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Authors: Sadili, Asep, Hidayat, Arief, Jakalalana, Supardi, Kurniawan, Adi, Sahroni, Deni, et al.

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Forest composition and structure after 200 years of succession following the eruption of Mount Tambora (Indonesia)

Asep Sadili^a, Arief Hidayat^b, Supardi Jakalalana^a, Adi Kurniawan^c, Deni Sahroni^a, Solikin^d and Francis Q. Brearley^e

^aBotany Division, Research Center for Biology, Indonesian Institute of Sciences, Cibinong Science Center, Cibinong, Indonesia; ^bResearch Center for Plant Conservation and Botanic Gardens, Indonesian Institute of Sciences, Bogor, Indonesia; ^cTambora National Park, Directorate General of Natural Resources and Ecosystem Conservation, Ministry of Environment and Forestry of Indonesia, Dompu, Indonesia; ^dPurwodadi Botanical Gardens, Indonesian Institute of Sciences, Pasuruan, Indonesia; ^eDepartment of Natural Sciences, Manchester Metropolitan University, Manchester, UK

ABSTRACT

We examined the changes in tropical forest diversity, structure and trait composition during primary succession after volcanic disturbance. Whilst many studies have examined early stages of succession, fewer have looked at a precisely dated older location: 200 years old in this instance. To do this, we established a 0.5 ha plot on the lower slopes of Gunung (Mount) Tambora (Sumbawa, Indonesia) in which we enumerated and identified all trees ≥ 10 cm dbh, determined their key traits and calculated forest above-ground biomass. Saplings (1.5–3.0 cm dbh) were enumerated in one quarter of this area. We recorded 214 stems ≥ 10 cm dbh within 21 taxa contributing to an above-ground biomass of 135 Mg ha⁻¹. Most trees had light wood and broad distributions suggestive of early successional traits, but leaves were generally small; most trees were insect pollinated and animal dispersed as expected at later stages of succession. Saplings were variable in their density and showed some floristic similarity with adult trees, but differences indicated the future trajectory of succession. Our floristic and structural data from the poorly studied drier forests of eastern Indonesia show that this 200-year-old forest is still undergoing succession at a slow rate.

RÉSUMÉ

Nous avons examiné les changements de diversité, de structure et de composition des traits dans une forêt tropicale pendant la succession primaire suite à une éruption volcanique. Tandis que plusieurs études ont examiné les premiers stades de la succession, peu se sont attardées à des stades plus avancés: 200 ans dans le cas présent. Pour ce faire, nous avons établi un quadrat de 0,5 ha sur le bas de la pente du Gunung (Mont) Tambora (Sumbawa, Indonésie), à l'intérieur duquel nous avons énuméré et identifié tous les arbres ≥ 10 cm dhp, déterminé leurs traits principaux et calculé la biomasse forestière aérienne. Les gaulis (1,5 – 3,0 cm dhp) ont été dénombrés dans un quart du quadrat. Nous avons relevé 214 tiges ≥ 10 cm dhp appartenant à 21 taxons contribuant à une biomasse aérienne de 135 Mg ha⁻¹. La plupart des arbres avaient du bois clair et une répartition étendue, suggérant des traits de début de succession, mais leurs feuilles étaient généralement petites et la plupart des espèces étaient pollinisées par des insectes et zoochores, tel qu'attendu pour les stades plus avancés de la succession. Les gaulis avaient une densité variable et une certaine similarité floristique avec les arbres adultes. Des différences indiquaient toutefois la future trajectoire successione. Les données floristiques et structurales que nous avons amassées concernant les forêts sèches peu étudiées de l'est de l'Indonésie montrent que la succession s'y poursuit, à un rythme lent, 200 ans après une éruption volcanique.

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Introduction

Volcanic activity is a major disturbance to ecosystems, regularly destroying existing communities and creating new substrates for colonisation. Understanding how vegetation changes following disturbance is a central goal of much ecological research and, thus, succession in volcanic landscapes can be informative in this regard. We have information on changes in species composition and diversity during post-volcanic succession from many

sites globally (e.g., Aplet et al. 1998; Kamiyo et al. 2002; Dale et al. 2005; Elias and Dias 2007; Walker et al. 2013; Karadimou et al. 2018) including South-east Asian tropical regions such as Indonesia (Whittaker et al. 1989; Sutomo and Cramer 2011), Papua New Guinea (Taylor 1957; Harrison et al. 2001) and the Philippines (Marler and Del Moral 2011, 2018).

