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Biodiversity restoration potential: a comparative study of native species regeneration in natural forests and *Liquidambar excelsa* plantation forests

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Abstract

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The identification of natural succession and regeneration processes is crucial for the preservation of biodiversity and ecosystem stability in sustainable forest management. This study investigated the biodiversity and regeneration of natural forests and *Liquidambar excelsa* (Noronha) Oken plantations. Tree species richness (dbh ≥ 10 cm) in natural forests was found to be significantly higher (44 species) than in plantation forests (5 species, 4 of which were natural recruits). Although tree density was higher in natural forests, basal area was lower than in plantations. At the regeneration (sapling) level, species richness did not differ significantly between the two forest types, with a moderate diversity index and high evenness, and a species similarity of 60.7%. However, sapling density and basal area were higher in the plantation forests. For understory vegetation, species richness was also not significantly different, but the diversity index was higher in the natural forests. Both shared a very high species similarity (75.6%), despite the greater density and cover in the natural forests. The successful recruitment of native species into plantations is more influenced by environmental factors such as proximity to natural forest seed sources and topography, rather than by the forest type itself. This is demonstrated by the discovery of *L. excelsa* seedlings in natural forests and the presence of several native species that have successfully regenerated in plantation forests, indicating the potential for biodiversity restoration.

Keywords

Bali, biodiversity, ecosystem stability, natural forest, plantation forest regeneration

Introduction

Deforestation and forest degradation continue to occur at alarming rates, e.g. France at 93.9 thousand ha per year and Turkey at 81.2 thousand ha per year, contributing significantly to the loss of biodiversity, including flora, fauna, and microorganisms (Austin et al., 2019; FAO and UNEP, 2020; Voigt et al., 2022). It is estimated that only 3% of primary forests remain worldwide, with a decline of more than 8% since 1990 (Nichol and Abbas, 2021). Compared

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with other tropical countries, Indonesia has made significant progress in recent years in preventing deforestation. However, Indonesia still ranked third out of the ten tropical countries with the highest primary forest loss in 2019 (Weisse and Goldman, 2021). Forest destruction is largely driven by land clearing for oil palm plantations, industrial timber plantations, and mining (Austin et al., 2019). Currently, law enforcement to prevent forest fires and land clearing is considered the most effective policy to reduce deforestation (Wijaya et al., 2019). However, ecosystem restoration efforts in areas that have already been damaged have also attracted considerable attention (Holl et al., 2017).

Even, the development of plantation forests to restore degraded forest areas continues to increase, reaching 29% between 1990 and 2020 (Sainge et al., 2020). However, there is still a perception that the development of plantation forests, especially using monoculture systems, cannot fully support the richness of native species like natural forests (Heinrichs et al., 2016; Rédei et al., 2020) and even hinders the regeneration of local species (Heinrichs et al., 2016; Nichol and Abbas, 2021). Diversity, species richness, dominance, and evenness of natural forests are recorded as being higher in natural forests than in monoculture plantations. Similarly, mixed-species plantations are still superior to monoculture forests (Akoto et al., 2015). For example, a global meta-analysis by Hua et al. (2022) found that monoculture tree plantations can achieve higher short-term carbon storage, but mixed-species plantations consistently contribute more significantly greater biodiversity and often enhance long-term ecosystem resilience and multifunctionality (Zhang et al., 2012). As well, tree height, diameter at breast height and aboveground biomass were higher at multispecies plantation than single species plantation (Feng et al., 2022). However, a different opinion suggests that plantation forests, whether single-species or mixed, can still have a positive impact on biodiversity recovery in severely degraded landscapes, such as those in tropical and subtropical Australia (Kanowski et al., 2005) and serve more ecological purposes (Tariq et al., 2024).

Indonesia has developed various restoration schemes for degraded forest areas. One such scheme is the application of monoculture planting of *Liquidambar excelsa* (Noronha) Oken (Syn. *Altingia excelsa* Noronha) in the eastern part of Bukit Tapak, Batukahu Nature Reserve, Tabanan Regency, Bali Province, Indonesia. The use of *L. excelsa* in restoration and reforestation schemes is supported by several key considerations. Ecologically, this species is well adapted to mountainous environments, occurring at elevations of about 200 to 1,700 m in humid hill and montane forests, and shows relatively rapid growth, reaching up to 60 m in height with a diameter of up to 1.5 m (Handayani and Hidayati, 2021). Its dense canopy plays an important role in maintaining microclimatic humidity, reducing soil erosion, enhancing water infiltration, and contributing to carbon sequestration. In addition to its ecological functions, *L. excelsa* has high economic value. Its timber is widely used for construction, and the species also produces a non-timber product in the form of balsam exudate that is utilized for food and medicinal purposes (Carolina et al., 2024). The combination of economic value and ecological functions makes *L. excelsa* one of the priority species for forest rehabilitation programs in Indonesia's mountainous regions. *L. excelsa* is native to Assam, Bangladesh, Cambodia, South-Central China, East Himalaya, Java, Laos, Lesser Sunda Islands, Malaya, Myanmar, Sumatra, Thailand, Tibet, Vietnam, particularly in highland areas (POWO, 2026). The habitat fragmentation and anthropogenic pressures, despite its current Least Concern status on the IUCN Red List (Beech et al., 2019) reinforce the urgency of studies to develop genetic conservation strategies.

The contrasting conditions between monoculture plantation forests and the edge of nature reserves, both of which had similar land cover histories but different reforestation practices, have piqued our interest in studying their succession. This study aimed to compare the successional pathways of plantation forests (after 40–60 years of natural growth) and natural forests, with particular focus on species diversity restoration and growth rates. Therefore, we tested the following hypotheses: (1) plantation forests undergoing natural succession will show lower species diversity restoration rates compared to natural forests, and (2) the basal area growth rates in late-successional plantation forests will converge with those of natural forests. The findings will aid in promoting meaningful restoration strategies and provide information on monoculture plantation forests succession in mountainous areas.

