Research article

Plant community structure and composition in secondary succession following wildfire from *Nuèes Ardentes* of mount Merapi, Indonesia

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Abstract: Patterns of plant community structure and composition during secondary succession following volcanic-fire induced disturbance of *nuées ardentes* was examined in Mount Merapi National Park, Indonesia. Five sites with different age (time since fire) and one undisturbed site were sampled. Species richness, diversity, turnover and importance value index (IVI) were calculated. Sixty one species belonging to 29 families were recorded in the study sites. The highest number of species belonged to the Poaceae (10), followed by Fabaceae (9) and then Asteraceae (6). The number of species present varied as time progressed with a rising trend of species richness and diversity over time and significant differences in species richness and diversity among sites (ANOVA, $p = 0.05$). Species turnover was highest between the 2006 and 1998 sites, and then between the 1997 and 1994 sites. Species turnover between the 1998-1997 sites was similar to the turnover between the 1994 site and the reference site. In terms of vertical structure, four strata were identified in the fire sites whereas in the reference site, all five stratums (A, B, C, D, and E) were present. In terms of quantitative structure based on IVI, each site had different dominating species for tree, groundcover and seedling layers. Non metric multidimensional scaling (NMDS) ordination of plots and analysis of similarity (ANOSIM) test results showed that there were significant differences in species composition between sites (Global $R_{ANOSIM} = 0.93$, P < 0.001). In the Mount Merapi succession, the changes in abundance of some invasive species such as *I. cylindrica*, *Brachiaria* spp., and *Eupatorium* spp. are important to note. These invasive species have different timing in entering the system, but *Imperata cylindrica* was noted almost constantly in every stage of succession except in the undisturbed site.

Keywords: Plant community - Volcanic fire - Disturbance - Secondary succession.

INTRODUCTION

In active volcanoes, volcanic activity remains the most significant threat to forest vegetation (Lavigne & Gunnell 2006, Whitten *et al.* 1996). Fire is an integral part of volcanic disturbance and has shaped community composition in montane forests of Java (van Steenis 1972, Whitten *et al.* 1996). On Mt. Merapi, the intense heat (often more than 700° C) released from *nuées ardentes* ignites wildfires (Bardintzeff 1984). A *nuè ardente* (French for "glowing cloud") is the "rapid movement of extremely hot (often more than 700° C) turbulent gases and fragmental material across a land surface from a volcanic vent. The denser part of a pyroclastic flow, hugs the ground and follows topography and moving with great force and speed (up to 200 km h^{-1})" (Dale *et al.* 2005a).

The montane forests of Java and Bali are not resistant to fire (Marrinan *et al.* 2005). The forests are easily ignited under conditions of prolonged drought, and when lightning strikes oil-rich species such as *Vaccinium* spp. On Mt. Merapi, *nuées ardentes* are the primary cause of forest fire (Simon 1998, Whitten *et al.* 1996). Recovery of the montane forest following fire is usually slow (Horn *et al.* 2001). Fire destroys the aboveground

part of shrubs and some surviving species may be covered with ash, which could slow the rate of the secondary succession (Antos & Zobel 2005, Whitten *et al.* 1996). Severely burned areas on mountains in Java and Bali are usually characterized by the increase in abundance of invasive species, such as *alang-alang* grass (*Imperata cylindrica*), and also white-leaved 'edelweis' (*Anaphalis longifolia*) and bracken fern (*Pteridium aquilinum*) (Whitten *et al.* 1996). *Homalanthus giganteus* is also a common pioneer tree species that occurs during secondary succession in these areas (van Steenis 1972).

Li *et al.* (1999) stated that many succession theories were based on intensive work in temperate forests. Gomez-Pompa and Vasquez-Yanes (1981) and Chazdon *et al.* (2007) studied secondary succession that occurs in the tropics; however their findings were based on work on old fields or in lowland tropical forests. Other forest types such as volcanic tropical montane forest have received little attention (Tsuyuzaki & Hase 2005, Whittaker *et al.* 1999). Furthermore, it is increasingly acknowledged that 'one model fits all' is not appropriate for all communities and ecosystems due to the complexity of each system (Hobbs *et al.* 2007).

The objective of this study was to describe plant community structure and composition in secondary succession using a chronosequence of sites that had been burnt by fires caused by *nuées ardentes* in the tropical montane forest of the Merapi Volcano National Park. We were particularly interested in whether there are any differences in species diversity, turnover, and community structure and composition across sites of different ages, and which species contributed the most to these differences.