Indonesia is an island nation lying on the 'Ring of Fire' and, as such, much of the country has been, and continues to be, influenced by volcanic processes from one

CONTACT Francis Q. Brearley  f.q.brearley@mmu.ac.uk  Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, UK

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of the many active volcanoes present. Whilst post-disturbance secondary forests have been well-studied across Indonesia (e.g., Brearley et al. 2004; Samsedin and Heriyanto 2010; Stas et al. 2017) primary succession has been less well studied although described from Gunung (Mount) Merapi on Java (Sutomo and Cramer 2011) and the particularly well-known Krakatau Islands (Whittaker et al. 1989; Thornton 1996). Furthermore, the forests of western Indonesia have been much better studied than the drier forests of the south-eastern regions of the country (Brearley et al. 2019) with only a few quantitative floristic studies from these seasonal forests (Laumonier and Nasi 2018; Mansur 2020; Sutomo et al. 2020).

The April 1815 eruption of Gunung Tambora was one of the most powerful and destructive in recorded history with a huge amount of material released into the atmosphere leading to subsequent global climatic anomalies and the infamous 'year without a summer' (Stothers 1984; de Jong Boers 1995; Oppenheimer 2003). More locally, areas in the immediate vicinity of the volcano were subject to extremely destructive pyroclastic flows and likely completely destroyed and sterilised. The eruption formed the largest caldera in Indonesia with a diameter 6 to 7 kilometres, a depth of about 950 m and with the highest point of the crater rim 2850 m above sea level. The area around Gunung Tambora was designated a conservation area since 1937 and, in commemorating the 200th anniversary of the eruption, Gunung Tambora National Park with an area of 71,646 hectares, was inaugurated on 11 April 2015. The national park is one of the youngest national parks in Indonesia and research is still minimal (Santika and Hidayat 2017); therefore, the aim of this study was to describe the vegetation structure, species diversity and species traits on the northern slopes of the volcano within the national park. Our study provides data on forest composition in an area of Indonesia that is generally poorly studied and leads to improved knowledge on post-volcanic tropical forest succession more generally.

Methods

Study site

Gunung Tambora is found in north-central Sumbawa, an island in the Lesser Sunda chain of Indonesia, where it forms the majority of the Sanggar peninsula. Mean annual precipitation is poorly documented but is around 1600 to 2200 mm and seasonal, with the greatest rainfall in January and the driest month in July with the climate classified as Köppen's Aw; precipitation appears to

increase with elevation on the mountain. The research location is lowland forest at Kawinda To'i Village (Tambora District, Bima Regency, Nusa Tenggara Barat Province). The study site is about 1 km east of the Oi Maray river near the border of the National Park (8° 07'00"S 118°01'24"E) at an altitude of 50 m a.m.s.l. The volcanic deposits under the forest may be tens of metres thick composed of layers of pyroclastic flows, ash and pumice from trachyandesitic lava (Self et al. 1984; Sigurdsson and Carey 1989; Sutawidjaja et al. 2006).

Field sampling

We established a permanent sampling plot measuring 50 m x 100 m (0.5 ha), with 50 subplots of 10 m x 10 m, in which all trees ≥ 10 cm dbh (diameter at breast height; 1.3 m) were recorded; lianas were not present and thus not enumerated. The plot was located in undisturbed forest considered representative of the north side of the volcano and close to a path to the summit. The slope was about 10° with the plot long axis running perpendicular to it. We marked each tree permanently with an aluminium tag and recorded their diameters (at 1.3 m) using a measuring tape or taking the measurement 10 cm above the buttress for buttressed trees. Tree height was measured using a Haga meter. Each individual was identified with the aid of local assistants using the name of the species in the local (Bima) language. Voucher specimens were then collected for subsequent naming at Herbarium Bogoriense where the vouchers were deposited. Most individuals (86%) could be identified to species with two taxa identified to genus only. For saplings, (diameter 1.5 to 3.0 cm) we recorded all individuals in a 5 m x 5 m area within each larger 10 x 10 m subplot. Again, 86% could be identified to species with two taxa (one of which was the same as above) identified to genus only.

