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Long-term changes in floristic diversity, composition and stand structure in *Acacia auriculiformis* plantation in Mount Makiling Forest Reserve, Philippines

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Abstract. *Hernandez JO, Ata JP, Combalicer MS. 2022. Long-term changes in floristic diversity, composition and stand structure in* Acacia auriculiformis *plantation in Mount Makiling Forest Reserve, Philippines. Biodiversitas 23: 3630-3637.* There have been continuous debates about whether exotic tree plantation facilitates vegetation succession. In the Philippines, the potential for the re-establishment of native plant communities and improvement of the plant community structure under exotic tree plantations has not yet been evaluated adequately. Thus, the study investigated the dynamics in floristic diversity, composition and stand structure of a reforested area using *Acacia auriculiformis* Benth. in Sitio Kay Inglesia, Mount Makiling Forest Reserve (MMFR), Philippines. The changes in basal area, stem density, biomass growth, species diversity, species evenness and richness, and canopy closure were determined between two study periods, i.e., 1993-2008 and 2009-2019. Results revealed significant changes in stem density (i.e., 1324 to 2135 trees ha^{-1}) and canopy closure (i.e., 18% to 10%) for mature trees and seedlings/saplings in 2009-2019. The changes in basal area and aboveground biomass were not significant between the two study periods. The species richness was significantly higher in 2009-2019 (i.e., 55 species) than in 1993-2008 (i.e., 22 species). The species diversity also significantly increased from low (i.e., H' = 1.99, S = 23) to moderate (i.e., H' = 2.88, S = 55). Moreover, the number of exotics decreased (i.e., 60 to 40% or 15 to 9 species) as the number of native ones increased (i.e., 27 to 72% or 15 to 40 species). Therefore, the findings of the present study show that re-establishment of native species is possible when restoring degraded land with *A. auriculiformis* plantation. However, monitoring studies on other key ecosystem attributes (e.g., ecosystem functionality, external exchanges, structural diversity) of the plantation are recommended to enhance our understanding of the species' potential for restoration.

Keywords: Exotic species, monoculture plantation, nitrogen fixers, restoration, succession

Abbreviations: AGB: Aboveground biomass; AS: area sampled; BA: basal area; DBH: diameter at breast height, IV: importance values; MMFR: Mount Makiling Forest Reserve; MVSP: Multivariate Statistical Package; RDen: relative density; RDom: relative dominance; RFre: relative frequency; SDen: species density; SDom: species dominance; SFre: species frequency

INTRODUCTION

There has been an extensive addition to forest plantations in the tropics by 57 million ha, about a 70% increase over the last 25 years, with more than 100 countries reportedly using exotic species to establish plantations (MacDicken et al. 2015). In the Philippines, previous national reforestation programs used fast-growing, economically important exotic species as one of the immediate approaches to begin restoring degraded forestlands. The rapid growth rates and the capacity of exotic tree species to restore forest structure and native species-rich communities in the understory have led them to be selected for reforestation use (Ismael and Metali 2014; Meira-Neto et al. 2018). Several studies have supported this by reporting that natural recolonization by native trees occurs under the canopy of exotic species (e.g., Zhou et al. 2015).

In contrast, other studies highlight the negative impact of exotic plants on native plant regeneration by suppressing seed production leads to declining species abundance (Cook-Patton and Agrawal 2014; Zahra et al. 2020). Plantation forestry using fast-growing species has also been observed to impair the survival of endemics and promote plant invasions (Braun and Vogt 2014). Furthermore, the regeneration of native species under exotic plants may differ depending on climatic regions and microsites (Svriz et al. 2013). In order to resolve these contrasting results, long-term vegetational studies are, therefore, needed to evaluate the capacity of exotic plants in facilitating or inhibiting the regeneration of native tree species in an exotic species plantation. Long-term studies on exotic plantations across tropical countries, including the Philippines, are also little explored to date.