MATERIALS AND METHODS

Site description

Mt. Merapi (7º 35' S and 110º 24' E) is administratively located in two provinces, Central Java (Magelang, Boyolali and Klaten Districts) and Yogyakarta (Sleman District). In Yogyakarta Province, Mt. Merapi (± 2,900 m asl) is located approximately 30 kilometres north of Yogyakarta. Mt. Merapi is representative of the landforms, soils and vegetation on a volcanic mountain that typify a large portion of montane ecosystems in Java (Whitten *et al.* 1996). Based on Schmidt and Fergusson's climate classification (1951), the Merapi area is classified as type B - tropical monsoon area, which is characterized by a high intensity of rainfall in the wet season (November–March) with a dry season that can often be very dry without any rainfall (April–October). Annual precipitation varies from 2,500–3,500 millimetres (Anonym 2004). The variation of rainfall on Mt. Merapi's slope is influenced by orographic precipitation. As in many other tropical monsoon areas, there are minor temperature and humidity variations during the year. Relative humidity on Mt. Merapi varies from 70%–90%, with daily average temperatures from 19° to 30° C (Dinas Kehutanan DIY 1999). Soils of the study area are mainly of young volcanic-ash origin (regosol) with shallow and/or deep, low to medium fertility solums with a profile not yet developed (Anonym 2004, Darmawijaya 1990). The soil textures are granulated, whereas the structures are crumbly (Anonym 2004, Dinas Kehutanan DIY 1999).

On Mt. Merapi, areas which have been completely buried by the *nuées ardentes* deposits undergo primary succession. These areas usually occur along the streams, channels or valleys created by the solid material flow paths of *nuées ardentes*. The secondary succession areas were located adjacent to the primary succession areas. These areas are the adjacent forest on either side of the valley or deposit channel which escapes burial and is mainly scorched by the extreme temperature of the *nuées ardentes*. Sites or areas of different ages (years since last *nuée ardente*) were selected to obtain a chronosequence. Identification of site age was conducted by studying aerial photographs, topography maps, and *nuée ardente* history maps (obtained from the Merapi Volcanology Observatory) to date sites affected by recent *nuées ardentes*. Identification was also conducted by reconnaissance study, interviewing long-term residents of the surrounding villages, personal communication with the national park's ranger and managers, and also field site visits. Sites also had to show no obvious signs of human disturbance and be at least 50 metres from any human activities or structures. Based on these, we chose four sites that were affected by *nuées ardentes* at different times (2006, 1998, 1997 and 1994) and one forest area that was mostly undisturbed and had not been affected by *nuées ardentes* for at least 50 yr as a reference site (Fig. 1). The five sites were located in a lower montane zone and were located at a range of altitudes from 1,000 to 1,600 metres. Chronosequence assumptions were met within these sites as they had similar environmental conditions such as climate, substrate, topography and geomorphology, although we acknowledge the limitations of the chronosequence approach and the potential for site-specific factors to be