Materials and methods

Study site

Batukahu Nature Reserve is notable for its representation of natural forests (NF) and a *L. excelsa* monoculture plantation or plantation forests (PF). The *L. excelsa* (Noronha) Oken (Syn. *A. excelsa* Noronha) plantation is a prime example of a successful plantation situated in the eastern part of Bukit Tapak, Batukahu Nature Reserve, Tabanan Regency, Bali Province, Indonesia. The forest is in relatively good condition with no visible evidence of logging or damage. This PF was previously an area of fields, scrub, and open land between a nature reserve to the west and an agricultural area to the east (currently the Bali Botanical Gardens). The history of *L. excelsa* planting and contract terms was obtained from the surrounding community. For the first five years, the community provided care for *L. excelsa* in exchange for the land between the *L. excelsa* seedlings being planted with agricultural crops using an intercropping system. After five years, the area was left to reforest, where it remains today. The edge of the nature reserve bordering the plantation forests was also previously covered with scrub and medium-sized trees, but no planting intervention was undertaken and the area was allowed to grow naturally. The plantation forest served as a buffer zone for the nature reserve, which was still under state control. *L. excelsa* planting took place in three stages: 1938, 1958, and 1974 (Siregar, 1987; Siregar et al.,

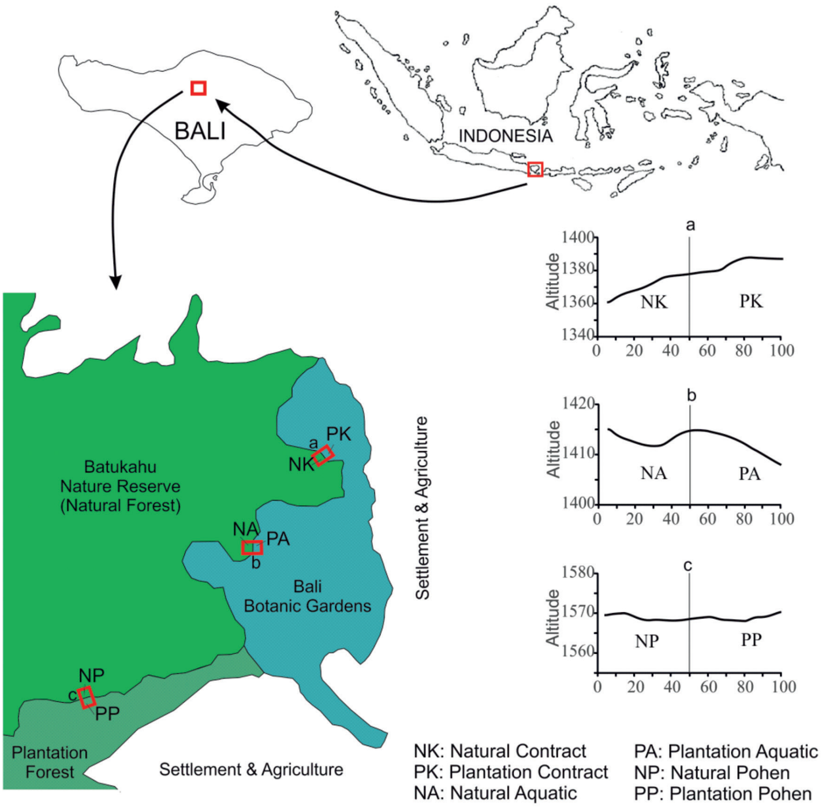


Fig. 1. Study site and topographic plot in natural forests (NF) and plantation forests (PF), Baturiti, Tabanan – Bali.

1989; Siregar and Undaharta, 2014) (Fig. 1).

Candikuning, Baturiti, Tabanan is located at 08°28'00"S and 115°16'00"E with an altitude ranging from 1,000 to 1,247 m asl. The average annual temperature ranges from 18 °C to 24 °C and the humidity is consistently high, ranging from 80% to 95% throughout the year. The average annual rainfall in Candikuning, Baturiti ranges from 2,500 mm to 3,300 mm, which makes this area one of the wettest areas in Bali (BMKG, 2023). The dominant natural vegetation in this area is moist, moss-rich montane forest vegetation. However, the current landscape is a mix of NF remnants, including *L. excelsa* plantations and agricultural land. The soils in this area are Andosols and Regosols, while the slope gradients are within the steep class (30–45%) and very steep (>45%) classes (Kariasa et al., 2018).

Vegetation sampling

In both PF and NF, plots 50 m × 50 m (0.25 ha) in size were created side by side. The study employed a comparative paired-site design with three independent replicates. Each replicate consisted of a matched pair of plots, one in the plantation and the other in the adjacent NF. Plots of the same size were replicated at three locations (Contract, Aquatic, and Pohen) with different topographies, resulting in three plots in each forest type (Fig. 1). The total plot area was 1.5 ha. Each plot was divided into 25 subplots of 10 m × 10 m for enumerating trees with a stem diameter at breast height (dbh) ≥ 10 cm. Within the 10 m × 10 m subplot, a 5 m × 5 m subplot was created for sampling at the sapling level (2 cm ≤ dbh < 10 cm), and within the 5 m × 5 m subplot, a 1 m × 1 m subplot was created for sampling understory vegetation (dbh < 2 cm and height < 1.5 m). All species found in each subplot were recorded for their scientific name, the number of individuals observed, the stem diameter of trees and saplings, and the percentage of canopy cover for understory vegetation. Plant specimens from each forest type were collected for identification purposes. Elevation and slope of the land in each main plot were also recorded.

