ORIGINAL RESEARCH

Burn severity and proximity to undisturbed forest drive post-fire recovery in the tropical montane forests of northern Vietnam

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Abstract

Background In recent decades, fire has increasingly occurred in the tropical montane rainforests of northern Vietnam. However, there are few studies of the effects of fire on forest composition and recovery in this region, and understanding these effects is critical for effective forest fire management and conservation. Forest plant species richness, structure (density, basal area), and composition were quantified for 133 forest plots randomly located in unburned (> 20 years since last fire) and recently burned (3–9 years since fire) vegetation associated with ten selected wildfires in three provinces of northern Vietnam where fires since 2000 were most frequent. Linear mixed effect models and nonmetric multidimensional scaling (NMDS) ordination were used to explore the structure, richness, and composition of burned and unburned forests and their environmental drivers, and to explore the key drivers of regeneration patterns in burned forest, including time since fire occurrence, fire severity, and distance to unburned forest edge.

Results Total species richness and diversity, tree species richness, tree density, and basal area were higher in unburned (vs. burned) forest plots, low (vs. high) severity burn areas, near (vs. far) from the closest unburned forest edge, and longer (vs. shorter) time since last fire. Results suggest that while burned forests were recovering on a trajectory back towards unburned forest composition, recovery was likely to be markedly slowed where fires were large (distance from edge effects) and/or of high severity, and forests may shift towards a different state (i.e., composition and structure) where more than one fire affects the same area over short time intervals.

Conclusions This study provides insights into the effects of fire and other environmental factors on forest composition and recovery in the tropical montane forests of northern Vietnam, crucial for informing policymakers involved in forest conservation and management.

Keywords Burn severity, Distance, Time since fire, Species richness, Unburned forest, Short interval fire

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Resumen

Antecedentes En décadas recientes, ha habido un incremento en la ocurrencia de incendios en los bosques montanos tropicales lluviosos del norte de Vietnam. Sin embargo, hay muy pocos estudios sobre los efectos del fuego en la composición y recuperación en esta región, y el entender estos efectos es crítico para un efectivo manejo del fuego y conservación de estos bosques. La riqueza de especies del bosque, su estructura (densidad y área basal) y composición, fueron cuantificadas en 133 parcelas ubicadas al azar en áreas no quemadas (> 20 años desde el último incendio) y en vegetación quemada recientemente (3–9 años desde el último incendio) asociadas a 10 incendios seleccionados en tres provincias del norte de Vietnam donde los incendios fueron más frecuentes desde el año 2000. Modelos de efectos mixtos lineales y análisis de ordenación no métricos multidimensionales (NMDS) fueron usados para explorar la estructura, riqueza, y composición en áreas quemadas y no quemadas y sus conductores ambientales clave de los patrones de regeneración en las áreas quemadas, incluyendo el tiempo desde el último incendio, la severidad de esos incendios, y la distancia a los bordes de las áreas no quemadas.

Resultados La riqueza total de especies y la diversidad, la riqueza de especies leñosas, la densidad y área basal de árboles fueron mayores en las áreas no quemadas (vs áreas quemadas), en bajas (vs altas) severidades, en áreas cercanas (vs alejadas) de los bordes no quemados más cercanos, y en los quemados más antiguos (vs recientes). Estos resultados sugieren que si bien los boques se estaban recuperando en una trayectoria hacia una composición previa del mismo, esa recuperación fue marcadamente más lenta en lugares que experimentaron grandes incendios (efecto de la distancia desde el borde del no quemado), y/o alta severidad, y esos bosques podrían desviar su trayectoria a un diferente estado (en cuanto a estructura y composición), en aquellos lugares en los que el fuego afecta recurrentemente la misma área en un período corto de tiempo.

Conclusiones Este estudio provee de perspectivas sobre el efecto del fuego y otros factores ambientales en la composición del bosque y su recuperación en bosques tropicales montanos del norte de Vietnam, cruciales para informar a los decisores políticos involucrados en conservación y manejo de bosques.

Introduction

Tropical forests occupy only 7% of the earth's land surface but contain nearly two-thirds of global floral and faunal diversity (Estoque et al. 2019). South East Asia contains nearly 15% of the world's tropical forests (Stibig et al. 2013) and includes four of twenty-five global biodiversity hotspots (Sodhi et al. 2010). In recent decades, biodiversity in the region has been adversely affected by multiple global environmental change factors, including increased forest fire (Cochrane 2003; Hughes 2017; Prestes et al. 2020), attributed to a range of human activities including anthropogenic climate change (Cochrane 2003; Goldammer 2007; Corlett 2016; Juárez-Orozco et al. 2017).

