats above 1,800 mare in the cloud zone, where humidity increases due to horizontal precipitation, and solar radiation decreases (Hamilton, 1995; Jarvis and Mulligan, 2011; Hsu, 2015). Consequently, $NHS_{13–16}$ consists mainly of subtropical herbaceous species, but the presence of temperate species increases with cooler temperatures and higher humidity, while tropical species decline (Fig. S3). This explains the distinct difference in suitable species (< 0.5) between $NHS_{13–16}$ and $NHS_{5–12}$ (Fig. 8B).

At the higher elevations of 2,000–3,100 m, PLHs transition to temperate or cool temperate climate, where temperate species dominate, with a few subtropical species like *Plantago asiatica* and *Oxalis corniculata* adapting to the colder temperatures. The average temperature in this zone (8–14°C) is below the optimal range for most plants, resulting in a significant species richness reduction in $NHS_{17–20}$ (Fig. 8A). Low temperatures and limited light hinder tropical and subtropical species' growth (Long *et al.*, 1983; Baker *et al.*, 1988), which explains the low similarity (< 0.2) between $NHS_{17–20}$ and other PLHs (Fig. 8B). However, some C4 species, such as *Miscanthus transmorrisonensis* and *Miscanthus floridulus*, can rapidly increase their photosynthetic capacity in short-term temperature rises and exposure to sunlight to enhance their cold resistance (Beale *et al.*, 1996; Jiao *et al.*, 2017). This phenomenon aligns with Su's (1984) vegetation zone classification.

Since the PLH subgrouping in this study only covers elevations between 0 and 3,100 m, the recommended NHS_{LR} species in Table 3 may not apply to landslides above 3,100 m. However, preliminary research suggests only a few species, like *Sedum morrisonense*, *Festuca ovina*, and *Deschampsia flexuosa*, are present in early-stage landslide succession above 3,100 m (Chen *et al.*, 2022). Additionally, based on the analysis of landslide characteristics (Fig. 3A), landslides above 3,100 m in Taiwan account for less than 3% of the total, making them relatively rare cases.

CONCLUSION

Further research on the practical application and adaptability of NHS_{LR} in landslide areas is crucial for maximizing their role in soil and water conservation. With rising temperatures and increasing extreme rainfall due to climate change, drought stress in PLHs and landslide frequency are expected to rise. The species traits of NHS_{LR} can help guide the selection of suitable species for revegetation in high-elevation or high-latitude areas. Utilizing these species for ecosystem restoration in landslide-affected areas offers potential benefits for biodiversity and ecological sustainability. While this study has identified key NHS_{LR} traits that allow survival in PLHs, further exploration is needed on seed production and the economic viability of large-scale revegetation. Given the variability of environmental factors across different PLH types, on-site seeding and germination experiments are vital to confirm plant growth and revegetation success. Mastering these techniques will enhance soil conservation and disaster management, providing broader environmental and societal benefits.

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