Data analysis

Vegetation data were analyzed to determine the frequency of occurrence, individual density, and dominance of each species. The sum of the relative values of these three values revealed an importance value index (IVI) for each species in each forest type at the tree, sapling, and seedling levels (Mueller-Dombois and Ellenberg, 1974). Shannon's species diversity index (H') was calculated to determine the level of species diversity. The most commonly used formula (Kent and Coker, 1996) was employed: $H' = -\sum(ni/N)\ln(ni/N)$, where ni is the number of individuals of the i^(th) species and N is the total number of individuals of all species. Mathematically, H' has a theoretical range from 0 to ln(S), where S is the number of species (Magurran, 2004). Species diversity is categorized as low if $H' < 1$, moderate if $1 < H' \leq 3$, and high diversity if $H' > 3$ (Odum, 1993). Community stability was assessed using the species evenness index (E), calculated as E = H′/ln(S), where H′ is the Shannon diversity index and S is the number of species. The evenness index ranges from 0 to 1. An E value approaching zero indicates a more uneven distribution of species in the community. Conversely, an E value approaching one means the more even the distribution of species in the community (Krebs, 2014). The community is categorized as stressed if the E value is < 0.50, unstable if $0.50 < E < 0.75$ and as stable if $0.75 < E < 1.00$ (Pielou, 1966). Differences between the two forest types were tested by t-tests for species richness, individual density, basal area of saplings and percentage of understory cover. Grouping was conducted based on floristic similarity of natural regeneration at the sampling level and ground vegetation in six main plots. Multivariate ordination analysis, Non-Metric Multidimensional Scaling (NMDS) based on the Bray-Curtis index, was performed using PAST 4.03 software (Hammer et al., 2001). The NMDS stress value was < 0.05, indicating a very good fit and a highly reliable ordination. Species turnover or the magnitude of changes in species composition between one plot and another was also analyzed using Whittaker's index.

Results

Trees in plantation forests vs. natural forests

Tree species richness: A total of 45 tree species (dbh ≥ 10 cm) were recorded across all study plots. Of these, 44 species were found in NF and 5 species in PF, including 4 recruits (*Bischofia javanica, Engelhardia spicata, Homalanthus giganteus,* and *Sphaeropteris glauca*). The Shannon diversity index (H') in PF was low (H' = 0.318), while in NF it was high (H' = 3.091). The evenness index in PF was low (E = 0.198), while in NF it was high (E = 0.817). Total basal area per hectare in PF (44.34 m^2) was higher than in NF (38.36 m^2). The condition of the trees based on the division of sub-plots (100 m^2) can be seen in Table 1.

The tree species similarity index based on the Bray-Curtis formula for both forest types was only 16.3%. All four shared species recorded in PF were also present in NF. Two of these species, i.e. *H. giganteus* and *S. glauca*, were also recorded as main species in NF based on their IVI values (Table 2).

Tree species composition in NF is dominated by late secondary species, which is defined as an advanced stage of forest succession. This is characterized by the dominance of late secondary species adapted to shaded conditions under a closed canopy. The prevalence of these species indicates that NF at this stage has progressed toward mature forest conditions.

Based on the importance value index (IVI), *H. giganteus* emerged as the primary species. This species has the highest density (80 trees ha^{-1}) and the widest distribution frequency (16.7%) of all species. *Strobocalyx arborea*, which ranks second, has the largest basal area (6.7 m^2 ha^{-1}). These two species, along with *Trema orientale*, *S. glauca*, and *Saurauia reinwardtiana*, the five species with the largest IVI, control 45.5% of the total IVI (Table 2).

Density and population structure

Tree density (dbh ≥10 cm) is higher was NF, while the basal area was lower than in PF (Table 1). The diameter distribution of trees based on dbh class in NF, particularly in tropical regions, often shows a reverse-J pattern with a higher proportion of individuals in smaller diameter classes, which indicates continuous regeneration and is well documented in recent studies (Getie et al., 2026; Susanto et al., 2025; Li et al., 2024; Rahayu et al., 2022). In PF, the tree density forms a normal curve with the largest proportion in the dbh class of 30–39 cm (Fig. 2). When evaluated based on tree height, both forest types generate a normal curve, but with different peaks. In NF, the largest proportion was in the 10–19 m height class, while in PF, it was in the 20–29 m height class. The species with high dbh (dbh > 100 cm) in NF are *Dacrycarpus imbricatus*, *E. spicata*, *Ficus fistulosa*, *S. arborea*, and *T. orientale*. These species are also noted as prominent species and occupy the main layer of the forest canopy. In PF, in the low dbh class (dbh < 20 cm), in addition to *L. excelsa*, there are also *B. javanica*, *E. spicata*, *H. giganteus*, and *S. glauca*, which are recruit species. These four recruit species occupy the understory of the forest canopy.

Saplings

The total number of sapling species (dbh 2–9.9 cm) in the two forest types studied was 62 species. The number of species in NF was 42 species, 39 genera and 34 families, whereas in PF was 47 species, 41 genera and 30 families. The average number of species per subplot (25 m^2) was not significantly different (t = 1.661, df = 148) between the two forest types. Significantly different (t = 2.777 and 3.064, df = 148) were found in the average density and basal area per subplot, with higher numbers in PF (Table 3). The diversity index (H') for both forest types was classified as moderate (2.897 in PF and 2.998 in NF), and the evenness index (E) was high (0.752 in PF and 0.802 in NF).