important. The fieldwork was conducted from March to August 2008. Average environmental conditions in each site are summarized in table 1.
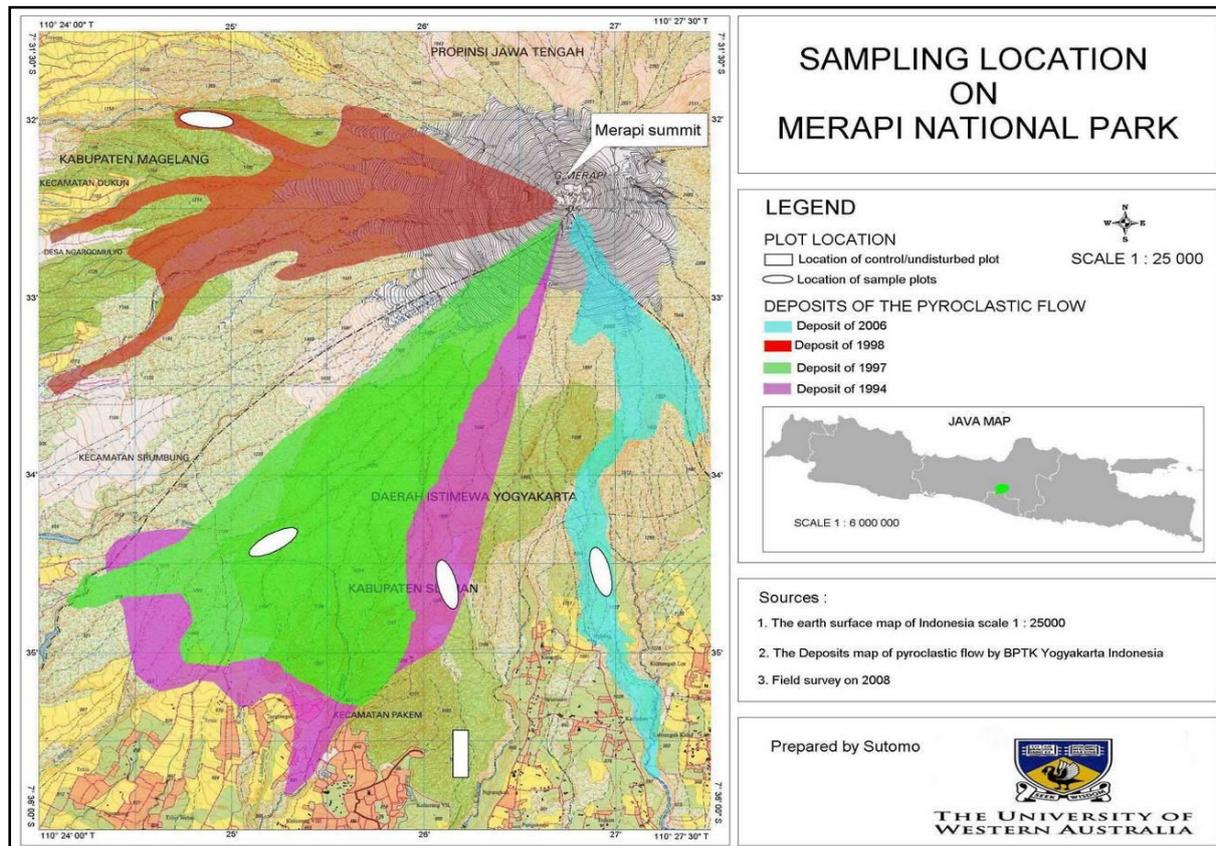
Figure 1. Map of mount Merapi National Park's eruption deposit sites (Circular symbols refer to the position of sampling sites in each deposit. The rectangle refers to the site position of an undisturbed forest in Kaliurang).

Table 1. Site location, *nuées ardentes* history and environmental information in each study sites at Mt. Merapi National Park.

Location	Year of *nuée ardente*	Site age (years)	Soil type	Elevation (m)
Kaliadem	2006	2	Regosol	1,220
Kalilamat	1998	10	Regosol	1,579
Kalibedog	1997	11	Regosol	1,207
Kalikuning	1994	14	Regosol	1,180
Kaliurang	-	-	Regosol	1,000

Vegetation sampling

In April 2008, vegetation was sampled in each of the four sites burnt by fire from *nuées ardentes* in 1994, 1997, 1998 and 2006. One area of unburnt forest (the reference site) was also sampled. The position and altitude of each site were recorded using a GPS, and slope was measured using a clinometer. At each site, an area of approximately 2.5 hectares was chosen and five circular plots (diameter range approximately 60 metres) were randomly placed in the chosen area. In each of these larger plots, three sets of circular plots of 10, 5 and 2 metres diameter were nested within each other to measure trees (10 metre plots), groundcover (5 meter plots) and seedlings (2 metre plots) (Isango 2007, Supriyadi & Marsono 2001). The species name, height and diameter of trees (dbh ≥ 10 cm) and young trees (dbh 2.0–9.9 cm, height ≥ 1.3 m) were recorded. Understorey plants and seedlings were counted (Kent & Coker 1992). All plants were identified to species level when possible. Identification was conducted at the dendrology laboratory, Faculty of Forestry, Gadjah Mada University Yogyakarta, Indonesia. Identification was done using flora books such as "The Flora of Java" (Backer & van den Brink 1963) and "Mountain Flora of Java" and the results were confirmed by a botanist in the Faculty.

Data analysis

Species diversity at each site was calculated using the Shannon-Wiener diversity index. Differences in diversity between sites were tested for significance using a one-way ANOVA in SPSS package V.11.5. To examine short term species turnover (beta diversity), a modified Sorensen's community correspondence index or CCI was used (Barbour *et al.* 1980, Cook *et al.* 2005) with the formula as follows:

$$CCI = \frac{2c}{a+b}$$

Where, a = the number of species present in the first community, b = the number of species present in the second community, and c = the total number of species found in both communities.

