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Characteristics and dynamics of *Alnus nepalensis* dominated forests in the subtropical region of Yunnan, southwestern China

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ABSTRACT: *Alnus nepalensis* is a deciduous broad-leaved tree species. It commonly appears in patchy distributions following the destruction of evergreen broad-leaved forests or the abandonment of agricultural land in the subtropical region of Yunnan, southwestern China. This versatile and ecologically important tree species plays a crucial role in the environment. Studying its community characteristics and succession trends is vital for understanding diverse forest types and secondary succession in the subtropical areas. Through our field vegetation investigation, we identified six forest types, i.e., 1: *Alnus nepalensis* deciduous broad-leaved forest; 2: *Alnus nepalensis-Schima wallichii* deciduous and evergreen broad-leaved mixed forest; 3: *Alnus nepalensis-Pinus armandii* deciduous broad-leaved and evergreen coniferous mixed forest. 4: *Alnus nepalensis-Litsea monopetala* deciduous and evergreen broad-leaved mixed forest. 5: *Alnus nepalensis-Quercus aliena-Pinus yunnanensis* deciduous broad-leaved and evergreen coniferous mixed forest. 6: *Alnus nepalensis-Quercus delavayi* deciduous and evergreen broad-leaved mixed forest. Among the six forest types, the Shannon-Wiener diversity ranged from 1.1 to 2.1. In all the forest types, *A. nepalensis* trees were predominantly found in DBHs of 10-30 cm with ages of ca. 10-30 years. Its maximum age reached ca. 95 years with a DBH of 132 cm. In central Yunnan, the successional pathways: transitioning from *Alnus nepalensis-Quercus aliena- Pinus yunnanensis* deciduous broad-leaved or evergreen coniferous mixed forest, *Alnus nepalensis-Pinus yunnanensis-Quercus aliena* mixed forest, or *Alnus nepalensis* deciduous broad-leaved forest, gradually shifting to *Alnus nepalensis-Quercus delavayi* deciduous and evergreen broad-leaved mixed forest, and ultimately progressing to *Quercus delavayi* evergreen broad-leaved forest.

KEY WORDS: Forest types, forest structure, species diversity, population structure, secondary succession.

INTRODUCTION

Old-growth tropical forests are being extensively deforested and fragmented worldwide. Forest recovery through succession has led to an expansion of secondary forests in human-modified tropical landscapes (HMTLs). Secondary forests thus emerge as a potential repository for tropical biodiversity, and also as a source of essential ecosystem functions and services in HMTLs (Arroyo-Rodríguez *et al*., 2017). From a restoration perspective, a secondary forest has higher species diversity than shrubland or a plantation in subtropical regions (Tang *et al*., 2010, 2024).

Dynamics of plant communities occur in areas previously covered by forests, often on abandoned agricultural land, large-scale clear-cut areas, and sites affected by fire (Tang *et al*., 2010, 2013; Molles, 2016). Different types and timings of disturbances determine different succession pathways (Kurkowski *et al*., 2008). Natural or human disturbances often change land use patterns, thereby altering the vegetation types in an area (Sullivan *et al*., 2019; Osburn *et al*., 2021). When the native vegetation type in an area is destroyed or altered, a long-term process of vegetation recovery and succession ensues (Tang *et al*., 2010; Tang, 2015; Zhong *et al*., 2020; Wang *et al*., 2022). Currently, under the influence of human activities, the area of primary forests has significantly decreased, replaced by secondary forests growing after the destruction of native vegetation. Globally, changes in vegetation affect the climate and ecological environment (Walker and Wardle, 2014; Oliver *et al*., 2021), hence forest dynamics and succession has long been a focal point in the field of ecology.

Due to its unique topography and complex climatic conditions, Yunnan boasts a diverse range of vegetation types. However, since extensive development and logging had occurred to meet economic needs in the past. This has led to unprecedented destruction of primary evergreen broad-leaved forests, resulting in a drastic reduction in the subtropical area. In their place, secondary vegetation has formed after the destruction of the original forests. Yunnan's zonal forest vegetation includes tropical rainforests, subtropical evergreen broad-leaved forests, and temperate coniferous forests. However, Yunnan lacks deciduous broad-leaved forests equivalent to those in the northern regions of China. The deciduous broad-leaved forests in the subtropical region of Yunnan mainly consist of transitional patchy formations of deciduous broad-leaved forests that naturally formed during the secondary succession process following the destruction of evergreen broad-leaved forests or abandoned agricultural land. They are mainly distributed in low to mid-elevation mountainous, hilly, and sub-mountainous regions in Yunnan, ranging from 1000 to 3500 m above sea level. The dominant deciduous broad-leaved tree species include *Alnus nepalensis, Quercus aliena, Quercus variabilis, Quercus acutissima*, *Pinus yunnanensis* and *Betula alnoides*. *A. nepalensis* plays an important role in maintaining the stability of forest ecosystems, agroforestry ecosystems, and the sustainable development of forestry in subtropical regions (Xia *et al.*, 2023). *A. nepalensis* is found throughout the Himalayas, ranging from 500 to 3000 meters in elevation, extending from Pakistan and Nepal to northern India, Bhutan, Upper Burma, southwestern China, and Indochina (Winrock International, 2024). The species forms a symbiotic relationship with nitrogen-fixing *Frankia* bacteria in its root nodules, which enhances soil nitrogen content, improves soil fertility, and facilitates the establishment of other plant species that thrive in nitrogen-rich soils. This characteristic makes *A. nepalensis* a key early colonizer in degraded or nutrient-poor soils (Sharma *et al.*, 1998; Varghese *et al.*, 2003; Joshi and Garkoti, 2020). In the central Himalayas, *A. nepalensis* often forms pure stands, though it can also grow in association with species such as *Quercus leucotrichophora*, *Schima wallichii*, *Symplocos ramosissima*, and *Daphniphyllum himalayense* at various stages of forest succession following disturbance (Singh, 2014; Joshi and Garkoti, 2020; Balami *et al.*, 2023). *A. nepalensis* forests are a widely distributed and highly adaptable type of secondary deciduous broad-leaved forest in southwestern China (Chen *et al.*, 1995).