Dendrocnide stimulans is the most prominent species in both forest types. This species has the highest distribution frequency, basal area, and density of any other species. Two species were shared among the five dominant

Table 1. Tree-level quantitative data in plantation forests (PF) and natural forests (NF)

Parameters	PF	NF	t
Average no. of species 100 m^{-2}	1.2 ± 0.4	3.1 ± 1.5	10.463*
Average density 100 m^{-2}	4.0 ± 1.7	4.3 ± 2.5	0.686
Average basal area (m^2) 100 m^{-2}	0.44 ± 0.26	0.38 ± 0.44	1.015

Table 2. List of tree species (dbh ≥ 10 cm) in plantation forests and five dominant species in natural forests based on importance value index (IVI)

No.	Species	Freq.	RF (%)	Basal area (m^2 ha^{-1})	RDo (%)	Density (ind. ha^{-1})	RD (%)	IVI (%)
	Plantation forests							
1	*Liquidambar excelsa* (Noronha) Oken	1.00	82.42	43.65	98.44	370.67	92.05	272.91
2	*Sphaeropteris glauca* (Blume) R.M.Tryon	0.17	14.29	0.51	1.15	28.00	6.95	22.39
3	*Engelhardia spicata* Lechen ex Blume	0.01	1.10	0.12	0.27	1.33	0.33	1.70
4	*Homalanthus giganteus* Zoll. & Moritzi	0.01	1.10	0.04	0.08	1.33	0.33	1.51
5	*Bischofia javanica* Blume	0.01	1.10	0.03	0.06	1.33	0.33	1.49
	Natural forests							
1	*Homalanthus giganteus* Zoll. & Moritzi	0.52	16.74	3.22	8.39	80.00	18.75	43.88
2	*Strobocalyx arborea* (Buch.-Ham.) Sch.Bip.	0.24	7.73	6.77	17.66	28.00	6.56	31.95
3	*Trema orientale* (L.) Blume	0.11	3.43	6.04	15.76	12.00	2.81	22.00
4	*Sphaeropteris glauca* (Blume) R.M.Tryon	0.28	9.01	1.04	2.72	37.33	8.75	20.49
5	*Saurauia reinwardtiana* Blume	0.13	4.29	1.95	5.09	37.33	8.75	18.13

RF, relative frequency; RDo, relative dominance; RD, relative density; IVI, importance value index.

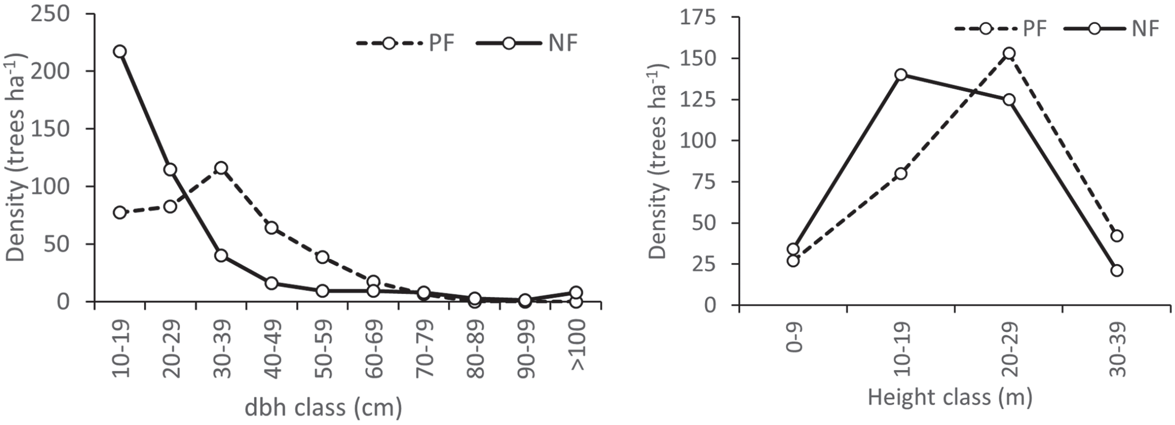


Fig. 2. Tree distribution based on dbh class (left) and height class (right).

sapling species in both forest types, namely *D. stimulans* and *Pinanga coronata* (Table 4). The sapling species similarity index, based on the Bray-Curtis formula, between PF and NF was 60.7%. The five sapling species in PF were also found in NF. A total of 44.7% of sapling species in PF were similar to tree species (dbh ≥ 10 cm) in NF.

Understory vegetation

The total understory vegetation observed in both forest types was 79 species, consisting of 65 species, 55 genera and 37 families in NF and 62 species, 56 genera and 43 families in PF. The species diversity index for understory vegetation in NF (H' = 3.060) was high, while in PF (H' = 2.787) it was moderate. The species evenness values of both were high, 0.675 in PF and 0.733 in NF respectively. The Bray Curtis similarity index was 75.6%, indicating a high level of similarity in species composition and community structure between the two forest types. The number of species and absolute crown cover per subplot did not dif-

Table 3. A statistical summary of quantitative data for saplings (2 cm ≤ dbh < 10 cm)

Parameters	PF	NF	t
Average no. of species 25 m^{-2}	4.5 ± 1.8	4.0 ± 1.6	1.661
Average density 25 m^{-2}	6.9 ± 6.8	4.3 ± 4.6	2.777*
Average basal area (cm^2) 25 m^{-2}	26.4 ± 27.5	14.9 ± 17.7	3.064*

Table 4. List of the five dominant sapling species (2 cm ≤ dbh < 10 cm) in plantation forests and natural forests based on species importance value (SIV)

No.	Species	Freq. (%)	Basal area (m^2 ha^{-1})	Density (ind. ha^{-1})	SIV (%)
	Plantation forests				
1	*Dendrocnide stimulans* (L.f.) Chew	64	0.58	1,328	82.75
2	*Glochidion rubrum* Blume	30	0.08	224	17.26
3	*Pinanga coronata* (Blume ex Mart.) Blume	34	0.08	192	16.92
4	*Epicharis parasitica* (Osbeck) Mabb.	14	0.11	232	15.50
5	*Liquidambar excelsa* (Noronha) Oken	22	0.07	208	13.93
	Natural forests				
1	*Dendrocnide stimulans* (L.f.) Chew	56	0.22	536	59.51
2	*Cyrtandra aclada* Merr.	24	0.15	424	39.05
3	*Pinanga coronata* (Blume ex Mart.) Blume	30	0.06	152	20.72
4	*Ardisia japonica* Blume	24	0.04	144	16.37
5	*Acronychia trifoliolata* Zoll. & Moritzi	22	0.04	112	14.45

Table 5. Summary of quantitative data on understory vegetation (height < 1.5 m; dbh < 2 cm)

Parameters	PF	NF	t
Average no. of species m^{-2}	3.0 ± 2.6	2.6 ± 2.3	0.999
Average density m^{-2}	19.1 ± 19.5	29.1 ± 32.9	2.259*
Average absolute crown cover (%) m^{-2}	58.3 ± 18.5	63.9 ± 19.8	1.808

fer significantly between the two forest types (t = 0.999 and 1.808, df = 148). In contrast, understory vegetation density was higher in NF, and the difference was statistically significant compared to PF (t = 2.259, df = 148; Table 5).