Acacia auriculiformis Benth. is a large evergreen leguminous tree (Mimosoideae) that can reach 15-30 m in height and 50-60 cm in diameter (Combalicer et al. 2018; Haque et al. 2021). This fast-growing species can thrive in water logging, acidic, and degraded soils dominated by *Imperata* grass and other weeds (Haque et al. 2021; Lee and Woo 2012). *A. auriculiformis* and other *Acacia* species are some of the fast-growing exotic plants that are commonly used for reforestation in degraded tropical and subtropical regions, such as in Southern Benin (Aoudji et al. 2017), Indonesia (Sutomo et al. 2016; Koutika and Richardson 2019), South China, and in the Philippines (Lee and Woo 2012). Because of the large canopy and ability to fix nitrogen, the species has also been considered a nurse plant for understory native species (Tran 2014). Other characteristics that make *A. auriculiformis* one of the widely used species for greening programs include densely matted root systems that can help stabilize eroded land, evergreen foliage that improves site microclimate, especially during the dry season, rapid early growth, and tolerance to poor soil conditions (Lee and Woo 2012; Dubiez et al. 2019). It was also reported that *A. auriculiformis* could improve soil conditions and facilitate the establishment of native plant communities by minimizing intense radiation and heat loading, among others (Huong 2020).

The Mount Makiling Forest Reserve (MMFR) is a 4,224-hectare ASEAN Heritage Park located in the southern-central of Luzon Island, Philippines (Combalicer et al. 2018; Alcala 2019). It is subdivided into four sub-watersheds, namely, Molawin-Dampalit, Cambantoc, Tigbi, and the Greater Sipit. In the past, slash-and-burn and other encroachment activities have led to extensive deforestation in MMFR. Although forest regrowth and reduced fragmentation in the forest reserve have already been documented in some studies (e.g., Vergara et al. 2019), deforestation is still evident in some parts of the forest reserve, particularly along the edges near human settlements. Thus, *A. auriculiformis* was introduced in MMFR to reforest the degraded areas.

Until now, the potential for the re-establishment of native plant communities and improvement of stand structure where *A. auriculiformis* has been planted has not yet been evaluated adequately since its first introduction in the 1990s in MMFR. Thus, the present study investigated the impact of *A. auriculiformis* on the species diversity and stand structure of regenerating/recolonizing vegetation in Sitio Kay Inglesia, MMFR. Specifically, we analyzed the changes in species and stand structure of the plantation between the two study periods to understand the overall changes over the years. The fruit types and dispersal vectors of the identified native species were also determined to explain the presence of dominant species in the understory of the plantation.

MATERIALS AND METHODS

Study area

The study was carried out in Sitio Kay Inglesia on the southwest slope of Mount Makiling Forest Reserve (MMFR), Batangas, Philippines, at 480 to 535 m above sea level (m asl) (Figure 1). It is geographically located at 14°06’ to 14°15’ N and 121°9’ to 121°16’ E with moderately sloping to the rolling slope. The area has a tropical monsoon climate with two distinct seasons: dry (January to April) and wet (May to December). The annual temperature ranges from 23 to 29°C, and the annual precipitation ranges from 925.77 - 1600 mm (Figure 2), of which approximately 85% occurs from June to October. The mean monthly relative humidity ranges from 33% to 92 % (Combalicer et al. 2018).