Analyses

We calculated species diversity metrics (Chao1, Fisher's alpha, Shannon-Wiener) for all trees ≥ 10 cm dbh using the equations in Colwell (2009) and the importance value index (IVI) according to Mueller-Dombois and Ellenberg (1974). For plant traits, we used the Global Wood Density database of Zanne et al. (2009) (the genus mean was used for four species) and measured leaf area (length x width x $\frac{\pi}{4}$; Li et al. 2020) on herbarium specimens using the median leaf area (on a mean of $28.7 \pm \text{SD } 13.9$ leaves) to categorise leaf sizes according to Webb (1959). Species' distributions were assessed by reference to Plants of the World Online (POWO 2020) and pollination and dispersal syndromes were assessed

by reference to relevant literature. To estimate forest above-ground biomass, the pan-tropical M4 allometric equation of Chave et al. (2014) was used, as well as that of Stas et al. (2017) which was developed for old secondary forest on Seram and is therefore more appropriate biogeographically (Anitha et al. 2015).

Results

In the half-a-hectare permanent sampling plot, we enumerated 214 stems ≥ 10 cm dbh within 21 'species' and 14 families (Table 1). The most abundant species were *Palaquium amboinense* (Sapotaceae), *Mallotus philippensis* (Euphorbiaceae) and *Alstonia spectabilis* (Apocynaceae), and the family with most species was Malvaceae (four species) followed by Euphorbiaceae

(three species) (Table 1). All trees could be identified to genus but there was an unidentified *Syzygium* (Myrtaceae) and *Mallotus* (Euphorbiaceae) species that were both fairly common. Fisher's alpha was 5.77 and Shannon-Wiener H' was 2.45. Our sampling area appeared to be sufficient as the species area curve levelled off (Figure 1(a)) but the Chao 1 estimate of species richness was 48 species, as we had a relatively large number (8) of singletons (Figure 1(b)).

The stem size abundance showed a typical distribution for tropical forests (Figure 2(a)); there were only three stems greater than 60 cm dbh: one each of *Alstonia scholaris* (Apocynaceae), *Ficus racemosa* (Moraceae) and *Palaquium amboinense*. The five most important species (i.e., greatest IVI) had contrasting stem size distributions: *Palaquium amboinense* and

Table 1. Abundance and characteristics of tree species in a 0.5 ha sampling plot in a secondary forest on a 200-year-old volcanic substrate in Gunung Tambora National Park (Sumbawa, Indonesia). Species are ranked by their importance value index (IVI). * = genus mean wood density.

Species	Family	Bima name	No. Stems	IVI	Mean ($\pm$ s.d.) diameter (cm)	Wood density (g cm ⁻²)	Leaf size
<i>Palaquium amboinense</i>	Sapotaceae	Katowi	34	56.40	27.0 $\pm$ 11.9	0.38	Notophyll
<i>Mallotus philippensis</i>	Euphorbiaceae	Safiru doro	39	41.01	16.3 $\pm$ 3.7	0.60	Microphyll
<i>Alstonia spectabilis</i>	Apocynaceae	Tula	28	35.24	19.6 $\pm$ 6.6	0.63	Mesophyll
<i>Syzygium</i> sp.	Myrtaceae	Monggo merah	19	33.44	29.6 $\pm$ 13.5	0.67*	Notophyll
<i>Ficus racemosa</i>	Moraceae	Na'a	12	28.92	43.4 $\pm$ 15.0	0.36	Microphyll
<i>Grewia eriocarpa</i>	Malvaceae	Rino kafa	21	22.59	14.2 $\pm$ 2.2	0.67	Microphyll
<i>Schleichera oleosa</i>	Sapindaceae	Kusambi	16	21.06	22.5 $\pm$ 8.9	0.90	Microphyll
<i>Alstonia scholaris</i>	Apocynaceae	Rida	10	16.47	22.1 $\pm$ 15.0	0.38	Mesophyll
<i>Mallotus</i> sp.	Euphorbiaceae	Safiri	12	11.35	15.0 $\pm$ 2.7	0.50*	Mesophyll
<i>Buchanania arborescens</i>	Anacardiaceae	Pato	6	9.37	27.9 $\pm$ 5.5	0.45	Notophyll
<i>Pterospermum diversifolium</i>	Malvaceae	Sala	4	5.39	19.6 $\pm$ 8.6	0.57	Notophyll
<i>Gmelina asiatica</i>	Lamiaceae	Kenanga	3	4.01	21.4 $\pm$ 8.6	0.47*	Microphyll
<i>Ficus hispida</i>	Moraceae	Mpusu	2	2.70	14.2 $\pm$ 3.0	0.38	Mesophyll
<i>Schoutenia ovata</i>	Malvaceae	Luhu/ Walikunkun	1	1.99	-	0.79	Microphyll
<i>Protium javanicum</i>	Burseraceae	Loa ketimis	1	1.78	-	0.75	Microphyll
<i>Exocarpos latifolius</i>	Santalaceae	Ncawu wera	1	1.69	-	0.86	Microphyll
<i>Phyllanthus emblica</i>	Phyllanthaceae	Sarume maju	1	1.40	-	0.64	Leptophyll
<i>Homalanthus giganteus</i>	Euphorbiaceae	Danta dolo	1	1.30	-	0.28*	Mesophyll
<i>Diospyros maritima</i>	Ebenaceae	Haju api	1	1.29	-	0.56	Notophyll
<i>Glochidion zeylanicum</i> var. <i>arborescens</i>	Phyllanthaceae	Mbune	1	1.29	-	0.52	Microphyll
<i>Kleinhovia hospita</i>	Malvaceae	Ntana mee	1	1.29	-	0.43	Notophyll