The dominant species in PF were also found in NF, and similarly, the dominant species in NF were also found in PF. Based on their life form, herbaceous species were recorded as the most abundant in both forest types. Tree saplings ranked second, followed by shrubs, ferns, and climbers (Fig. 3). The richness of tree seedlings was recorded as higher (19 species) in PF compared to NF (13 species), indicating relatively good local tree species regeneration in the plantation forests. Based on Table 6, the species *Lysimachia laxa* dominated both PF (IVI = 74.86%) and NF (IVI = 42.60%), with the highest frequency and density compared to other species. Meanwhile, *Piper aberrans* and *Diplazium esculentum* were consistently present in both forest types but with lower IVI values.

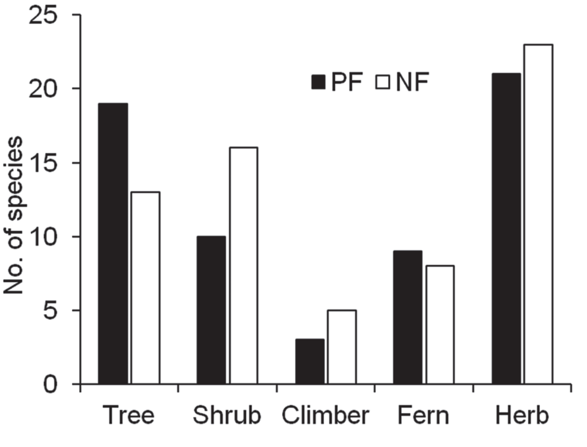


Fig. 3. Understory species richness based on life form in natural forests (NF) and plantation forests (PF).

Beta diversity of natural regeneration communities (saplings and understory vegetation) in PF and NF

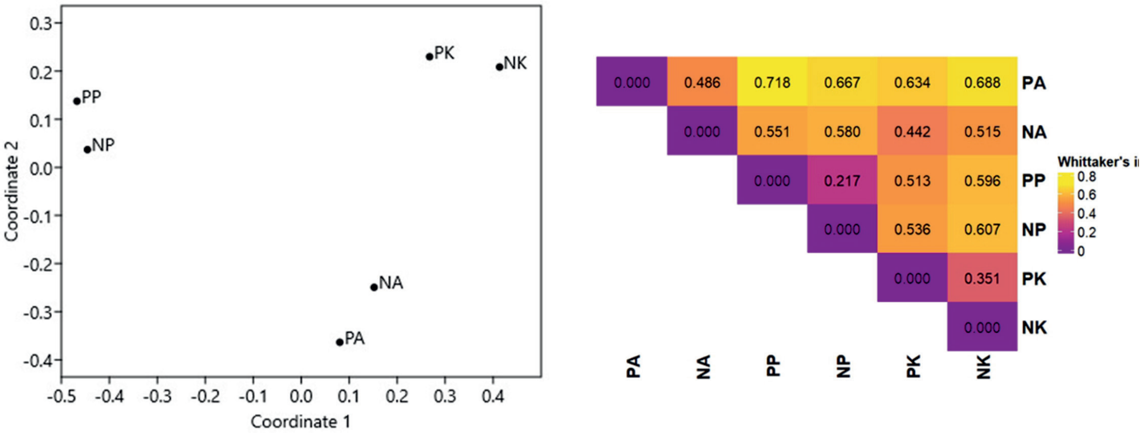
Floristic similarity analysis for saplings and understory vegetation was examined at six study sites (Fig. 4). The sites included NF plots (NK, NP, and NA) and PF plots (PK, PP, and PA). The NMDS stress value was 0.040, indicating a very good fit and a highly reliable ordination. NMDS results indicated that the clustering of study plots was largely influenced by edge effects. Based on Whittaker's index, species turnover was lowest between NP and PP (0.217), followed by NK and PK (0.351). The highest species turnover occurred between PA and PP (0.718) and between PA and NK (0.688). A Whittaker's index value close to zero indicates little or no change in species composition between plots. Conversely, if the value is 1, it means there is a significant change in species composition between plots, or the level of change in species composition is high (Whittaker, 1960).

Regeneration of *L. excelsa*

The *L. excelsa* planted as a monoculture around the Batukahu Nature Reserve originated from Java. There are no previous reports of this species growing naturally in the Batukahu Nature Reserve. At the time of the study, *L. excelsa* in PA and PP plots was 58 years old, and in PK plot it was 42 years old. Although *L. excelsa* is not included among the top five tree species in NF (Table 2), its tree density in NF is very low, reaching only 3 individuals ha^{-1}.