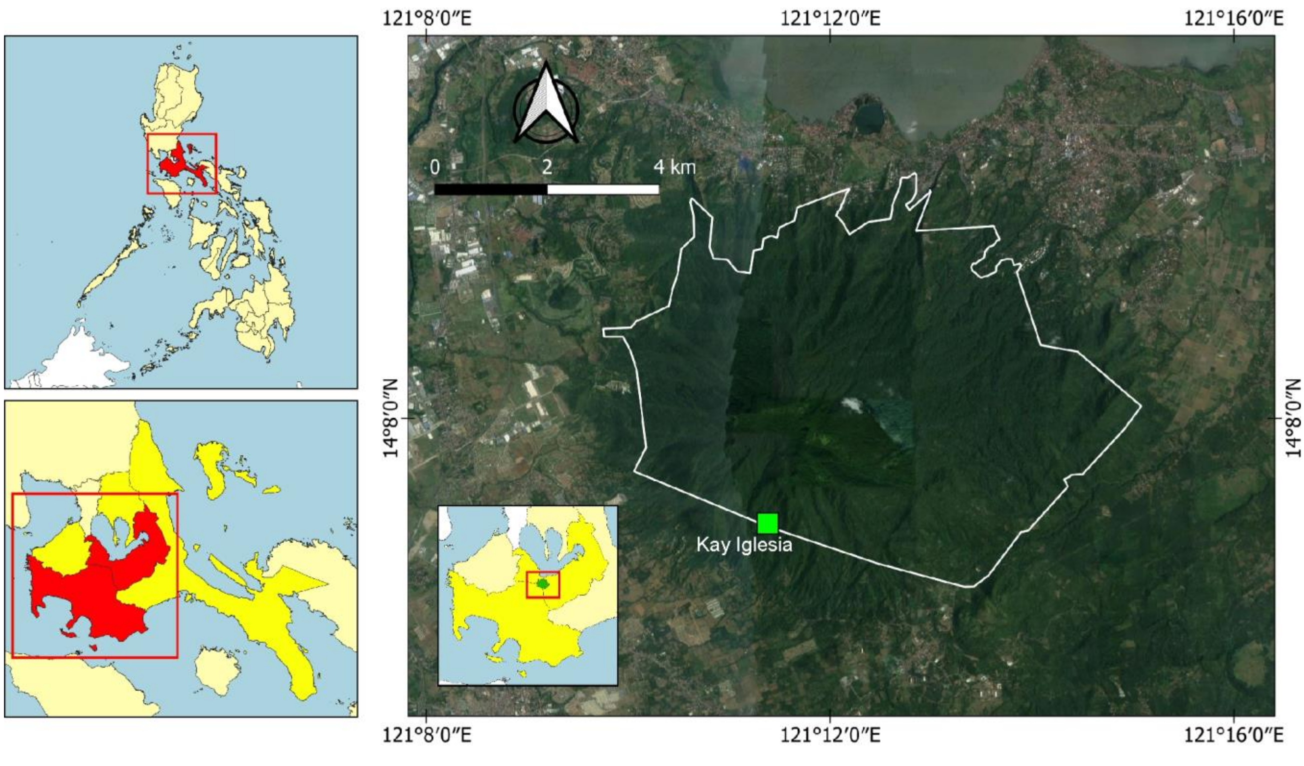

Figure 1. Study site at the *Acacia auriculiformis* plantation in Sitio Kay Inglesia, Mount Makiling Forest Reserve, Philippines

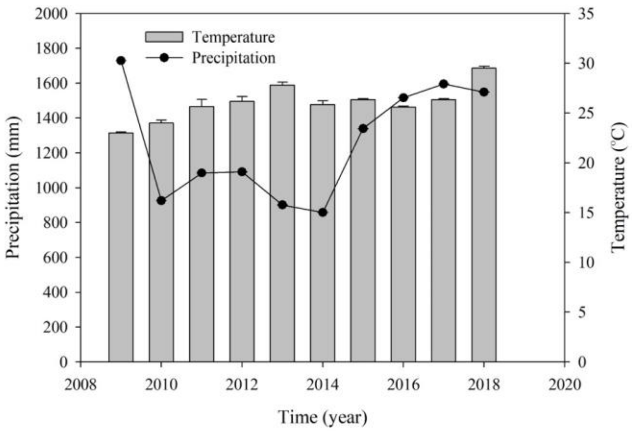

Figure 2. Annual temperature and precipitation in Batangas, Philippines. The data was obtained from the Weather World online

Sitio Kay Inglesia was a portion (c.a. 16 ha) of a 50-ha degraded portion of Sipit Watershed. Some forest patches in the watershed have been used for grazing goats and plantations of fruit crops. The annual incidence of forest fires had been a serious problem in the study site, attributed to repeated slash-burn activities, relatively dry climate, low soil moisture, and strong winds. Due to perennial forest fire, the study area was once an open grassland dominated by *I. cylindrica* and *Saccharum spontaneum*. The last time the study site was burned was in 1991. Although the original vegetation in the study site was cleared, the remnants of individuals of *Parashorea malaanonan*, *Shorea guiso*, and *Shorea contorta* in the adjacent forests (c.a. 50-100 m away from the study site) may indicate that a dipterocarp forest was possibly present in the area. *A. auriculiformis* was then introduced in 1993 to restore the fire-degraded area in Sitio Kay Inglesia, and this was monitored and managed with intensive protection from fire. Several interventions in forest restoration of Sitio Kay Inglesia site were already implemented, including programs on (i) forest fire protection, (ii) volunteer-based tree planting, and (iii) corporate sponsorship, forest protection, and follow-up planting (Combalicer et al. 2018).