I then calculated D, which is an index of how much a species list changes across sites with the formula as follows (Cook *et al.* 2005):

$$D = 1 - CCI$$

This index ranges from 0 to 1, and a low value indicates little change in the species composition between sites whereas a high value indicates the opposite.

In order to examine the vertical structure, forest vegetation was divided into five strata (A, B, C, D and E), as recognized for humid tropical forests (Simon 1996). Stratum A consisted of emergent trees more than 35 metres tall. Stratum B was the main canopy layer with trees 18–35 metres in height. Stratum C consisted of young trees 8–18 metres tall. Stratum D consisted of shrubs and sapling (of trees) with height ranges from 1.5–5.0 metres. Stratum E was the groundcover layer, including grasses, herbs, tree seedlings and fern allies (Simon 1996). The number of trees, young trees (poles), sapling and shrubs that have the characteristics of stratum A, B, C and D were noted, while the number of groundcover species was noted for the E stratum in each of the study sites.

Importance Value Index (IVI) (Curtis & McIntosh 1950, Kent & Coker 1992) was used to describe the quantitative structure of the community. This statistic represents the contribution that a species makes to the community in terms of the number of plants within the plots (density), its contribution to the community through its distribution (frequency), and its influence on the other species through its dominance. Importance Value Index was calculated for each species of tree and groundcover in each of the study sites. The formula for tree IVI is as follow:

$$IVI = RD + RF + RDm$$

Where, RD = relative density of a species, RF = relative frequency of a species and RDom = relative dominance of a species.

$$\text{Relative Density of species A} = \frac{\text{Number of individual of A species}}{\text{Total number individual of all species}} \times 100\%$$

$$\text{Relative Frequency of species A} = \frac{\text{Frequency value of A species}}{\text{Total frequency value of all species}} \times 100\%$$

$$\text{Relative Dominance of species A} = \frac{\text{Dominance value of A species}}{\text{Total dominance value of all species}} \times 100\%$$

Dominance values for a tree species were obtained by dividing the basal area of the tree with the size of the plot (Simon 1996, Supriyadi & Marsono 2001). The IVI formula for groundcover species (including seedlings) was similar to the tree layer but without the calculation of relative dominance (Kusmana 1995), and so the formula is as follow:

$$IVI = RD + RF$$

Where, RD = relative density of a species, and RF = is relative frequency of a species.

Species abundance data were square root transformed prior to all multivariate analyses. A resemblance matrix based on a Bray-Curtis similarity index was generated as a basis for the subsequent ordination and cluster analyses. Plant species composition and abundance at each site were compared using non-metric multidimensional scaling ordination (NMDS) (Clarke 1993). Statistically significant differences in species composition and abundance between the sites were determined by analysis of similarity (ANOSIM), which tests the null hypothesis that there is no difference in species composition and abundance among groups (Clarke

1993). SIMPER, an analysis that calculates the average Bray-Curtis dissimilarity between all samples, was used to identify the species that differentiate sites (Clarke 1993). These analyses were done using PRIMER V.6 (Clarke & Gorley 2005).

RESULTS

Sixty one species belonging to 29 families were recorded in the study sites. The highest number of species belonged to the Poaceae (10), followed by Fabaceae (9) and then Asteraceae (6). There were significant differences in species richness between sites (ANOVA *P* = 0.05, table 2). Species richness was lowest at the 2006 site and highest at the 1994 site. Species richness in the reference site (undisturbed site) was much lower when compared to the 1994 site. Species richness in the reference site was significantly lower than in all but the 2006 site.

Table 2. Species richness and diversity in the burnt sites and reference site in mount Merapi National Park. Superscript letters (a-c) after mean values (±SD) indicates significant difference between sites as assessed with Tukey's HSD test. Dates are those in which the site was burnt by fire generated by *nuées ardentes.*

ANOVA group/years since fire	Species richness	Species diversity
2006 site	9.20 (±1.48)[a]	1.91 (± 0.19)[a]
1998 site	14.0 (±3.39)[b]	2.13 (± 0.27)[ab]
1997 site	15.4 (±1.51)[b]	2.41 (± 0.19)[bc]
1994 site	19.4 (±2.96)[c]	2.7 (± 0.21)[c]
Reference site	10.6 (±1.67)[a]	2.21 (± 0.27)[ab]

The changes in species diversity are not as distinct as the changes in species richness over time (ANOVA *P* = 0.05). The reference site is significantly different to the 1994 site, but not significantly different from 2006, 1998, and 1997. The 1998 site is not significantly different from 2006 and 1997 sites and also the 1997 site is not significantly different from the 1994 site.