Table 6. List of the five dominant understory plant species (height < 1.5 m; diameter < 2 cm) in plantation forests and natural forests based on species importance value (SIV)

No.	Species	Freq. (%)	Relative dominance (%)	Density (1,000 m^{-2})	SIV (%)
	Plantation forests				
1	*Lysimachia laxa* Baudo	70.7	22.3	7,307	74.86
2	*Piper aberrans* C.DC.	24.0	6.7	1,587	19.84
3	*Diplazium esculentum* (Retz.) Sw.	30.6	6.7	840	17.37
4	*Cardamine hirsuta* L.	30.6	6.4	867	17.19
5	*Grona heterophylla* (Willd.) H.Ohashi & K.Ohashi	28.0	4.2	853	14.36
	Natural forests				
1	*Lysimachia laxa* Baudo	49.3	14.3	5,267	42.60
2	*Selaginella* sp.	24.0	8.1	4,627	28.93
3	*Piper aberrans* C.DC.	38.7	7.9	2,480	24.46
4	*Diplazium esculentum* (Retz.) Sw.	28.0	6.1	1,707	17.76
5	*Digitaria abludens* (Roem.&Schult.) Veldkamp	20.0	4.7	1,653	14.5



	PA	NA	PP	NP	PK	NK
PA	0.000	0.486	0.718	0.667	0.634	0.688
NA		0.000	0.551	0.580	0.442	0.515
PP			0.000	0.217	0.513	0.596
NP				0.000	0.536	0.607
PK					0.000	0.351
NK						0.000

Fig. 4. Results of NMDS analysis based on the Bray Curtis index (left) and Whittaker's index (right) values at six sample locations.

In contrast, in PF, *L. excelsa* was a dominant tree species with a density of approximately 371 individuals ha^{-1}. Despite the low abundance of adult trees in NF, *L. excelsa* showed successful regeneration in both forest types. The density of *L. excelsa* seedlings in PF reached 405 individuals ha^{-1}, while in NF it reached 443 individuals ha^{-1}. This indicates that *L. excelsa* has penetrated NF. The distribution of individuals based on stem diameter showed the largest proportion in small diameter classes and decreased with increasing diameter classes, indicating good regeneration (Fig. 5). The largest stem diameter encountered was 2.9 cm.

Discussion

Composition and structure of trees

Reforestation is one way to restore forest function (Nichol and Abbas, 2021). While, natural restoration efforts are widely regarded as being more effective in restoring biodiversity than monocultures (Parrotta et al., 1997; Akoto et al., 2015). Centuries of regeneration are required to reestablish large numbers of native species (Bowd et al., 2019). In this study, which was conducted on 58- and 42-year-old *L. excelsa* plantations, only four native species were reached tree size (dbh ≥ 10 cm) from recruitment. These four species are *B. javanica*, *H. giganteus*, *S. glauca*, and *E. spicata* (Fig. 6), which also inhabit the surrounding NF and exemplify distinct ecological strategies

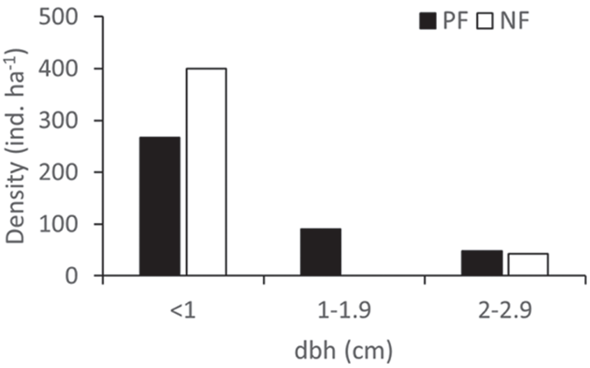


Fig. 5. Regeneration of *L. excelsa* in natural forests (NF) and plantations (PF).

Fig. 6. Native species (dbh ≥ 10 cm) recruited in the study area *Sphaeropteris glauca* (a), *Homalanthus giganteus* (b), and *Engelhardia spicata* (c).

that facilitate initial colonization.

Homalanthus giganteus represents a rapidly proliferating pioneer tree endemic in the rainforests. This species is particularly adept at colonizing extensive gaps and disturbed sites, thereby playing a pivotal role in the early stages of ecological succession by swiftly stabilizing environments and altering microclimates. However, this species ultimately succumbs to shading. Its capacity to flourish in disturbed environments has prompted the International Union for Conservation of Nature (IUCN) to classify it as of Least Concern, but its enduring viability is inherently tied to the conservation of the primary rainforest matrix, which faces significant threats from extensive deforestation driven by agricultural expansion and logging activities throughout its indigenous range (Van Welzen and Silk, 2021; Floyd, 1977; de Kok, 2024).

The second species, *S. glauca* is categorized as a pioneering tree fern. It flourishes under open, high-light conditions on well-drained slopes and ridges, with its establishment frequently linked to considerable soil disturbance. Its spores are capable of long-distance dispersal, enabling it to colonize degraded environments where it contributes to the formation of shaded, humid microsites conducive to the germination of later successional tree seedlings (Large and Braggins, 2004; Johns, 1982). Lastly, *E. spicata* epitomizes a later successional light requiring canopy tree. This species is widely distributed across both secondary and primary forests throughout Southeast Asia. Although its fruits are dispersed by wind, allowing it to penetrate open plantations, its establishment and growth indicate a more advanced phase of structural and compositional recovery towards a mature forest assemblage (Zhang et al., 2020; Manos and Stone, 2001). The presence of these four species, ranging from a transient pioneer to a potential canopy tree candidate, exemplifies the nascent yet gradual trajectory of natural succession within these monoculture plantations, thereby underscoring a critical bottleneck in the recruitment of a diverse native flora.

Thus, there are only 5 tree species (dbh ≥ 10cm) consisting of 5 genera and 5 families in PF. This is significantly different with NF which has 44 species, 38 genera and 30 families. The number of species (species richness) recorded in this study is higher than in the previous report, which was conducted in the same area on a 0.5 ha plot. The previous study documented about 33 species (Siregar and Undaharta, 2018; Siregar, 1987). This discrepancy is probably attributable to variations in plot size (Saha et al., 2016). It has been established that the dominant species from three studies within this area, conducted in different years, are similar and differ solely in their order of dominance. The main species in NF are still dominated by species that usually inhabit old secondary forests, while recruitment in PF was dominated by these same species. However, these species will presumably be gradually replaced by climax species as the forest ages (Siregar and Undaharta, 2018). This finding suggests that over the past 40 years, succession in the lower montane forests of Batukahu, Bali, has not seen significant changes in the composition of primary species.