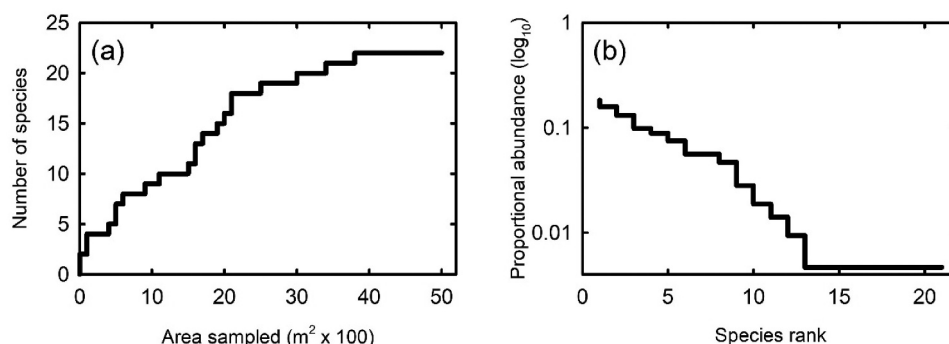


Figure 1. (a) Species-area and (b) rank abundance curve for trees in a secondary forest on a 200-year-old volcanic substrate in Gunung Tambora National Park (Sumbawa, Indonesia).