Species turnover was highest (lowest species similarities) between the 2006 and the 1998 sites, and then between the 1997 and 1994 sites (Table 3). Species turnover between the 1998–1997 sites was similar to the turnover between the 1994 site and the reference site.

Table 3. Species turnover rates (D) between pairs of sites in the chronosequence on mount Merapi.

	2006-1998	1998-1997	1997-1994	1994-Ref site
D	0.89	0.63	0.83	0.66
Sorenson Index	0.11	0.37	0.17	0.34

In terms of vertical structure, the number of individuals found in each stratum indicates the presence of the particular stratum in each site (Table 4). In the 2006 site, stratums B, C, D, and E were recorded. The 1998, 1997 and 1994 sites also had four stratums (B, C, D, and E) whereas in the reference site, all five stratums (A, B, C, D, and E) were present.

Table 4. Number of individuals in each stratum for each site of secondary succession at mount Merapi. Stratum A refers to the number of trees that are more than 35 m in height. Stratum B is number of trees that are 18 to 35 m in height. Stratum C comprises of trees that are 8 to 18 m tall. Stratum D is the total number of saplings and Stratum E is the total number of groundcover species.

Stratum	2006 site	1998 site	1997 site	1994 site	Ref site
A	-	-	-	-	41
B	3	5	16	25	28
C	5	45	18	17	1
D	4	10	15	6	11
E	12	20	23	25	16

In terms of quantitative structure, tree and groundcover species in the sites were compared on the basis of the Importance Value Index, (IVI) (Table 5). In the 2006 site, the tree layer was dominated by *Pinus merkusii*, whereas in the 1998 and 1997 site, *Homalanthus giganteus* and *Paraserianthes falcataria* were the most important tree species. In the oldest site (1994), *Schima wallichii* and *P. merkusii* were the most important tree species whereas in the reference site, *Altingia excelsa* was the most important tree species. In the groundcover layer, the 2006 site was dominated by *Imperata cylindrica,* whereas *Eupatorium riparium* was the most important species in the 1998 and 1997 sites. In the oldest site (1994) *Brachiaria reptans* was the most

important species, while in the reference site, *Selaginella doederleinii* was the most important species in the groundcover layer. In the tree seedling layer, *Acacia decurrens* was the most dominant tree seedlings species in the 2006 site, followed by *P. merkusii*. *Albizia lopantha* dominated the seedling layer in the 1998 site, while in the 1997 and 1994 sites *Calliandra callothyrsus* was the most important seedling. In the reference site, *A. excelsa* was the dominant seedling.

Table 5. Importance Value Index (IVI), and shade tolerance for the most important species in each stratum at each of the study sites. Asterisks indicate exotic species.

Species	Shading tolerance	2006 site	1998 site	1997 site	1994 site	Reference site
Trees						
*Acacia decurrens**	Intolerant	17.27	6.17	-	58.88	-
Albizia lopantha	Intolerant	-	33.68	-	-	-
Altingia excelsa	Tolerant	60.63	-	-	8.44	217.51
Erythrina sp	Intolerant	-	12.51	-	-	-
Homalanthus giganteus	Intolerant	-	148.65	-	-	-
Macaranga javanica	Intolerant	-	31.55	-	-	-
Paraserianthes falcataria	Intermediate	-	-	116.20	46.83	-
Parkia sp	Intolerant	-	6.53	29.32	-	-
Pinus merkusii	Intermediate	222.09	-	-	87.85	54.05
Schima wallichii	Intermediate	-	-	104.92	89.0	21.80
Groundcover						
*Brachiaria reptans**	Intermediate	-	2.19	19.90	16.54	2.23
Eleusine indica	Intermediate	-	-	8.82	14.49	3.11
*Eupatorium riparium**	Intermediate	-	55.35	57.03	-	13.43
*Eupatorium odoratum**	Intermediate	-	8.69	4.70	1.95	-
Imperata cylindrica	Intolerant	73.77	14.18	23.51	9.55	-
*Polygala paniculata**	Intermediate	26.83	-	2.35	7.60	-
Selaginella doederleinii	Tolerant	-	-	0.87	0.56	61.80
Seedling						
*Acacia decurrens**	Intolerant	99.04	13.88	-	13.57	-
Albizia lopantha	Intolerant	-	77.77	-	-	-
Altingia excelsa	Tolerant	9.52	-	11.05	7.46	33.35
Calliandra callothyrsus	Intermediate	-	-	146.56	84.04	-
Pinus merkusii	Intermediate	62.85	-	-	41.31	-
Schima wallichii	Intermediate	-	-	17.10	19.69	22.40