The forest communities containing *A. nepalensis* as the most dominant belong to patchy deciduous broad-leaved forests formed after the destruction of or human alteration to evergreen broad-leaved forests or montane rainforests, leading to fallow land or slash-and-burn cultivation in the subtropical region of Yunnan. This type of forest represents a stage in the secondary succession process that many forests are currently undergoing. Especially in the current subtropical region of Yunnan, the original distribution area of primary evergreen broad-leaved forests has sharply decreased. Understanding how pioneer communities transition to late successional communities is crucial for vegetation restoration and biodiversity conservation in evergreen broad-leaved forests. In spite of wide distribution, there is no data record and analysis for its forest types and there is little information on the ecology and dynamics of the forests dominated by *A. nepalensis*.

Our study aims to (i) conduct a comprehensive geographical investigation across the entire Yunnan Province, focusing on forests where *A. nepalensis* is the dominant species; (ii) classify and characterize the forest types in these regions; (iii) analyze the population structure of *A. nepalensis*; and (iv) test the hypothesis that *A. nepalensis* readily colonizes disturbed areas, facilitating the establishment of both coniferous and evergreen broad-leaved species, which in turn leads to the gradual transition towards a primary evergreen broad-leaved forest in central Yunnan.

METHODS

Study areas

We established 62 plots located in central, southern, western and eastern Yunnan (Fig. 1). The plot locations in detail and environmental characteristics are shown in Supplementary Table S1.

The climate of study areas is largely controlled in summer by the Indian Ocean monsoon. For the plot sites, the annual mean temperature is 5.4–20.6˚C. The mean temperature of the warmest month, July, is 9.8–25.1˚C and of the coldest month, January, is 0.4–13.6˚C. The annual mean precipitation is 797–1739 mm, and the evapotranspiration is 490–920 mm. The moisture index is 0.8-1. These data on the plot sites were extrapolated from the observed data during 50 years (1950–2000) of local climatological stations.

The main human disturbances include the conversion of primary evergreen broad-leaved forests to agricultural land, logging for timber or cutting for firewood. The natural disturbances are landslides.

Species

Alnus nepalensis is a deciduous tree with a straight trunk, up to 30 m in height and 60 cm (rarely to 2 m) in diameter. It is commonly known as Nepal alder, Indian alder, Himalayan alder, southwest alder, dry winter melon, alder, etc. Internationally, it is distributed in India, Sikkim, Bhutan, Nepal, China and Vietnam. In China, it is found in Tibet, Yunnan, Guizhou, southwestern Sichuan, and Guangxi, with a vertical altitude range of 400–3600 m (Zhou and Yang, 1988). Its bark is gray-brown, its leaves are ovate or long-elliptic, with both sides of the leaves green, the inflorescence is a panicle, and the fruit is a winged, obovate-elongated shape (Li *et al.*, 2008). It is a wind-pollinated plant, capable of spreading pollen and seeds with the help of wind. *A. nepalensis* is a fast-growing pioneer species of degraded lands and is moderately shade tolerant (Storrs and Storrs, 1984). It is a typical nitrogen-fixing tree species, commonly used in afforestation for maintaining or restoring soil fertility (Li *et al.*, 2022). Its wood is hard and widely used in furniture making, construction, and wood product processing. Additionally, this species is rich in tannins, flavonoids, and triterpenoids, which can be widely used in traditional medicine (Li *et al.*, 1999).

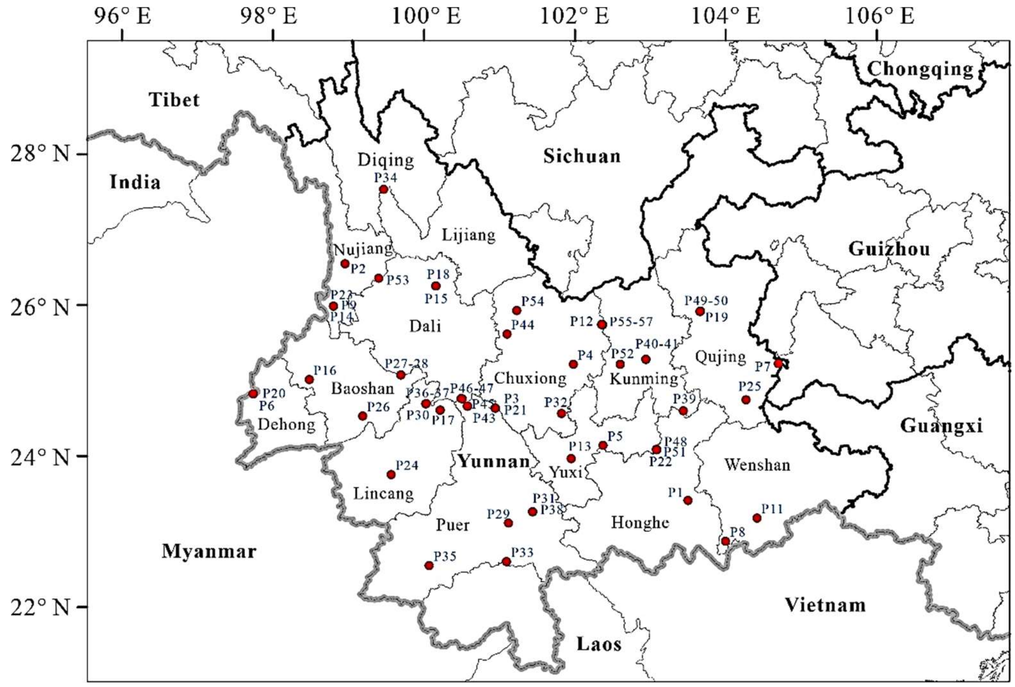

Fig. 1. Study areas and plot locations in Yunnan, southwestern China.

Data collection and analyses

Plots and subplots

We established 57 plots across various forests in Yunnan where *A. nepalensis* is the primary dominant species. Additionally, we set up two plots where *Quercus aliena* is the secondary dominant, and three plots of primary evergreen broad-leaved forests dominated by *Quercus delavayi* (formerly *Cyclobalanopsis delavayi*) in central Yunnan. From these, we selected 15 of the 57 plots as case studies to analyze succession dynamics. The 20 selected plots were chosen to be as similar as possible in terms of environmental variables and disturbance histories within central Yunnan.