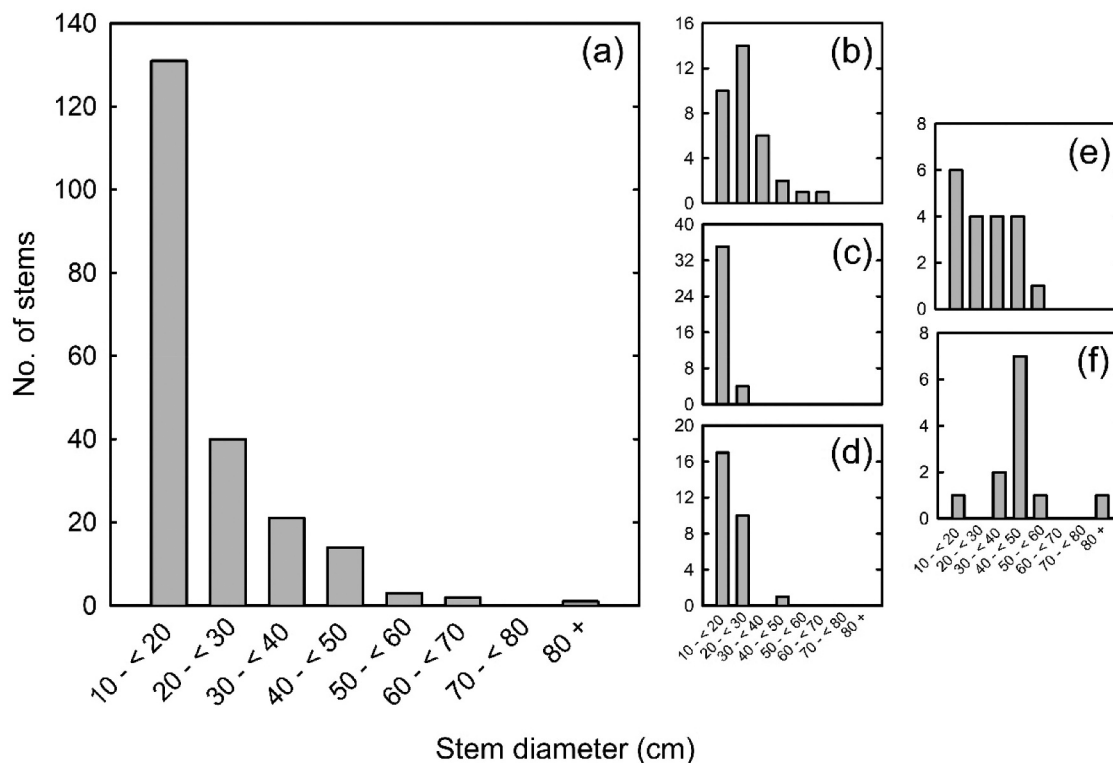


Figure 2. Stem diameter distribution for trees in a secondary forest on a 200-year-old volcanic substrate in Gunung Tambora National Park (Sumbawa, Indonesia). Panel (a) shows all trees, whereas panels (b) to (f) show diameter distributions for the five most important (i.e., with greatest IVI) species: (b) *Palaquium amboinense* (c) *Mallotus philippensis* (d) *Alstonia spectabilis* (e) *Syzygium* sp. and (f) *Ficus racemosa* (note different scales on the y-axis for each species).

Syzygium sp. showed typical distributions (Figure 2(b,e)) although there were fewer trees in the smallest size class for *Palaquium amboinense* (Figure 2(b)); *Mallotus philippensis* was truncated towards the smaller size classes (Figure 2(c)), as was *Alstonia spectabilis* indicating more recent colonisation and/or generally smaller trees (Figure 2(d)); *Ficus racemosa* showed a random distribution across the tree size classes (Figure 2(f)).

Forest basal area was $20.8 \text{ m}^2 \text{ ha}^{-1}$ and above-ground biomass was 135 Mg ha^{-1} using the equation of Chave et al. (2014), which was very similar to 142 Mg ha^{-1} using the Stas et al. (2017) equation; the species that contributed most to the forest biomass were *Palaquium amboinense* and *Syzygium* sp. The forest canopy height was approximately 20 m with some emergents, which were mostly *Palaquium amboinense* or *Syzygium* sp., up to 27 m tall.

About half of the species, and stems, had microphyllous leaves and around 40% were light wooded (i.e., less than 0.50 g cm^{-3}). The median leaf size across all stems was notophyllous and the mean wood density was 0.57 g cm^{-3} (Table 1). Two-thirds of the species had broad distributions that also included areas outside of Malesia; in many cases these included India, China and/

or Australia. Some of these species (three) had an eastern Malesian centre to their distribution extending into Australia or the Solomon Islands whilst another group (two species) showed a dry tropical, but disjunct, distribution including the Lesser Sunda Islands and Indochina. Just two species, *Homalanthus giganteus* (Euphorbiaceae) and *Protium javanicum* (Burseraceae), had distributions restricted to Java and the Lesser Sunda Islands only. There was one naturalised species (*Gmelina asiatica*; Lamiaceae). *Mallotus* species appear to have attributes of wind-pollinated species whereas the rest of the species were insect pollinated. Similarly, the two *Alstonia* species were wind dispersed whilst the rest of the species were dispersed by a range of birds and small and large mammals.

Within one-quarter of the plot, we recorded 63 saplings (1.5 to 3.0 cm dbh) equivalent to $504 \text{ saplings ha}^{-2}$ although variation between subplots was high. Fourteen out of the 21 taxa present as adults (i.e., $\geq 10 \text{ cm dbh}$) were also present as saplings along with five others not found as adults. The most abundant sapling species was *Grewia eriocarpa* (Malvaceae) followed by *Palaquium amboinense* and *Syzygium* sp., and then *Leea aequata* (Vitaceae) that was not present as an adult (Figure 3).