Vegetation survey

At the study site, a systematic sampling design was employed for data collection by establishing six 20 m × 20 m permanent plots (c.a., 50 m apart) along a 2-km line transect, where undergrowth had grown undisturbed. The elevations of these plots ranged from 520-535 m asl. Two nested subplots were laid out inside the 20 m × 20 m plots to inventory all regenerants or wildlings, including *A. auriculiformis*. The subplots were laid out at 10-15 m apart. The vegetation surveys were conducted in 2008 (hereafter, 1993-2008 study period) and 2019 (hereafter, 2009-2019 study period). All trees encountered in each plot were identified and tagged with aluminum labels. The diameter at breast height (DBH) was measured at the height of 1.3 m above the ground using a diameter tape, and the height of each tree was measured using a meter pole. Individuals with a DBH less than 2.5 cm and a total height < 1.0 m were grouped as seedlings, and those with DBH < 2.5 cm with a total height within 1-2 m were recorded as saplings. Voucher specimens were collected for identification and authentication. Species nomenclature follows the correct and accepted name in The Plant List Database (i.e., www.theplantlist.org) and Co's Digital Flora of the Philippines (i.e., www.philippineplants.org). The fruit types and seed dispersal agents of the species were identified by a plant taxonomist, which was validated using herbarium samples.

Data analysis

For each study period, the species richness (S), Shannon-Weiner diversity (H'), and evenness (E) were calculated using Multivariate Statistical Package (MVSP) software version 3.2.2. The change in the vegetation structure of the plantation was determined following the formulae in Table 1. The frequency, stem density (trees ha^{-1}), and basal area (BA, $m^2 ha^{-1}$) were calculated for all trees. The importance values (IV in %) of regenerating woody species encountered in the sampled plots were computed by obtaining the summation of the relative values of frequency, stem density, and basal area. The IV measures a given species' dominance in a forest area based on species and stands structure. In this study, it was determined to describe the ecological significance of the species on the plantation.

Canopy closure percentage was measured at the center of each plot with the HemiView Forest Canopy Image Analysis software. The images were obtained by looking upwards from the forest floor using a fisheye lens and a high-resolution camera. Four readings were taken per plot and averaged.

The aboveground biomass (AGB) was estimated using the allometric equation (i.e., AGB = exp [-2.134 + 2.530 x log (DBH)] developed for a tropical forest in Southeast Asia using the DBH values (Walker et al. 2016).

Statistical analysis

The statistical analysis was performed using the R Statistical Package Software (version R-3.5.1) following the 95% confidence level. The basal area, stem density, biomass growth, species diversity, species evenness and richness, and canopy closure percent were compared using paired t-test.

RESULTS AND DISCUSSION

Results showed that floristic diversity and composition, and stand structure in the *A. auriculiformis* plantation improved in 2019 relative to 2008 (Figure 3; Table 2). Specifically, the 2019 survey had a significantly higher stem density than the 2008 survey, i.e., from 1,324 trees ha^{-1} to 2,135 trees ha^{-1} for individuals with DBH > 2.5 cm and from 403 trees ha^{-1} to 711 trees ha^{-1} for all seedlings and saplings (Table 2). This is consistent with the pattern reported in several studies in monoculture plantations of exotics, such as *Eucalyptus* and *Acacia* species (Zhang et al. 2016; Bekele and Abebe 2018). Moreover, the species diversity in the plantation significantly increased from low (H' = 1.99, E = 0.32, S = 23) to moderate (H' = 2.88, E = 0.77, S = 55). Planted and naturalizing stands of shade-intolerant introduced tree species of acacias facilitate the establishment of shade-tolerant native forest species (Geldenhuys et al. 2017). Similarly, an *Acacia* plantation in a subtropical zone has slowly transformed into a natural forest after 34 years of development because of the gradual increase in plant diversity (Ren et al. 2020).

The relative count of native species increased from only 15 (27.5%) in 2008 to 40 (72.4%) species in 2009-2019 (Table 3; Figure 4). Higher regeneration of native species than non-native ones in the exotic plantation was reported in several studies (Tulod et al. 2017; Combalicer et al. 2018). In Southern Ethiopia, monoculture plantations of four exotics species (*i.e*., *Cupressus lusitanica*, *Eucalyptus globulus*, *E. saligna*, and *Pinus patula*) recruited and enhanced the regeneration of native woody species (Goodale et al. 2012). Other exotic species plantations, however, might negatively control natural regeneration by suppressing or limiting the growth of native saplings and increasing competition for resources. For example, the *Swietenia macrophylla* plantation inhibited the growth of native wildlings due to the thick layer of leaf litter in the forest understory (Galano et al. 2021). Self-seeding characteristic of some exotic tree species has also been associated with low native plant regeneration in the understory (Firsov and Byalt 2016). Moreover, the nitrogen-fixing ability of *Acacias* in Australia interacted with the slow decomposition of phyllodes, which resulted in the alteration of soil nutrient cycling and hindered the competitive ability of native species (de Jesus et al. 2020). The shading effect of the large crown of *Acacias* may also have a negative effect on plant diversity and favor the emergence of herbaceous and grasses in the understory.