In addition to the IVI, table 5 also shows the presence and absence of the most important (dominant) species in each layer throughout the succession. In the tree layer, *A. excelsa* and *P. merkusii* were present at the youngest site (2006) and then absent in the next two older sites (1998 and 1997), and then reappeared in the oldest (1994) and the reference site. *Erythrina* sp., *H. giganteus, Albizia lopantha* and *Macaranga javanica* were only present at the 1998 site. In the groundcover layer, *I. cylindrica* was recorded in all four of the burnt sites, but was more dominant in 2006, 1998 and 1997 sites than in the 1994 site, and was absent in the reference site. In contrast, *Brachiaria reptans* was absent in the 2006 site and then present throughout the rest of the chronosequence and was at a very low abundance in the reference site. *Selaginella doederleinii* started to appear in the 1997 and, 1994 sites and became dominant in the reference site.

There was clear separation between the sites as shown by the NMDS ordination result (Fig. 2). Plots from the youngest site (2006) were separated from plots from the older sites (1998, 1997 and 1994), and from the undisturbed site. An analysis of similarity (ANOSIM) test confirmed that there were significant differences in Bray-Curtis species similarities between sites (Global $R_{ANOSIM} = 0.93$, $P < 0.001$).

Six pairwise comparison tests between sites (2006 and 1998, 2006 and 1997, 2006 and 1994, 2006 and reference site, 1998 and 1994, and 1994 and reference site) had an R value of 1.0 (Table 6). The comparison between the 1997-1998 sites and 1997-1994 sites had R-values of 0.72 and 0.86 and also, the comparison between 1997-undisturbed and 1998 undisturbed had R-value of 0.98 (Table 6).
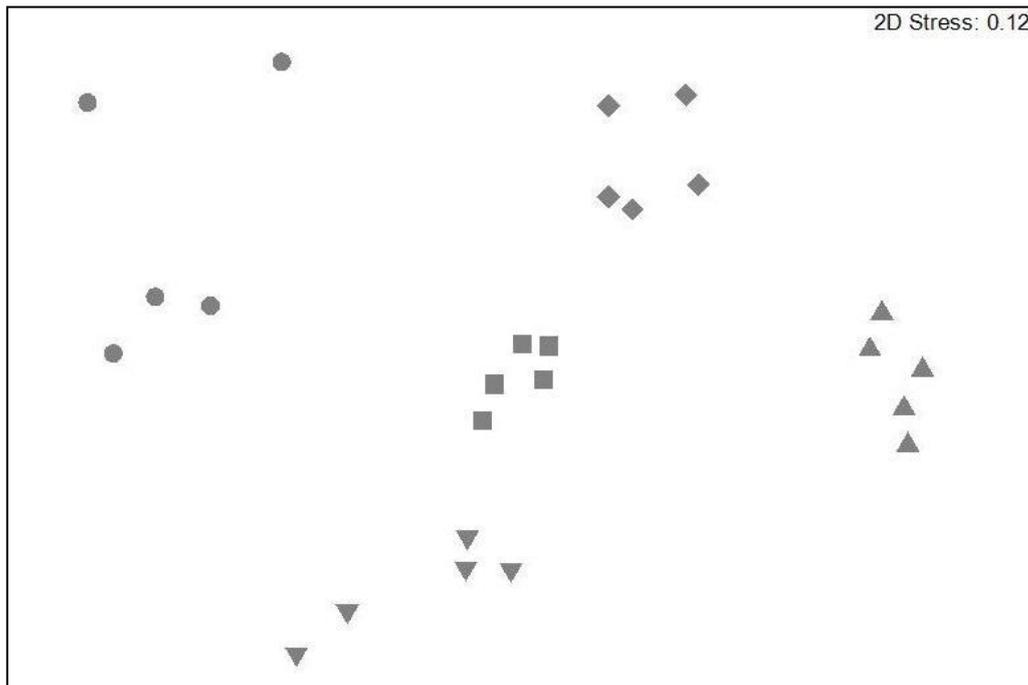
Figure 2. NMDS of sites based on vegetation composition and abundance: 2006 site (triangles), 1998 site (inverse triangles), 1997 site (squares), 1994 site (diamonds) and reference site (circles).

Table 6. ANOSIM pairwise test of NMDS vegetation plots ordination. Sample statistic (Global *R*): 0.93, significance level of sample statistic P < 0.001, number of permutation: 999.