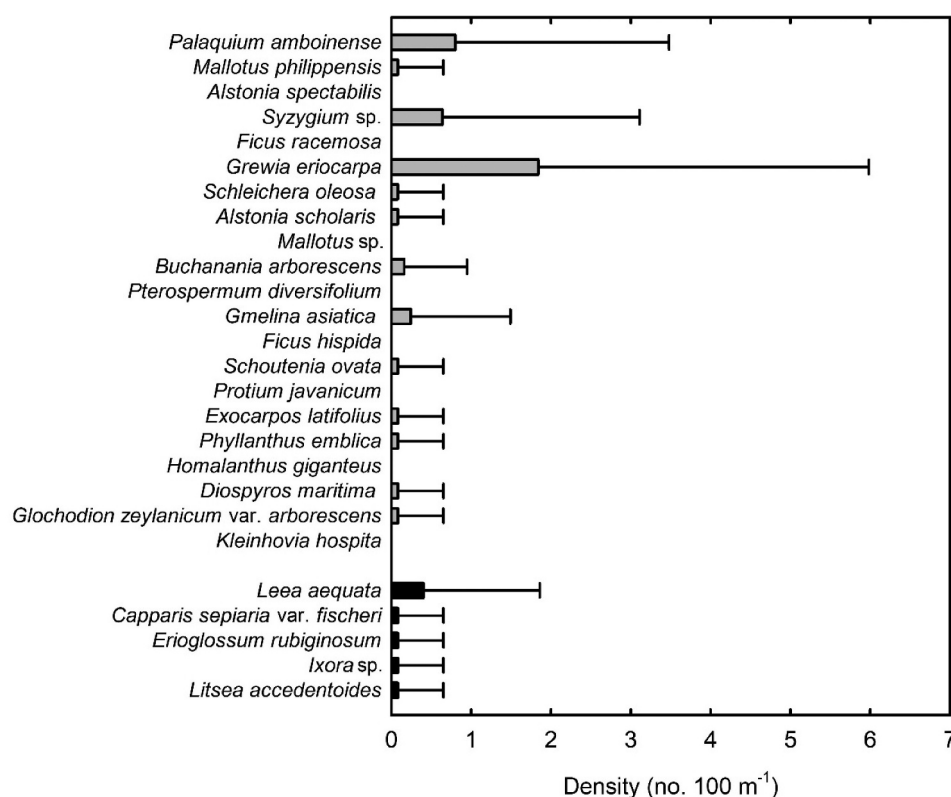


Figure 3. Sapling (1.5 to 3.0 cm dbh) density (mean $\pm$ standard error) in a secondary forest on a 200-year-old volcanic substrate in Gunung Tambora National Park (Sumbawa, Indonesia). Species are ranked according to their IVI as adults with those not present as adults depicted with black bars.

Discussion

The forest on a 200-year-old volcanic substrate that we studied on the northern slopes of Gunung Tambora in Indonesia is still undergoing succession. The tree diversity (Fisher's alpha of ca. 6) was very low when considering other forests of Sundaland (Brearley et al. 2004), Sulawesi (Trethowan et al. 2020) and Seram (Edwards et al. 1993) – indeed, this value is more typical of montane forests across Indonesia (Sulistiyawati et al. 2018). Succession appears to be slow on Tambora with the landscape described as ‘fairly barren’ in 1933, more than 100 years after the colossal eruption (de Jong Boers 1995, in de Jong Boers 1995). In some ways the area is isolated being at the end of a peninsula and surrounded by water on three sides, although some of the western Sanggar peninsular was not influenced by pyroclastic flows (Sigurdsson and Carey 1989) leaving potential re-colonisation nuclei. In comparison with the tree communities in other post-eruption successional environments, the communities in small plots (0.04 ha) on Long Island in Papua New Guinea (trees > ca. 5 cm dbh) showed a tree diversity (Fisher's alpha) similar or lower than the current study (Harrison et al. 2001).