The plot size is from 20 m × 20 m to 30 m × 20 m, based on the smallest area for the maximum number of species and the topography regarding the possibility to access. We divided each plot into subplots. The size of each subplot was 10 m × 10 m. For the species in each plot, all individuals at least 1.3 m tall were identified to species level, numbered and tagged, and their diameter at breast height (DBH) and height were recorded. In addition, general information about each plot was noted, such as slope position, altitude, slope exposure, slope inclination, as well as human disturbance history. Woody stems (≥ 1.3 m tall) in the overstory were classified into two categories based on their vertical position and height: arborous layer (height ≥ 5 m) and shrub layer (1.3 m ≤ height < 5 m tall). The arborous layer included canopy (height ≥ 15 m), subcanopy (5 m ≤ height < 15 m) sublayers. All woody species less than 1.3 m tall in the understory, each individual was identified to species level, counted, and measured for height and percent cover. We specifically noted microhabitats of *A. nepalensis* seedlings. Based on the classification on forest vertical layers, we elucidated forest stratification using the frequency distribution in height-classes of woody species (height ≥ 1.3 m).

In each plot, we set up five 1 m × 1 m squares selected for investigation for the herbaceous taxa in the understory. Five 1 m × 1 m squares were respectively located in the four corners and the center of each subplot. Herb taxa in the understory were identified and the coverage and number of individuals of each species were recorded.

Increment cores

We obtained 51 increment cores from *Alnus nepalensis* trees of varying DBHs in the study plots. For each tree trunk, a single increment core was taken from at 1.3 m above ground level. The length of time from the position at 1.3 m in height to ground level was estimated to be seven years based on the tree rings in the stem base of saplings with a height ≤ 1.3 m. The two years was added to the data of ages we obtained from each increment core. Tree age was determined using the software WinDENRO tree ring analysis system (Regent Instruments Inc., Canada). We used the data on ages and DBHs of the 51 tree samples to obtain a formula on correlation of ages and DBHs. Then we used the formula to calculate ages of *Alnus nepalensis* trees according to the measured DBHs of *Alnus nepalensis* trees in the study plots. From the tree ring analysis, we were also able to determine ring widths.

Data analyses

The classification of distribution area types for seed plant families and genera adopts Wu (1991, 2003).

For all woody individuals ≥ 1.3 m tall, DBH was used to calculate basal area and then basal area (BA) for each species found in a plot could be determined. To measure the abundance of species, we used relative importance value (RIV) = (Relative density + Relative basal area)/2 for species in the overstory, and RIV = (Relative density + Relative coverage)/2) for species in the understory (Tang *et al*., 2022). We used 20 plots including 15 of the 57 plots and the 5 additional plots (please see the subsection of plots above) in central Yunnan to analyze the plant community succession. Plant communities were classified using a floristic similarity dendrogram with Relative Euclidean and Ward's Method (McCune and Mefford, 2016). DCA (Detrended Correspondence Analysis) with the PC-ORD software (McCune and Mefford, 2016) was applied for studying on the secondary succession. Diversity indices were calculated for each forest stand using Shannon-Wiener's diversity index H′ and Pielou evenness index (Pielou, 1969), Simpson's diversity index D (Lande, 1996). Differences in species richness and diversity indices among forest types, were analyzed by the nonparametric Kruskal–Wallis all-pairwise comparisons test, using Analyse-it (version 5.11.3, Analyse-it Software, Ltd., 2019).

RESULTS

Floristic feature, forest types and stratification

The forests containing *Alnus nepalensis* as the 1st dominant were widely distributed in the subtropical region of Yunnan. Among 57 plots, there were 426 species belonging to 245 genera and 92 families.

Among the 236 genera of seed plants, they were classified into 12 distribution types and 10 variants, with the pantropical component being the most common, comprising 46 genera and accounting for 21.1%. This was followed by the north temperate distribution type, comprising 31 genera and accounting for 14.2%. The floristic composition of the forests is primarily tropical, with temperate elements being secondary, indicating a transitional nature from tropical to temperate regions (Table S2).

Cluster analysis of 57 plots identified six forest community types with a floristic similarity of approximately 74% (Fig. 2), and species composition is detailed in Tables S3-S5. Representative profiles for each type are shown in Fig. 3.

Forest Type 1: *Alnus nepalensis* deciduous broad-leaved forest. *A. nepalensis* dominated the canopy and subcanopy (RIV = 97.07%) with few associated species. The shrub layer featured *A. nepalensis* (25.16), *Colquhounia coccinea* var. *mollis* (RIV = 11.43%), and *Rubus alceifolius* (6.36%). The understory was dominated by *Ageratina adenophora* (28.86%) and *Pilea notata* (18.27%).

Forest Type 2: *A. nepalensis*-*Schima wallichii* deciduous and evergreen broad-leaved mixed forest. *A. nepalensis* (56.15%) dominated the canopy, with *S. wallichii* (12.14%) and other species in the subcanopy. The shrub layer included *Litsea martabanica* (5.96%) and *Ardisia thyrsiflora* (5.78%), while the understory featured *Ageratina adenophora* (10.27%) and *Oplismenus undulatifolius* (9.61%).

Forest Type 3: *A. nepalensis*-*Pinus armandii* deciduous broad-leaved and evergreen coniferous mixed forest. *A. nepalensis* (63.81%) dominated the canopy, co-dominating with *Pinus armandii* (30.33%) in the subcanopy. *Pyracantha fortuneana* (28.5%) dominated the shrub layer, while Achyranthes bidentata (16.01%) and *Ageratina* adenophora (11.01%) were common in the understory.

Forest Type 4: *A. nepalensis*-*Litsea monopetala* deciduous and evergreen broad-leaved mixed forest. *A. nepalensis* (39.9%) dominated the canopy, with a co-dominant *Litsea monopetala* (19.11%), along with other evergreen species. The shrub layer was dominated by *Hydrangea davidii* (25.5%), and the understory featured *Oplismenus compositus* (24.38%) and *Tetrastigma serrulatum* var. *puberulum* (8.39%).

Forest Type 5: *A. nepalensis*-*Quercus aliena*-*Pinus yunnanensis* mixed forest. *A. nepalensis* (41.9%) and *Quercus aliena* (14.68%) dominated the canopy, with co-dominance in the subcanopy. Rhododendron decorum (38.74%) was dominant in the shrub layer, and *Carex baccans* (9.24%) and *Pachysandra axillaris* (8.91%) were common in the understory.