Further, Table 3 shows the list of plant species recorded from the understory of the plantation between the two study periods. In the 1993-2008 period, the understory was dominated by grasses, undershrub, and shrubs (*I. cylindrica*, *Lantana camara*, and *Chromolaena odorata)* with IV ranging from 30 to 40%. This suggests that the area gradually transitioned from degraded grassland into a shrubland ecosystem because of the presence of shrub to small tree species with IV ranging from 37-52%. These species include *Calliandra calothyrsus*, *Ficus nota*, *Pipturus arborescens*, and *Trema orientalis* associated with *A. auriculiformis*. Later, the site became dominated by small to medium trees in the 2009-2019 study period, most of which are native species such as *Alstonia macrophylla, Antidesma bunius, Bridelia insulana, Diplodiscus paniculatus, Pterocarpus indicus, and Pterocymbium tinctorium* with IV of 19-33%. The dominance of *I. cylindrica*, *C. odorata*, and *L. camara* significantly declined from 37-38% in the 1993-2008 study period to less than 1.20% in the 2009-2019 period. These species may have been replaced by other plants, including palms (*Arenga* sp.), vines (*Arcangelisia* sp.*)*, subshrub (*Bombax* sp.), and rhizomes (*Zingiber* sp.) in the 2009-2019 study period, which were all absent in the previous study period.

Table 2. Stand characteristics of *A. auriculiformis* plantation of the 1993-2008 and 2009-2019 study periods

Items	1993-2008	2009-2019
Basal area ($m^2 ha^{-1}$)	46.33[a]	53.71[a]
Stem density (> 2. 5 cm DBH, trees ha^{-1})	1324[b]	2135[a]
Seedling density (≤ 2.5 cm DBH, trees ha^{-1})	403[b]	711[a]
Aboveground biomass growth (tons ha^{-1})	103.09[a]	122.10[a]
Species diversity (H')	1.99[b]	2.88[a]
Evenness (E)	0.32[b]	0.77[a]
Richness (S)	23[b]	55[a]
Canopy closure (%)	18[a]	10[b]

Note: different lowercase letters indicate statistical significance between the two study periods

Table 1. Parameters used to determine the floristic diversity and composition, and stand structure of the *A. auriculiformis* plantation.

Parameters	Description	Formula
Basal area	The cross-sectional area of trees at breast height.	BA = 0.7854 × DBH^2
Species stem density	The actual size or number of individuals of one species per unit area.	SDen = No. of individuals of one species/AS
Relative density	The density of one species as a percent of the total density of all species.	RDen = (SDen for a species/ total density for all species) × 100
Species frequency	The number of times a plant species is present in a given number of plots or quadrats.	SFre = No. of plots in which species occur/ total number of plots sampled
Relative frequency	The frequency of one species as a percent of the total frequency of all species.	RFre = (SFre for a species/ total frequency for all species) × 100
Dominance	A species that is most commonly found or dominant based on basal area or percent coverage.	SDom = BA of one species/AS
Relative dominance	The dominance of one species as a percent of the total dominance of all species.	RDen = (SDom for a species/ total dominance for all species) × 100
Importance values	The IV is a measure of how dominant a species is in a given forest area.	IV = RDen + RFre + SDom

Note: SDen: Species density; RDen: Relative density; SFre: Species frequency; RFre: Relative Frequency; SDom: Species dominance; RDom: Relative dominance; IV: Importance values; BA: Basal area; AS: Area sampled, DBH: diameter at breast height