Although the eruption was about 350 years ago on Long Island, the island is much more remote than Tambora (ca. 50 km from the mainland) leading to a slower recovery of the tree flora. Data from two plots (0.5 ha) at Ujung Kulon in west Java, near the location of the 1883 Krakatau eruption, had notably higher Fisher's alpha diversity (15.0 and 23.7) although this site likely just experienced heavy ash fall rather than extensive tree mortality from pyroclastic flows (Purwaningsih and Atikah 2018). Additionally, biomass of the Tambora dry forest at around 140 Mg ha⁻¹ is also low; the nearest comparable forest is a montane forest (0.18 ha studied) in west Sumbawa with nearly three times this biomass (Mansur and Kartawinata 2017). However, biomass is similar to a disturbed dry forest on Lombok with 122 Mg ha⁻¹ (0.64 ha; Mansur 2020) and 50-year-old secondary forest on Seram (1 ha; 140 Mg ha⁻¹; Stas et al. 2017) but much lower than a similar aged forest on Borneo (0.75 ha; 358 Mg ha⁻¹; Brearley et al. 2004). Similarly, Li et al. (2018), showed, through remote sensing analysis that vegetation NDVI (as a broad measure of productivity) was still showing

a linear increase up to 140 years after eruptions on three tropical African volcanoes indicating that they had not yet reached their maximum biomass.

We established our study plot exactly 200 years after the eruption of Gunung Tambora meaning that we obviously missed enumerating the earlier vegetation communities but we can make inferences regarding the recent successional processes. The composition of saplings is broadly similar to the trees indicating that change in the tree community is likely to be slow but there are some notable contrasts such as lack of saplings of *Alstonia spectabilis* and poor regeneration for *Mallotus philippensis*, both of which were common as adults; in contrast, *Grewia eriocarpa* had a high density of saplings that may persist to later stages of succession. The presence of a large proportion of broadly distributed trees is indicative of a generalist community and the generally light-wooded community confirms the forest is still undergoing succession. In contrast, wind pollination and wind dispersal are notable traits at the earliest stages of succession (Tsuyuzaki and Del Moral 1995; Karadimou et al. 2018) and there was only a small proportion of wind-pollinated (*Mallotus* species) or wind-dispersed (*Alstonia* species) trees among the community. The large proportion of trees with microphyllous leaves is indicative of a drier forest community in contrast to wetter Malesian forests with mostly notophylls or mesophylls (Becker et al. 1999; Milliken and Proctor 1999). The generally small leaves may also go some way to explaining the slow rate of forest succession if primary productivity, linked to leaf size (Li et al. 2020), is reduced compared to larger-leaved forests. As succession proceeds, we would expect forest biomass and species richness to increase although it is difficult to predict the course of succession as there are few studied 'reference' forests for comparison.

Although there are studies on similarly-aged tropical forest in Hawaii' (Aplet et al. 1998; Kitayama et al. 1995) It is difficult to make comparisons with other areas of biogeographically related forest as Sumbawa has been poorly studied floristically in comparison with other Indonesian Islands (Brearley et al. 2019). Previous studies on the vegetation of Sumbawa have been conducted by Kostermans (1965) and Wiradinata et al. (2013) among others, but there have been few quantitative studies save that of Mansur and Kartawinata (2017) at Gunung (Mount) Batulante in western Sumbawa which is notably wetter than Tambora. There is also floristic information from Lombok (Mansur 2020; Sutomo et al. 2021) which has dry forest and is therefore more comparable to our study site. Six tree species found in our Tambora forest community were also found at Gunung Batulante (Mansur and Kartawinata 2017) but only in

the secondary forests they studied, not the disturbed primary forest, further confirming the secondary nature of the forests on Gunung Tambora.

In conclusion, the primary successional process in this dry forest on Gunung Tambora appears to be slow as the species diversity and biomass accumulation is low compared to other comparable Malesian forests and the species composition and their traits show indications of a forest still undergoing succession. Succession post volcanic eruption may even take thousands of years as Takeuchi (2005) found a forest on the island of Ambitle (Papua New Guinea) influenced by a volcano that last erupted over 2000 years ago still dominated by early successional species. We hope to continue re-measurements of the Tambora plot for the foreseeable future and provide valuable ongoing data on tropical primary successional processes.

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Data availability

Data will be deposited at ForestPlots.net.

Disclosure statement

No potential conflict of interest was reported by the authors.

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