Groups	R Statistic
2006, 1998	1
2006, 1997	1
2006, 1994	1
2006, Reference site	1
1998, 1997	0.72
1998, 1994	1
1998, Reference site	0.98
1997, 1994	0.86
1997, Reference site	0.98
1994, Reference site	1

In table 7, *Eupatorium riparium* contributed most to the dissimilarity between the 2006 and 1998 sites (21.27%), 2006 and 1997 sites (20.96%), 1998 and 1994 sites (16.31%), and 1997 and 1994 sites (21.39%). *Brachiaria reptans* contributed most to the dissimilarity between the 2006 and 1998 sites (9.96%) and 1998 and 1997 sites (9.89%). *Dichantium caricosum* contributed most to the dissimilarity between the 2006 and 1994 sites (10.60%). *Selaginella doederleinii* was the most important species contributing to dissimilarities between the reference site and the burnt sites. *Imperata cylindrica* was the second most important species in the comparison between 2006 and 1998 sites and 2006 and the reference sites.

DISCUSSION

In the first decade after disturbance by fire there was a rapid recovery at the sites, with 54 species belonging to 23 families recorded in the secondary forest at the study sites. The highest number of species belonged to the Poaceae (10), followed by Fabaceae (9) and then Asteraceae (6). Species richness and diversity increased with time since the fire, however species richness and diversity in the reference site was not significantly different from the youngest (2006) site. This pattern was similar to that reported in other studies where species diversity reached its peak in older succession sites after most of the climax species had entered the system, and then decreased with the loss of the species present in early successional stages (Magurran 1988, Peet 1992, Zhu *et al.* 2009). The results support the hypothesis of Aubert *et al.* (2003) that species diversity will increase during the early succession stage, reach a maximum in the mid-succession stage and decrease in the late succession stage.

Table 7. SIMPER result. Percentage contribution of species to average Bray–Curtis dissimilarities in all pairs of sites. Only those species with a contribution to average dissimilarity of >5% are included. The average dissimilarity value (%) is also shown for each pair of the sites. Asterixis indicates exotic species.

Species	Site comparison									
	2006 and 1998	2006 and 1997	1998 and 1997	2006 and 1994	1998 and 1994	1997 and 1994	2006 and Ref site	1998 and Ref site	1997 and Ref site	1994 and Ref site
*Brachiaria paspaloides**	6.21	-	6.51	-	5.07	-	-	5.98	-	-
*Brachiaria reptans**	-	9.96	9.89	8.01	5.42	8.45	-	-	8.30	5.89
Calliandra callothyrsus	-	8.01	8.68	-	-	6.31	-	-	6.80	-
*Dichantium caricosum**	-	-	-	10.60	7.81	7.22	-	-	-	8.08
Eleusine indica	-	-	-	8.96	6.53	-	-	-	-	5.97
*Eupatorium odoratum**	-	-	-	9.84	5.29	6.42	-	-	-	7.42
*Eupatorium riparium**	21.27	20.96	5.76	-	16.31	21.39	6.15	13.94	13.60	-
Imperata cylindrica	9.89	-	7.41	9.02	-	5.63	15.14	5.83	9.89	5.13
*Polygala paniculata**	6.82	-	-	-	-	-	6.81	-	-	-
Selaginella doederleinii	-	-	-	-	-	-	18.45	16.94	13.77	14.33
Average dissimilarity (%)	88.98	79.38	61.51	75.50	85.38	60.75	95.56	83.35	80.67	87.82

A decrease in the light availability at the forest floor as the succession proceeds might be the cause of the decline of species diversity in the reference site (Gomez-Pompa & Vazquez-Yanes 1981). Direct shading of overstorey species inhibits the existence and regeneration or growth of less tolerant and intolerant understorey species in the reference site (Lepš 1990).

There was progressive development of forest structure over time. Although all of the burnt sites had four strata (B, C, D, E), the number of individuals in each stratum differed. The number of individuals of stratum B (tall trees 18–35 m) was lowest in the 2006 site, greater in the older sites, but was the greatest in the reference site. The reference site had five strata (A, B, C, D, and E) with the lowest number of individuals of stratum E compared with the proportion of stratum E in the burnt sites. There were also differences in the patterns of abundance of the most important species with different light requirement characteristics (shade tolerant/intolerant) in the groundcover layer. The gradual decrease in *Imperata cylindrica* (shade-intolerant species) abundance over time contrasted with the gradual increase in the abundance of *Selaginella doederleinii* (shade-tolerant species), suggesting that there was a decrease in the light availability at the forest floor as the canopy developed and the succession proceeded.