Forest Type 6: *A. nepalensis*-*Quercus delavayi* mixed forest. *A. nepalensis* (44.25%) and *Quercus delavayi* (23.76%) dominated the canopy, with *Pinus yunnanensis* (11.42%) in the subcanopy. The shrub layer was dominated by young *A. nepalensis* (27.28%) and *P. yunnanensis* (15.75%), while *Urtica fissa* (39.26%) and *Ageratina adenophora* (22.76%) were common in the understory.

Overall, *A. nepalensis* forests were widespread in Yunnan at altitudes of 1450–2590 m a.s.l., often appearing along roadsides and farmland edges, where human disturbance is high. These forests, which mixed with species of *Quercus*, *Schima*, and *Pinus*, were mainly found in less disturbed, protected areas in central and southwestern Yunnan. *Ageratina adenophora*, an invasive species, dominated the understory in Types 1-4, indicating habitat disturbance.

A. nepalensis and its typical forests and their habitats are shown in Fig. 4.

Species diversity

Among the six forest types, the average species richness, the Shannon-Wiener diversity, Simpson diversity and Pielou evenness ranged between 7–15, 1.1–2.1, 0.45–0.81, 0.62–0.81, respectively (Fig. 5). For species richness, forest Type 1 (*Alnus nepalensis* deciduous broad-leaved

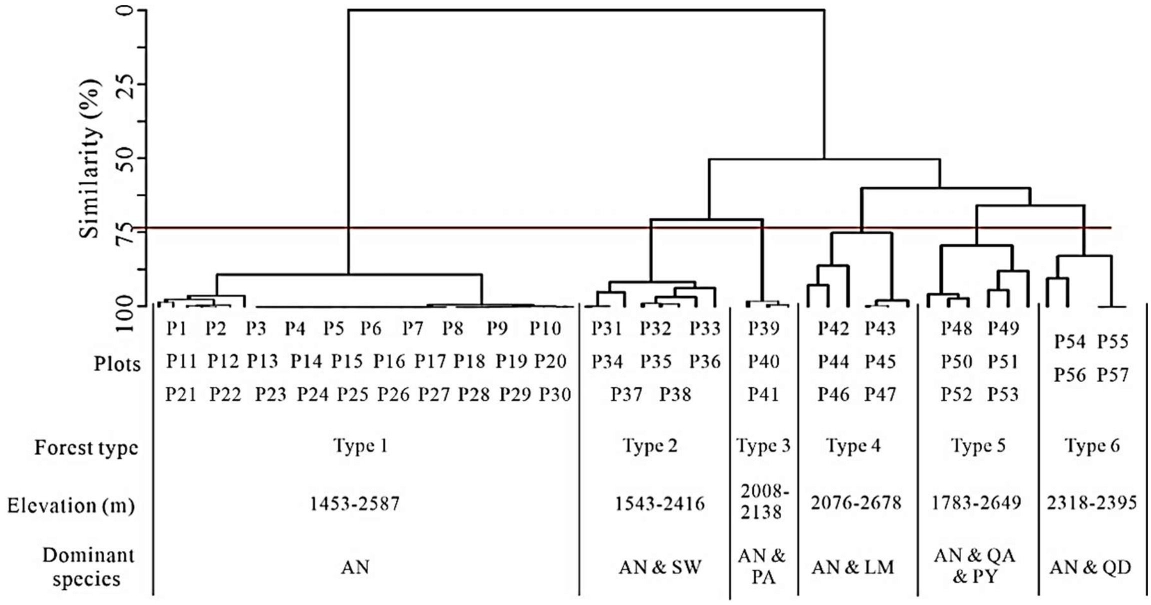

Fig. 2. Cluster analysis of the 57 plots. **AN**: *Alnus nepalensis*; **SW**: *Schima wallichii*; **PA**: *Pinus armandi*; **LM**: *Litsea monopetala*; **QA**: *Quercus aliena*; **PY**: *Pinus yunnanensis*; **QD**: *Quercus delavayi.* **Type 1**: *Alnus nepalensis* deciduous broad-leaved forest; **Type 2**: *Alnus nepalensis-Schima wallichii* deciduous and evergreen broad-leaved mixed forest; **Type 3**: *Alnus nepalensis-Pinus armandii* deciduous broad-leaved and evergreen coniferous mixed forest; **Type 4**: *Alnus nepalensis-Litsea monopetala* deciduous and evergreen broad-leaved mixed forest; **Type 5**: *Alnus nepalensis-Quercus aliena-Pinus yunnanensis* deciduous broad-leaved and evergreen coniferous mixed forest; **Type** 6: *Alnus nepalensis-Quercus delavayi* deciduous and evergreen broad-leaved mixed forest.