Another point of note is the decreasing trend of tree density and increasing trend of basal area. Siregar (1987) and Siregar and Undaharta (2018) noted a decrease in tree density from 640 trees ha^{-1} to 514 trees ha^{-1} and increase in basal area from 34.16 m^2 ha^{-1} to 38.33 m^2 ha^{-1}. Similarly, this study found that tree density was down to 403 trees ha^{-1} and basal area was up to 44.34 m^2 ha^{-1}. The specific factors contributing to these trends are unclear, but it is presumed that it might be due to the fall of older trees. Records during the study period indicate that damage from natural disasters or human disturbance was relatively minor, despite the findings of several stumps and fallen large trees were found. Dominant species such as *H. giganteus*, *S. arborea*, and *T. orientale* are known to inhabit secondary forests and are classified as fast-growing tree species with a relatively shorter lifespans than primary species (Jakovac et al., 2021). We suspect that not all trees in NF grew as a result of post-damage regeneration. Six individuals of five species with a dbh > 100 cm, i.e. *S. arborea*, *T. orientale*, *F. fistulosa*, *E. spicata*, and *D. imbricatus* are remnants of trees that grew before severe degradation occurred in this area. *D. imbricatus* is a native species of the Batukahu Nature Reserve, where it exhibited the highest population density and nearly formed a homogeneous community at an altitude range of 1,500 to 1,600 m asl.

Regeneration

In general, Table 2 shows that PF is dominated by *L. excelsa*, which had a very high IVI (272.91%), significantly different from the rest of the species. RF, RDo, and RD were also very dominant, indicating a monoculture PF dominated by a single species. Meanwhile, NF showed a more uniform and diverse range, with no species being particularly dominant. The five species with the highest IVI were *H. giganteus*, *S. arborea*, *T. orientale*, *S. glauca*, and *S. reinwardtiana* (Table 2). However, at the sapling level, both locations showed moderate species diversity index and high species evenness index (Table 3). Moreover, based on their life forms, the understory vegetation in PF contained a greater number of tree species (Fig. 3). The species composition of natural regeneration at the sapling level was also highly similar between the two forest types, at 60.7%, and at the understory level, at 75.6%. The main types of natural regeneration (saplings and understory) in both forest types showed similarities.

The similarity in sapling species composition between PF and NF reflects a moderate to high degree of overlap, suggesting that PF can support a substantial proportion of sapling species characteristic of NF. This compositional resemblance implies that PF may function as secondary habitats or ecological stepping stones, particularly in fragmented landscapes where NF patches are spatially isolated. It has been demonstrated that PF can create favourable microclimatic conditions, thereby facilitating the establishment and survival of native seedlings. Canopy cover provided by plantation stands has been shown to buffer microclimatic extremes, reduce moisture loss, and suppress aggressive understory vegetation. This creates shaded environments conducive to seedling growth. Similar patterns have been documented in tropical forest mosaics, where PF facilitate native species regeneration (Simões et al. 2024; Forbes et al., 2019). The higher average number of species recorded in PF further supports the role of these systems as secondary habitats that accommodate a mixture of planted and naturally regenerated species. Previous studies have demonstrated that PF can enhance native species recruitment by improving microclimatic conditions, increasing seed rain from adjacent NF, and facilitating seedling establishment through nurse effects (Forbes et al., 2019). The observation that more than 44% of sapling species in PF correspond to tree species (dbh ≥ 10 cm) in NF indicates a strong ecological linkage between regeneration processes in PF and the mature forest structure of NF. This overlap suggests that PF can facilitate the recruitment of species characteristic of NF, particularly in landscapes where connectivity and edge effects to NF seed sources are maintained (Lemenih and Teketay, 2005).

The dominant species in NF were also found to be the dominant species in PF, and vice versa. At the sapling level, both locations were dominated by *D. stimulans* (Table 4), this species is a successful and aggressive pioneer, considering that it is easy to grow, produces many seeds and grows well in open and disturbed areas. The low Whittaker's index between NF and PF were the most important numerical evidence. For example, the PP and NP values of 0.217 as the lowest values indicate a high similarity in species composition between plantation forests (PF) and natural forests (NF). Similarly, PK and NK values of 0.351 are considered low, indicating that geographic edge effects to seed sources (surrounding NF) is the main factor that shapes the regeneration community in PF, causing their composition to be similar to NF (Fig. 4).

The common assumption that NF are better at restoring biodiversity than monoculture plantations (Nichol and Abbas, 2021), fully align with this study especially in the categories saplings and understory vegetation. The plantations were previously a dryland agricultural areas and scrubland. The source of naturally regenerating seeds in PF is thought to come from the surrounding NF, indicating that proximity is the most dominant factor in determining the species composition of naturally regenerating in PF. Many factors influence the natural succession process, such as soil fertility (Buriánek et al., 2013) and management history (Rédei et al., 2020). Furthermore, disturbances (natural and human) also have significant ecological and functional implications (Bowd et al., 2019). Intensive disturbances can cause physical, chemical, and biological barriers to the natural succession process (Rosleine, 2013).

It appears that aboveground environmental factors, such as the relatively similar canopy cover between NF and PF, no longer play a significant role in differentiating the species composition of the understory (Siregar and Undaharta, 2014). This aligns with Andrew (2025), who demonstrated that canopy cover and soil conditions largely determine regeneration success (frequently to a greater extent than the plantation itself). This differs from the early stages of PF growth, which were dominated by light-demanding species (Siregar et al., 1989). After more than 40 years, as the forest canopy became denser, light-demanding plant species disappeared and were replaced by shade-tolerant species (Siregar and Undaharta, 2014).