Over the course of succession, the characteristics of species found at a site will change (Wills 2002). In the Mt. Merapi sites, the younger sites were characterized by shade-intolerant colonizer species with good dispersal capability. *I. cylindrica* is a widely distributed invader grass that has a long record of colonising cleared lands in Indonesia (Eussen & Soerjani 1975, Soerjani *et al.* 1983). *I. cylindrica* has wide-spread rhizomes and its seeds are wind-dispersed (Jonathan & Hariadi 1999), making it an effective colonizer following fire (Murniati 2002). *Acacia decurrens*, however, is a nitrogen-fixing shrub that is usually recruited after fire. At Mt. Merapi, it may have regenerated following the *nuées ardentes* fire from a soil seed bank (Hardiwinoto *et al.* 1998, Spurr & Barnes 1980). *I. cylindrica* and *A. decurrens* can also be found in other degraded areas on volcanoes in Java, such as in Mt. Bromo-Tengger and Mt. Semeru (Anonym 2009, Whitten *et al.* 1996). The species that occurred in the older sites and reference site on Mt. Merapi were characterized as intermediate to shade-tolerant species with greater longevity. In the older sites, *A. decurrens* was replaced by the leguminous tree, *Calliandra callothyrsus*, which occurred with other tree species such as *Altingia excelsa*. *A. excelsa* is a native emergent tree species and its seedlings are shade tolerant. Older sites were also characterized by the presence of the fern *Selaginella doederleinii* and the exotic invasive *Eupatorium* spp. in the groundcover layer. *Eupatorium* spp. is a fast growing species, usually found on steep slopes in a wide range of soil conditions and light availability (Heyne 1987).

Many studies have shown that generally species composition changes with time after a fire (Clearly *et al.* 2006, Reilly *et al.* 2006, Ross *et al.* 2002, Spencer & Gregory 2006). The result of NMDS ordination was

notable in that species composition differed among all sites, suggesting that the species composition changes with time after a fire. The 2006 and 1998 sites were different in terms of floristic composition and abundance with highest species replacement rate when compared with the replacement rate in the other sites ($D = 0.89$). *Altingia excelsa, Pinus merkusii*, and *Polygala paniculata* which were present in the 2006 site, dropped out in the 1998 site whereas there was an increase in the number of species from the Fabaceae family in the 1998 site with the colonization of *Albizia lopantha, Erythrin*a sp and *Parkia* sp. The differences in species composition between the 1998 and 1997 sites (short interval) was the lowest in all of the site pair-wise comparisons, but they were still significantly different from each other. Consistent with this, the species replacement rate was also lower ($D = 0.63$) when compared with the replacement rate in the other site comparisons. Although ANOSIM showed that the reference site and the 1994 site were significantly different, the turnover rate between these sites was more or less the same as the rate in the 1998-1997 sites ($D = 0.66$). This result indicates that some of the species that characterized the reference site, such as *Altingia excelsa, Schima wallichii* and *Selaginella doederleinii*, had appeared earlier in the 1994 site and thus suggested convergence of floristic composition in these sites.

In the Mt. Merapi succession, the changes in abundance of some invasive species such as *I. cylindrica*, *Brachiaria* spp., and *Eupatorium* spp. are important to note. *I. cylindrica* is an invasive native of south-east Asia. *I. cylindrica* dominated the early succession sites, but was not recorded in older sites as it was most likely shaded out by increasing canopy cover. In contrast, the invasive exotic species *Eupatorium* spp. remained in the system long after the fire had occurred and forest structures had developed. *Eupatorium* is native to South America, and this noxious and highly competitive species has become a problem elsewhere in Asia, such as in Nepal (Kunwar 2003). In the longer term, domination of invasive exotic species may limit the chance of recruitment of other native species including seedlings of woody species, thereby reducing diversity and even changing the successional trajectory and ecosystem functioning (Dale *et al.* 2005b, Hobbs & Huenneke 1992, Raghubanshi & Tripathi 2009, Standish *et al.* 2009).

This study suggested that the Merapi forest exhibited a high resilience for site recovery following *nuées ardentes*-induced wildfire with the rapid re-colonisation of plant species. It is also important to consider the potential problems of invasive species *Eupatorium* spp. as weeds, as these species remain abundant even in the much more developed sites. These findings may have important consequences for forest management as there is still much to learn about the capability of alien invasive species to change soil chemical properties, which can be crucial factors in driving the successional trajectory.

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