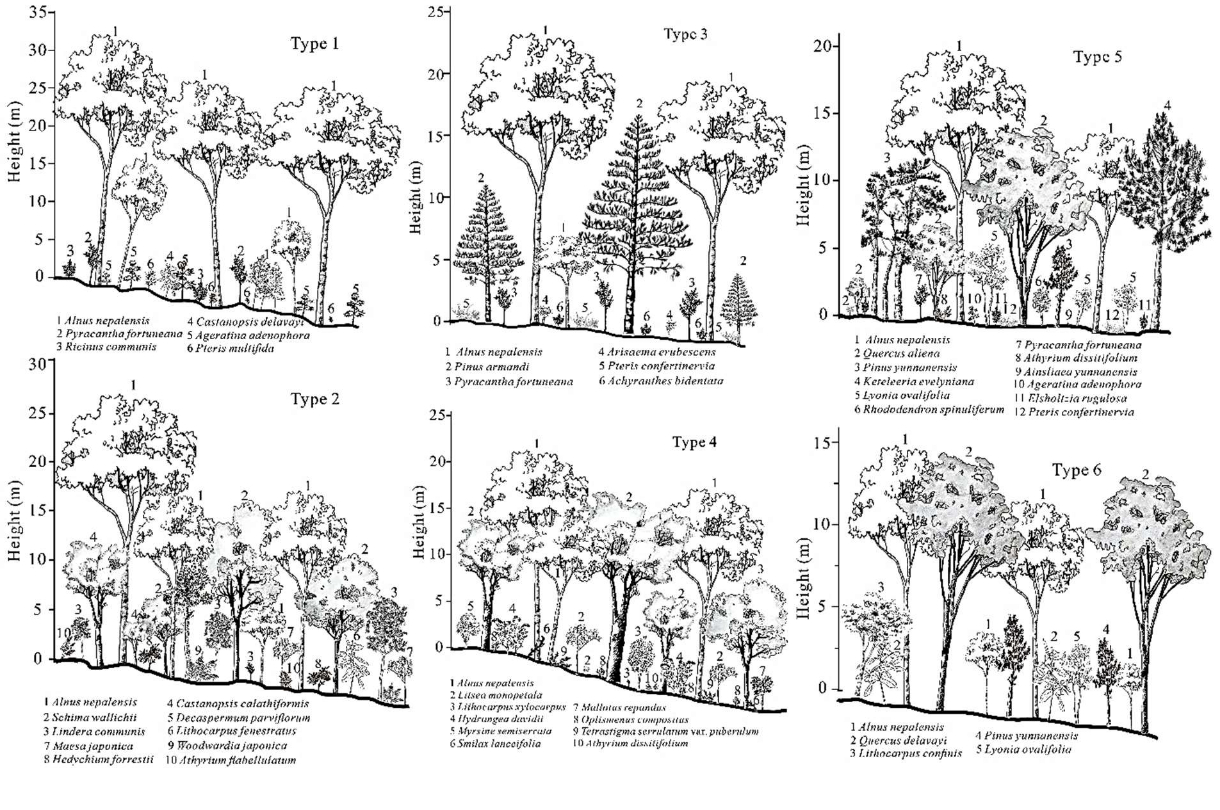

Fig. 3. Representative forest profile of each forest type. **Type 1**: *Alnus nepalensis* deciduous broad-leaved forest; **Type 2**: *Alnus nepalensis-Schima wallichii* deciduous and evergreen broad-leaved mixed forest; **Type 3**: *Alnus nepalensis-Pinus armandii* deciduous broad-leaved and evergreen coniferous mixed forest. **Type 4**: *Alnus nepalensis-Litsea monopetala* deciduous and evergreen broad-leaved mixed forest; **Type 5**: *Alnus nepalensis-Quercus aliena-Pinus yunnanensis* deciduous broad-leaved and evergreen coniferous mixed forest; **Type 6**: *Alnus nepalensis-Quercus delavayi* deciduous and evergreen broad-leaved mixed forest.

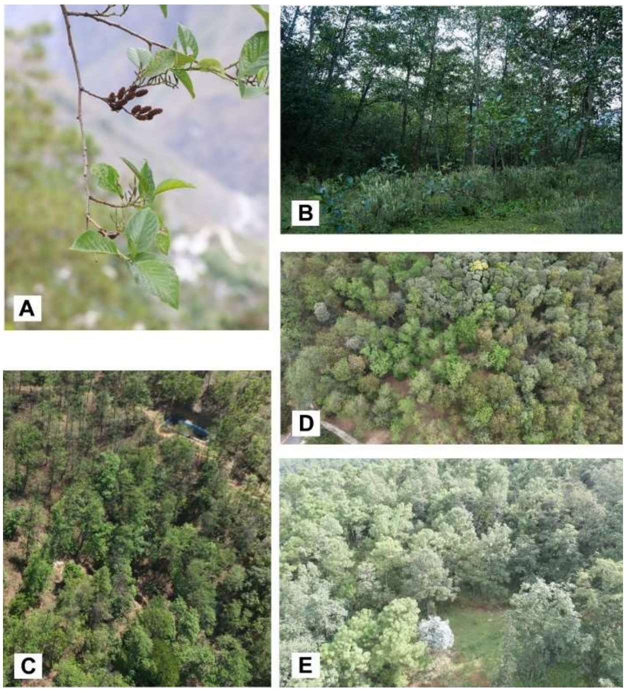

Fig. 4. ***Alnus nepalensis*** and its representative forest stands and habitats. **A.** Leaves and mature fruits of *Alnus nepalensis*; **B.** An *Alnus nepalensis* forest; **C-D.** A mixed forest of *Alnus nepalensis* and evergreen broad-leaved tree species including *Quercus delavayi* etc. **E.** A mixed forest dominated by *Alnus nepalensis* and coniferous *Pinus armandi*.

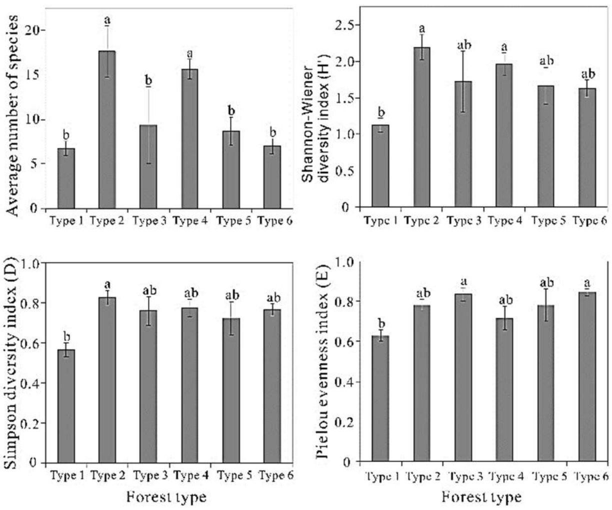

Fig. 5. Woody species (height ≥ 1.3 m) diversity of each forest type. Forest types with different letters mean significantly different, sharing the same letters do not differ significantly by the non-parametric Kruskal-Wallis all-pairwise comparisons test ($p < 0.05$). Bar: Standard deviation. **Type 1**: *Alnus nepalensis* deciduous broad-leaved forest; **Type 2**: *Alnus nepalensis-Schima wallichii* deciduous and evergreen broad-leaved mixed forest; **Type 3**: *Alnus nepalensis-Pinus armandii* deciduous broad-leaved and evergreen coniferous mixed forest; **Type 4**: *Alnus nepalensis-Litsea monopetala* deciduous and evergreen broad-leaved mixed forest; **Type 5**: *Alnus nepalensis-Quercus aliena-Pinus yunnanensis* deciduous broad-leaved and evergreen coniferous mixed forest; **Type 6**: *Alnus nepalensis-Quercus delavayi* deciduous and evergreen broad-leaved mixed forest.

forest) and Type 6 (*Alnus nepalensis-Quercus delavayi* deciduous and evergreen broad-leaved mixed forest) had the lowest value. In general, forest Type 1 had lower values of diversity indices than those in the mixed forests (forest Types 2-6). Among the mixed forest types (Types 2-6), the diversity indices did not have significantly difference.