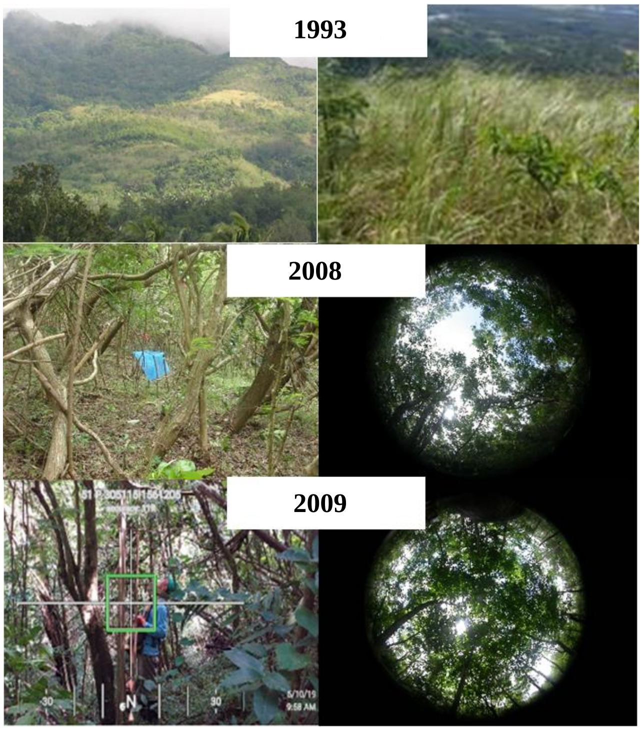

Figure 3. Changes in stand characteristics of *A. auriculiformis* plantation from 1993 to 2019 study periods

Overall, results indicate that the species and stand structure in the *A. auriculiformis* plantation have changed positively with time. Our results support previous reports that exotic tree plantations may play a key role in biodiversity conservation and forest restoration (Zhang et al. 2016; Veridiano et al. 2020). Previous studies attributed the results to the ability of *A. auriculiformis* to fix nitrogen and reduce photoinhibition of understory species. This nitrogen-fixing ability allows the species to adapt to a wide range of environmental conditions prevailing in the soils (Lipa and Janczarek 2020). Such a characteristic may have improved soil fertility in the area over time, creating more suitable microclimatic conditions for tree regeneration. Hence, the plantation may have facilitated the emergence of heliophilous (tolerates a high level of direct sunlight) pioneer species such as *C. odorata, Ficus nota, Ficus septica, L. camara, Macaranga tanarius, Pipturus arborescens, Tabernaemontana pandacaqui,* and *Trema orientalis*, which were initially absent in the area. Gradually, these species may have further improved the growing condition in the understory of the plantation.

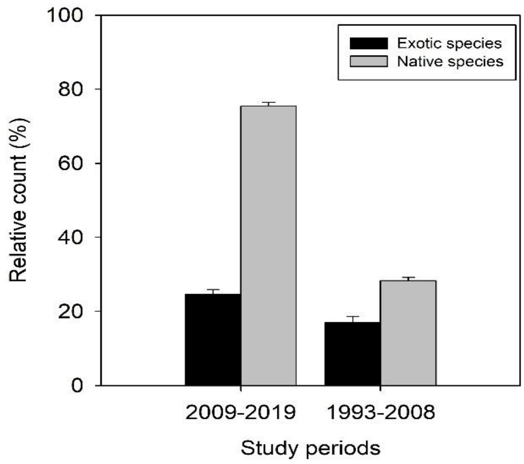

Figure 4. Relative count of naturally regenerated exotic and native species in *Acacia auriculiformis* plantation between 1993-2008 and 2009-2019 study periods. The bars indicate standard errors (n = 177).

Table 3. Regenerated plants in *Acacia auriculiformis* plantation of the 1993-2008 and 2009-2019 study periods

Scientific name	IVI 1993-2008	IVI 2009-2019	Geographic range	Dispersal mode
Anacardiacea				
Dracontomelon dao (Blanco) Merr. & Rolfe		6.89	Na	Zoochory
Apocynaceae				
Alstonia macrophylla Wall. ex DC		23.07	Na	Anemochory
Tabernaemontana pandacaqui Poir	1.5	3.51	En	Autochory
Voacanga globosa (Blanco) Merr.		1.05	En	Autochory
Wrightia pubescens R. Br.ssp. laniti (Blanco) Ngan		5.07		Anemochory
Asteraceae				
Chromolaena odorata (L.) R.M.King &H.Rob.	32.11	0.34	Ex	Anemochory
Bignoniaceae				
Spathodea campanulata Beauv.	0.1	0.63	Ex	Anemochory
Brownlowiaceae				
Berrya ammonilla Roxb		1.83	Na	
Diplodiscus paniculatus Turez		33.04	En	Anemochory
Burseraceae				
Canarium asperum Benth.		0.33	Na	Zoochory
Cannabaceae				
Trema orientalis (L.) Blume	35.09	1.01	Na	Zoochory
Combretaceae				
Terminalia microcarpa Steud.		0.71	Na	Zoochory