The main differences in forest regeneration between the two forest types at the understory vegetation level lie in individual density and understory vegetation cover, both of which are higher in NF. In contrast, at the sapling level, individual density and basal area are higher in PF than in NF. This suggests that habitat conditions beneath the canopy of *L. excelsa* in PF are relatively conducive to the growth of pioneer saplings (Keenan et al., 1999). Meanwhile, the herbaceous- and shrub-dominated understory in NF appears to suppress the growth of these tree species (Fig. 3).

The success of natural regeneration in PF is strongly influenced by the initial species composition, planting density, and initial site conditions (Sansevero et al., 2011).

The greater abundance of saplings in PF may also be due to less competition for space in the understory (10–19 m) compared to NF, which tend to be dense from the understory to the top of the canopy (Fig. 2). The success of *H. giganteus*, *S. glauca*, and *E. spicata* in growing to tree level (dbh ≥ 10 cm) under the canopy of *L. excelsa* in PF offers hope that the recruitment of new species from the surrounding NF will continue in the future. However, although reforestation programs have been able to create favorable environments for the regeneration of pioneer tree species, it appears that the ability of PF to recruit climax species, particularly those with large seeds that require special assistance from animal dispersal agents, remains to be seen.

Additionally, Moslehi et al. (2025) demonstrated that even non-invasive plantation species may have long term ecological consequences. In PF located on the slopes beneath NF, seed recruitment from NF appears to be less challenging. However, species enrichment initiatives through planting to accelerate the regeneration of local, large-seeded species could be attempted (Parrotta et al., 1997). Succession in NF as demonstrated in this study shows that more than 40 years after the damage occurred, the tree species composition is still dominated by secondary species. Erskine et al. (2006) have suggested that multi-species plantations can produce more productivity and create ecological benefits, and should be more widely pursued than monoculture as a reforestation method.

Liquidambar excelsa invasion

The findings of this study indicate that *L. excelsa* seedlings have penetrated NF areas with an individual density of up to 443 individuals ha^{-1}. Even at the sapling level, *L. excelsa* emerged as one of the 10 dominant species in both forest types. The presence of abundant *L. excelsa* seedlings plays a crucial role in forest ecosystem function and can influence long-term succession patterns (Royo and Carson, 2006). However, invasion can cause changes in forest structure and composition, potentially disrupting key ecosystem functions (Lodge and Shrader-Frechette, 2002). Invasion by alien species can even lead to a decline in plant diversity in NF (Heinrichs et al., 2016). Other studies have shown that the fall of large trees of local species, a natural mechanism in NF, actually stimulates the development of exotic species, especially invasive ones, where the growth rate of exotic plant species is greater than that of endemic species (Utomo et al., 2007).

In this study, no invasive species other than *L. excelsa* were found, either under the gaps or under the forest canopy. This pattern suggests that *L. excelsa* currently represents the primary ecological risk associated with species invasion in the Batukahu forest landscape. The potential for *L. excelsa* expansion into NF of Batukahu is great. In addition to its abundant seedlings, the submontane zone is an area of distribution in its natural habitat (Dahlan et al., 2018; Istomo and Sari, 2019). Given its high regeneration capacity and suitability to local environmental conditions, *L. excelsa* has potential to become ecologically dominant and outcompete native species if left unmanaged. Therefore, a deeper study is needed to examine the ecological impact of the presence of the introduced species *L. excelsa* in NF of the Batukahu and consider its potential to cause environmental and economic damage (Lodge and Shrader-Frechette, 2002).

From a management perspective, this finding highlights the need for early detection, continuous monitoring, and selective control measures, particularly the removal of seedlings and saplings within NF boundaries to prevent further spread of *L. excelsa* into conservation areas. For the record, *L. excelsa* was found growing up to tree level (dbh ≥ 10 cm) in the Contract (NK) and Pohen (NP) of NF. Batukahu Forest is a nature reserve area whose species purity is strictly maintained according to Government Regulation Number 28 of 2011 as amended by Government Regulation No. 108 of 2015 concerning the Management of Nature Reserves and Nature Conservation Areas. This also proves that although forest rehabilitation through the development of plantations took place outside the nature reserve area, it was able to spread into the nature reserve area. Interestingly, the distribution of *L. excelsa* in NF was only found in NK and NP. Meanwhile, it was not found in the NA. This may be related to the topography where the altitude of NK is lower than PK and the relatively flat area between NP and PP, which allows *L. excelsa* seeds to be easily carried by surface flow into NF. Meanwhile, NA is positioned above PA (Fig. 1). However, the absence of *L. excelsa* seedlings in NA and PA can be caused by the extent of anthropogenic disturbance.

Conclusions

While monoculture plantings offer quick and visible results in land restoration, they often decline at the tree level. In contrast, multiculture is a highly effective strategy for initiating forest recovery. It builds more resilient ecosystems resistant to disease, drought, and climate change by enhancing multiple attributes simultaneously and setting a trajectory toward a more NF state. A major practical constraint to this approach is the limited availability of native seedlings for large-scale reforestation, which often leads to the selection of exotic species with higher economic value and better seed supply.

For example, *L. excelsa* is native to western Indonesia but is introduced in central and eastern regions. Our study found that even planting *L. excelsa* in degraded areas still facilitated the regeneration of local species. This regeneration showed a high degree of similarity to nearby NF, a success strongly influenced by edge effects and topography. Quantitative analyses (NMDS and Whittaker's Index) confirmed that regeneration in plantations over 40–60 years was more similar in composition to nearby NF (indicated by low species turnover values of 0.217 between NP and PP) than to similar plantations at more distant locations (high turnover values, of 0.718 between PA and PP). Plantations downslope from NF showed particularly strong compositional similarity.

However, a significant concern emerged which is *L. excelsa* invading adjacent NF. This indicates that restoration using non-native species, especially in areas bordering or topographically above NF, risks causing ecological damage. The full impact of this invasion in the Batukahu, Bali, remains to be determined, but it underscores a potential ecological threat.

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