Growth patterns and population structure

The average annual ring width growth of *Alnus nepalensis* was 7.06 mm/year. The first 9 years, it was 5.5 mm/year, from the 10th year to the 27th year, it was 6.12 mm/year, from the 28th year to the 37th year, it was 9.8 mm/year. Overall, there was an increasing trend in growth (Fig. 6A). The relationship of age and DBH of *A. nepalensis* is shown in Fig. 6B.

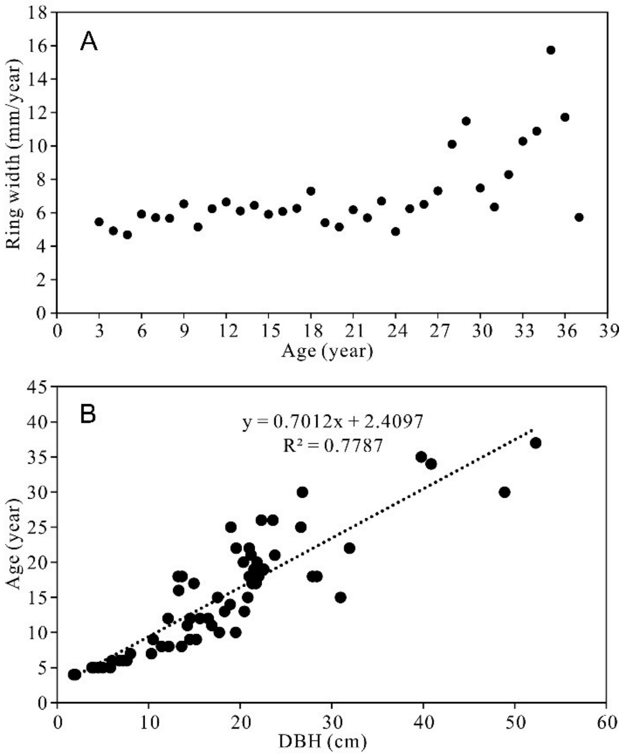

Fig. 6. Growth patterns of ***Alnus nepalensis*** trees (height ≥ 1.3 m). **A.** Changes in ring width with age; **B.** The relationship of DBH and age.

The individual frequency distribution in DBH-class of dominant species in each forest type is shown in Fig. 7. *Alnus nepalensis* exhibited a multi-modal pattern across all forest types, indicating sporadic regeneration. Its maximum DBH reached 110 cm. The number of individuals was concentrated in the 10–40 cm DBH range (forest Types 1, 2, 4, and 6) and the 15–40 cm DBH range (forest Types 3 and 5). *A. nepalensis* showed better regeneration in forest Type 1 (*Alnus nepalensis* deciduous broad-leaved forest), with relatively more young trees having a DBH of less than 10 cm, compared to the mixed

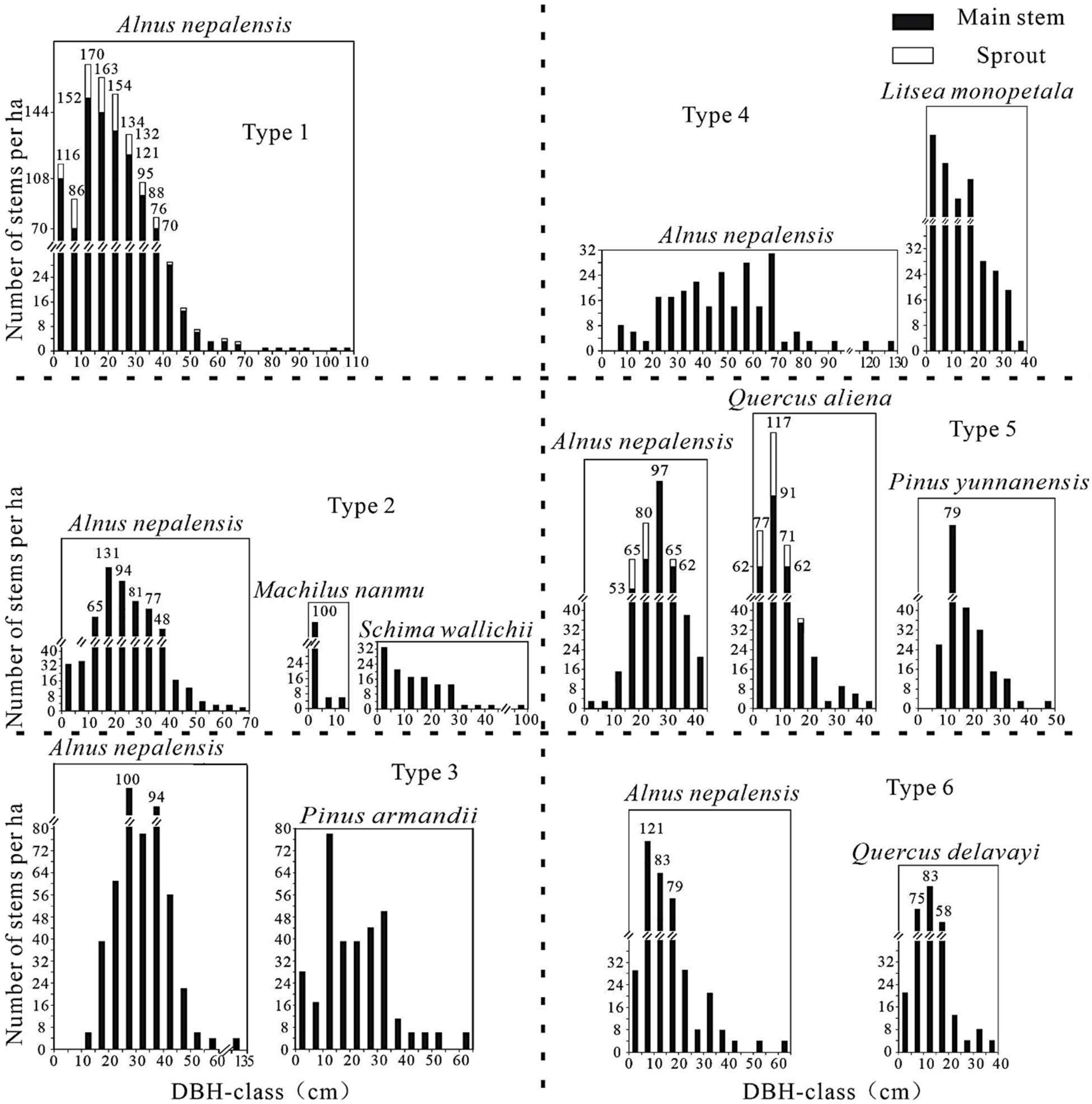

Fig. 7. The DBH-class structure of representative species in each forest type.