Euphorbiaceae				
Acalypha amentacea Roxb.	5.53	0.2	Na	Anemochory
Macaranga bicolor Müll.Arg.	1.53	6.29	En	Anemochory
Macaranga tanarius (L.) Muell.-Arg.	1.07	2.7	Na	Anemochory
Neotrewia cumingii (Muell.-Arg) Pax & Hoffm.		0.83	Na	Zoochory
Fabaceae				
Aeschynomene americana L.	0.54	0.32	Ex	
Calliandra calothyrsus Meissn.	36.97	5.52	Ex	Autochory
Gliricidia sepium (Jacq.) Kunth ex Walp	7.54	16.67	Ex	Autochory
Leucaena leucocephala (Lam.) de Wit	1.33	1.41	Ex	Autochory
Pterocarpus indicus Rojo	1.72	18.8	Na	Anemochory
Wallaceodendron celebicum Koord.		18.16	En	Autochory
Lamiaceae				
Callicarpa formosana Rolfe		0.11	Na	Zoochory
Clerodendrum intermedium Cham.	5.01	6.13	Na	Zoochory
Gmelina arborea Roxb.	0.12	18.09	Ex	Zoochory
Hyptis suaveolens (L.) Poit.		1.11	Ex	Anemochory
Lauraceae				
Cinnamomum camphora Nees & Eberm		1.05	Ex	Zoochory
Litsea cordata (Jack.) Hook.f.		1.33	Na	Zoochory
Meliaceae				
Aglaia edulis (Roxb.) Wall		0.72	Na	Autochory
Melia dubia Cav.		0.49	Ex	Zoochory
Moraceae				
Ficus ampelas Burm.f.		4.2	Na	Zoochory
Ficus nota (Blanco) Merr.	52.02	7.29	Na	Zoochory
Ficus septica Burm.F.	6.58	6.01	Na	Zoochory
Malaisia scandens (Lour.) Planch.		1.6	Na	Zoochory
Myristicaceae				
Myristica elliptica Wall. Ex. Hook.f.&Thoms		0.34	Na	Zoochory
Myrsinaceae				
Ardisia squamulosa Elmer		0.62	En	Zoochory
Myrtaceae				
Psidium guajava L.		6.21	Na	Zoochory
Phyllanthaceae	0.11			
Antidesma bunius (L.) Spreng		30.06	Na	Zoochory
Antidesma pentandrum (Blanco) Merr.	0.62	1.3	Na	Zoochory
Bridelia insulana Hance		31.07	Na	Zoochory
Phyllanthus urinaria L.		1.45	Na	Zoochory
Poaceae				
Imperata cylindrica (L.) Beauv.	40.92	0	Na	Anemochory
Primulaceae				
Ardisia pyramidalis (Cav.) Pers.		0.28	Na	Zoochory
Putranjivaceae				
Drypetes maquilingensis (Merr.) Pax & K. Hoffm.		1.88	Na	Zoochory
Rubiaceae				
Coffea arabica L.	4.52	1.11	Ex	Zoochory
Sapindaceae				
Ganophyllum falcatum Blume		1.88	Na	Zoochory
Sapindus saponaria L. forma *microcarpa* Radlk.		1.25	Ex	
Scrophulariaceae				
Buddleja asiatica Lour.		0.34	Na	Anemochory
Sterculiaceae				
Pterocymbium tinctorium (Blanco) Merr.		22.03	Na	Anemochory
Sterculia oblongata R.Br.		0.49	Na	Anemochory
Thymelaeaceae				
Wikstroemia lanceolata Merr.		1.37	Na	Zoochory
Urticaceae				
Maoutia setosa Wedd.	1.95	0	Na	Zoochory
Pipturus arborescens (Link) C.B. Rob.	33.01	0.59	Na	Zoochory
Verbenaceae				
Lantana camara L.	30.12	1.2	Ex	Zoochory