forests (forest Types 2-6). *Schima wallichii* in forest Type 2 and *Litsea monopetala* in forest Type 4 demonstrated a good regeneration with an inverse-J pattern. *Pinus armandii* in forest Type 3, *Pinus yunnanensis* in forest Type 5, and *Quercus delavayi* in forest Type 6 also exhibited a multi-modal pattern, indicating sporadic regeneration.

The age structure of *A. nepalensis* was also a multi-modal pattern which was similar to that of DBH structure (Fig. 8).

Dynamics

Twenty plots in central Yunnan as a case study for secondary succession as shown the dynamics of the plant communities were analyzed. In the DCA analysis, along Axis 1 (the eigenvalue: 0.785, the percentage of contribution: 61.96%) from the left side in the horizontal direction to the right side, five forest communities were distinctive with the decreasing of disturbance intensity (Fig. 9). The broad range of 0-80 on Axis 1 reflects strong variation in species composition across the five forest communities and captures a wide gradient of disturbance intensity, from very high to very low. Axis 1 also indicates the time elapsed since disturbances. The succession stages were clearly divided into three phases.

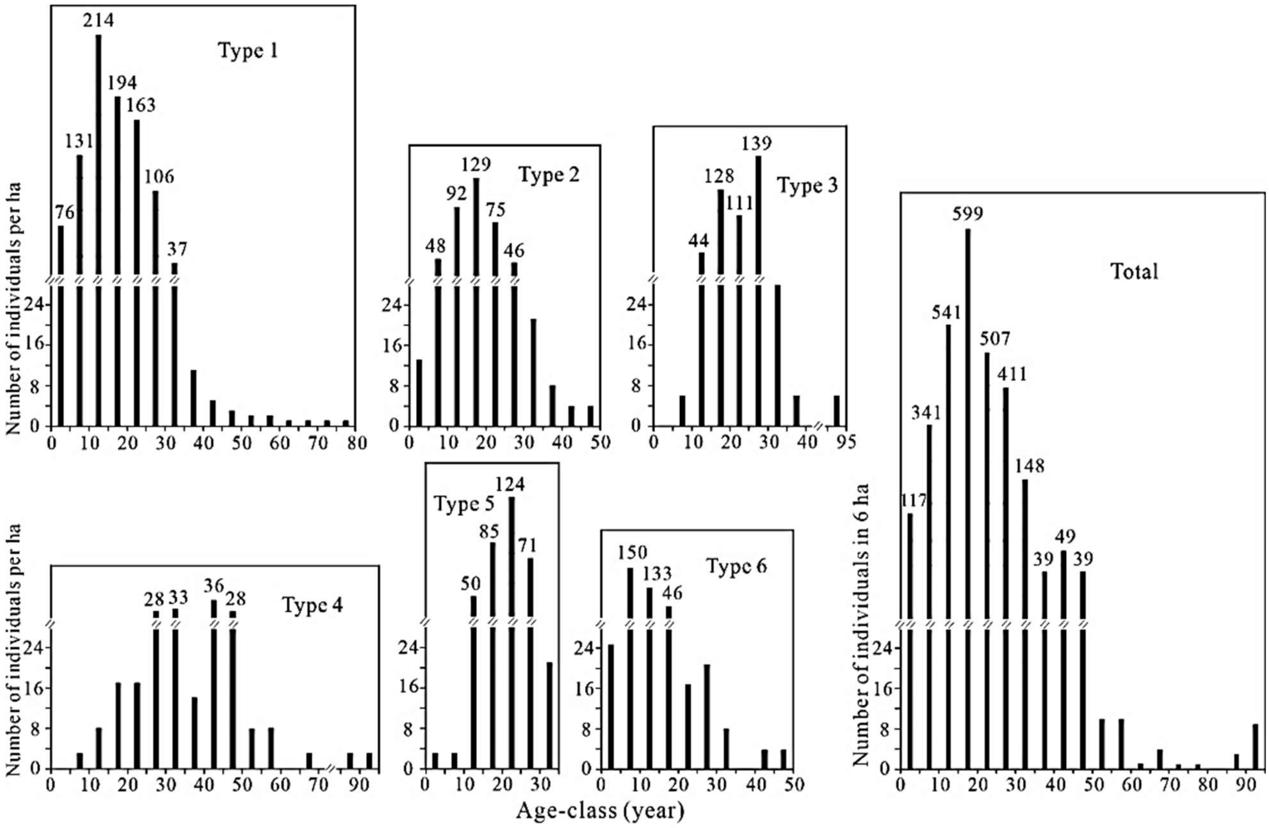

Fig. 8. The age-class structure of ***Alnus nepalensis***.

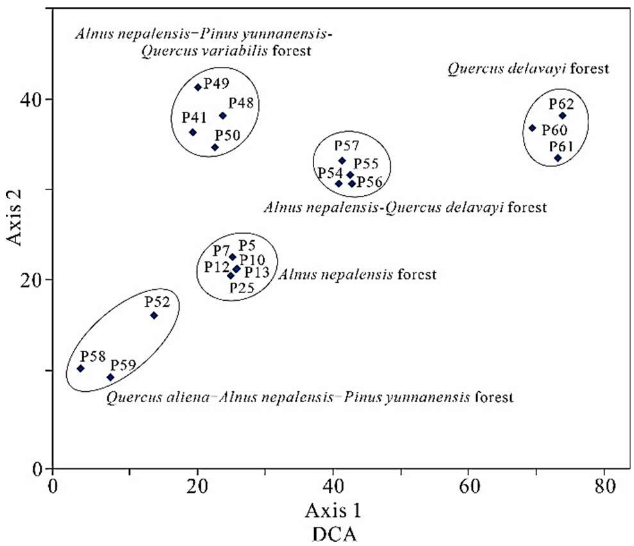

Fig. 9. The DCA ordination of 20 plots showing succession pathways in central Yunnan.

Early succession stage: the deciduous broad-leaved and coniferous mixed forest or deciduous broad-leaved forest. This included *Alnus nepalensis*-*Quercus aliena* - *Pinus yunnanensis* mixed forest (P52, P58, P59) or *Alnus nepalensis*-*Pinus yunnanensis* - *Quercus aliena* mixed forest (P41, P48, P49, P50) or *Alnus nepalensis* forest (P5, P7, P10, P12, P13, P25). When evergreen broad-leaved forests were disturbed or abandoned agricultural land, pioneer species such as *Alnus nepalensis, Quercus alien*, and *Pinus yunnanensis* quickly grew under sufficient light conditions, forming mixed forests or deciduous broad-leaved forests dominated by these species.

Mid-succession stage: the mixed deciduous and evergreen broad-leaved forest, represented by *Alnus nepalensis–Quercus delavayi* (P54, P55, P56, P57) mixed forest. As canopy density increased, pioneer species, which were heliophytes, became less suited to high-density conditions. Shade-tolerant evergreen broad-leaved species from Fagaceae such as *Quercus*, *Lithocarpus*, and *Castanopsis* grew in the understory. While the pioneers remain fewer in number, the shade-tolerant evergreen broad-leaved species increase in number. Over time, the shade-tolerant species become a codominant with deciduous broad-leaved *A. nepalensis*, forming mixed deciduous and evergreen broad-leaved forests.

Late succession stage: the evergreen broad-leaved forest, represented by *Quercus delavayi* evergreen broad-leaved forest (P60, P61, P62). As the light-intolerant pioneer species (*A. nepalensis, Pinus yunnanensis, Quercus variabilis*) died off, shade-tolerant species like *Quercus delavayi* or *Lithocarpus fenestratus* became dominant, forming late-successional evergreen broad-leaved forests.

DISCUSSION

Ecological characteristics

In the subtropical region of Yunnan, *Alnus nepalensis* is a key species that often colonizes disturbed sites, such as landslides and areas with human activity. This species is light-demanding and fast-growing, making it well-suited to open, sunny areas. It thrives in moist, well-drained soils, but its adaptability allows it to grow in poor, dry, rocky, and gravelly soils, which are common in disturbed habitats. Our study confirms that *A. nepalensis* not only coexistes with evergreen broad-leaved and/or coniferous tree species in mixed forests but can also form a forest dominated by a single species-*A. nepalensis* in disturbed sites. For instance, in southeastern Tibet, the Himalayan region, *A. nepalensis* rapidly colonizes areas after natural disturbances, such as landslides, establishing single-species stands (Sun *et al*., 1996). This ability to quickly occupy disturbed habitats is partly due to its symbiotic relationship with *Frankia* bacteria in root nodules, which enables the fixation of atmospheric nitrogen, thereby improving soil fertility (Varghese *et al*., 2003).

The nitrogen fixation process enhances soil organic matter, increasing nitrogen and phosphorus availability (Chaudhry *et al*., 1996; Mishra *et al*., 2018), which further promotes the growth of *A. nepalensis* and other plant species. This process plays a crucial role in early succession by enriching the soil, which not only benefits *A. nepalensis* but also facilitates the establishment of other species, eventually leading to more diverse plant communities. In disturbed areas, this ecological service accelerates the recovery of ecosystems by improving the habitat for other species, highlighting the critical role of *A. nepalensis* in forest regeneration and ecosystem services.

Dynamics

Plant community dynamics are driven by the process of secondary succession, where species composition evolves over time as a result of environmental changes and interactions. Succession is a continuous process that is influenced by both biotic and abiotic factors, and each species plays a role in shaping the environment for subsequent colonizers (Miura *et al*., 2001). In central Yunnan, early-stage succession is often triggered by disturbances such as landslides, agricultural abandonment, and deforestation. Pioneer species, including *A. nepalensis*, *Pinus yunnanensis*, and *Quercus aliena*, rapidly colonize disturbed areas such as mountainsides and farmland edges, forming broad-leaved and coniferous mixed forests or deciduous broad-leaved forests. Based on tree core ages and local knowledge, these pioneer communities usually take 15-40 years to establish.

As succession progresses, the role of pioneer species diminishes, and they are gradually replaced by more shade-tolerant species, such as *Castanopsis* and *Cyclobalanopsis* (currently classified under the genus *Quercus*) (Tang *et al*., 2010; Tang 2015). This transition occurs over a span of about 40–80 years, as canopy closure increases and light availability decreases. Eventually, a stable evergreen broad-leaved forest is established, taking 80–180 years to fully develop.

Our analysis of successional pathways in central Yunnan reveals that secondary forests in the early to mid-succession stages eventually give way to zonal evergreen broad-leaved forests, such as those dominated by *Quercus delavayi*, provided no major disturbance occurs. The decline in the importance value of *A. nepalensis* throughout succession is evident, as its dominance in the canopy and subcanopy decreases from 97.1% in the early stages to just 3.5% in the late stages. As the canopy density increases, the competitive advantage of light-demanding species weakens, and semi-shade-tolerant and shade-tolerant species, such as *Quercus delavayi*, begin to dominate. The importance value of *Q. delavayi* increases significantly, from 20.9% in the early stages to 72.5% in the late stages. Other species from the Fagaceae family, such as *Lithocarpus confinis* and *Castanopsis orthacantha*, also become more prominent in late-succession communities.

Mechanistically, the decline of pioneer species like *A. nepalensis* and the rise of shade-tolerant species are driven by competitive dynamics, including light, nutrient availability, and soil conditions. As the canopy becomes denser, the light that reaches the forest floor is reduced, favoring species that can thrive in lower light conditions. Additionally, the soil nutrient changes brought about by nitrogen fixation in the early stages of succession—facilitated by *A. nepalensis*—create a more favorable environment for the establishment of later successional species. The increased soil fertility supports a wider range of species, promoting biodiversity and stability in the forest ecosystem. Over time, these species outcompete *A. nepalensis*, leading to a more complex and structured forest community.

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