Notes: IVI: Important Value Index (%); Na: native; En: endemic; and Ex: exotic

Areas with *Ficus* trees increased soil fertility via litterfall compared to areas where they were absent (Berhe et al. 2013; Dhanya et al. 2013). Another example is *C. odorata,* considered a good heliophyte during ecological succession by acting as a nutrient sink and alternative source of organic matter and macronutrients in degraded lands (Seyni et al. 2021). This continuous site improvement possibly led to the unsuccessful self-regeneration or naturalization of *A. auriculiformis*, consistent with Nghiem et al. (2015). No wildlings of *A. auriculiformis* were observed in the study site during both study periods. The result can be ascribed to the created canopy gap (increased light transmittance) and the death of sexually mature trees due to super typhoon Glenda (*Rammasun*) that hit the plantation in July 2014 (rainy season). The number of remaining *A. auriculiformis* trees in the 28-year study period decreased to only 83%. Such an effect of the typhoon can be supported by the observed lower canopy closure in 2019 than in 2008. Shade-intolerant species which could not regenerate under shaded conditions may have been given a chance to regenerate after the canopy was opened due to the typhoon. Further, the wet season may have facilitated the decomposition of litterfall in the area, which may have advanced the emergence of pioneer species in the understory but suppressed the regeneration of the *A. auriculiformis*. Based on the gap dynamics theory, shade-intolerant species can reestablish their populations by regeneration within gaps (Zhu et al. 2014), but the environment should be suitable for their regeneration (Hernandez et al. 2020). Overall, the canopy gap creation caused by Typhoon Glenda could partially explain the higher proportion of shade-intolerant species in the 2009-2019 study period, including *P. tinctorium, M. dubia, T. microcarpa,* and *D. dao.* These species are shade-intolerant based on crown structure, growth strategies, height growth rate, foliar phenology, and root depth (Nguyen et al. 2014). In contrast to our findings, the density of early settled heliophilous pioneer species significantly declined as the canopy of *A. mangium* plantation developed with age, and these species were replaced by mesophytes and shade-tolerant plants (Ren et al. 2021). This could imply that the result obtained could have differed without disturbance (*i.e.*, typhoon). Thus, silvicultural management, such as thinning and pruning, may also be conducted in *A. auriculiformis* plantation to facilitate the regeneration of shade-intolerant species.

Further, the *A. auriculiformis* plantation is only 50-100 m away from the undisturbed adjacent forest, explaining the dominance of animal-and-wind-dispersed trees in both study periods. High dominance of naturally growing animal-and-wind-dispersed species (e.g., *F. nota*, *Neonauclea bartlingii*, and *Pterocarpus indicus*) was also recorded in a portion of the Sipit Watershed near the study site (Castillo et al. 2020). Hence, we could also infer that the seeds of *A. bunius, B. insulana, C. intermedium,* and *F. nota* may have been deposited into the plantation via zoochory and high regeneration of small-medium trees in the 2009-2019 study period, such as *A. macrophylla, P. indicus,* and *P. tinctorium* with winged fruit type, by anemochory. *A. macrophylla* is a shade-tolerant pioneer species common across a wide range of disturbance environments (Goodale et al. 2012). *P. tinctorium* can have advanced regeneration in both gap and non-gap areas in the forest; hence, it is also considered both gap maker and gap filler in MMFR. In this study, *D. paniculatus* and *Wallaceodendron celebicum* with high IV of 33 and 18% were observed, respectively, only in the 2009-2019 study period. These species have capsule fruits that split when mature to release the seeds on their own (autochory), which has a short-distance scope (Sádlo et al. 2018). *A. auriculiformis* plantation was once a dense forest and was converted to grassland due to massive deforestation in the 1970s-1980s. Seeds of *D. paniculatus* and *Wallaceodendron celebicum,* common in MMFR, may have long been deposited in the soil seed bank and germinated when the environment became favorable for germination and/or a typhoon opened the canopy. In our previous work in MMFR, we found that the species composition of emergent seedlings from soil seed banks was similar between natural forest (control plot) and Mahogany plantations, and most of these species are autochorous and/or animal-dispersed plants.

In conclusion, the species and stand structure in the plantation changed significantly with the plantation age. The number of native species was higher in 2009-2019 than in 1993-2008. Thus, results suggest that *A. auriculiformis* plantations can allow the restoration of species and stand structure of degraded lands in MMFR. However, monitoring studies on the other key ecosystem attributes (e.g., ecosystem functionality, external exchanges, structural diversity) of the plantation are recommended to enhance our understanding of the species' potential for restoration.

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