 Many ecosystems worldwide show adaptations to fire, with species traits facilitating rapid recovery, including resprouting and seedling recruitment from in situ seed banks (Bellingham and Sparrow 2000; Bond and Midgley 2001). However, in ecosystems where fire is infrequent and in which species are less well adapted and resistant to fires, such as rainforests (Mueller-Dombois 1981; Kauffman and Uhl 1990), fire can negatively impact regeneration by killing extant saplings and seedlings, seeds and other underground regenerative plant parts near the soil surface (Kennard et al. 2002), as well as trees, most of which have thin bark (Pinard et al. 1999; Balch et al. 2013). As a result, there is little or no regeneration from on-site propagules (Kauffman 1991) and recovery is likely

to be slowed as it must occur from the in-migration of seeds from surrounding unburned forest areas (Tesfaye et al. 2004; Mayke et al. 2017).

 The post-fire characteristics of forest ecosystems depend on the fire regime and the suite of plant traits represented among extant forest species (Keeley et al. 2011). Fire frequency, burn severity, time since fire occurrence, and distance from unburned forest are four key parameters that can strongly affect post-fire recovery (Cochrane and Schulze 1999; Barlow and Peres 2008; Numata et al. 2017). Fire frequency is one of the most important factors influencing ecosystem composition and structure (Gill 1975). Ecosystems are less likely to return to their pre-disturbance state under increased short-interval fires (Díaz-Delgado et al. 2002; Tessler et al. 2014). Stand structure can be changed by repeated short-interval fire, reducing tree density and height (Hutchinson et al. 2012), depleting the seed bank (Kennard et al. 2002; Balch et al. 2013; Prestes et al. 2020) and removing fire-sensitive species (Cochrane and Barber 2009; Brando et al. 2012). It can lead to system state changes, and to dominance by fire-tolerant species (Cochrane and Schulze 1999; Goldammer 1999). While repeat short interval fires are infrequent in wet tropical forests, they are likely to increase as climate changes and have been reported to negatively affect diversity and community composition in Amazonian forests

(Cochrane and Schulze 1999; Barlow and Peres 2008; Balch et al. 2015; Verma and Jayakumar 2015).

Time since fire (TSF) is a key determinant of the composition and structure of forests. Species richness, species diversity, and aboveground biomass generally increase with time since fire (Mayke et al. 2017; Numata et al. 2017; Verma et al. 2017), whereas the presence and abundance of pioneer species declines (Mayke et al. 2017; Numata et al. 2017). The recovery time of tropical forests after fire is highly dependent on the severity of fire and the presence or absence of surviving trees, resprouting, seedling banks, seed banks (Kennard et al. 2002; Primack and Corlett 2005; Mayke et al. 2017), and the particular forest attribute considered. Uhl et al. (1981) reported that species richness had recovered after 22 months and stem density after 10 months following simulated slash-and-burn events in the upper Rio Negro region of the Amazon basin, and Verma et al. (2017) found that tree diversity reached the level of unburnt stands after 15 years in tropical dry deciduous forest of the Western Ghats, India. On the other hand, Mayke et al. (2017) estimated that at least 190 years was required for complete forest recovery (structure and composition) after high severity fires in seasonally dry tropical forest fragments in southeastern Brazil. These examples highlight that different measures of forest recovery vary in their recovery times, among forest types, and in relation to fire severity.

Burn severity also affects forest recovery and may be influenced by topography (e.g., slope, aspect), vegetation composition and structure, and fuel moisture. Drivers and effects are well described for temperate forests (Turner et al. 1997; Lentile et al. 2007; Odion et al. 2010; Kane et al. 2015; Harris and Taylor 2017; Fang et al. 2018) but not for tropical forests (Cochrane and Schulze 1999; Verma and Jayakumar 2015). High severity burns are more likely to occur in extreme weather (i.e., dry, hot, and windy), on upper slopes and on warmer aspects (Alexander et al. 2006; Fang et al. 2018). All trees may be killed in high severity burns, increasing opportunities for ground layer early secondary species, while there may be selective mortality in low severity burn areas, depending on species, size and bark thickness of trees (Cochrane and Schulze 1999; Zhong 2006; Donato et al. 2009). The severity of fire also affects post-fire regeneration through its impact on seed sources both above and below ground (Turner et al. 1998; Donato et al. 2009).

Finally, distance to the nearest unburned forest edge is another key factor influencing vegetation recovery following disturbance and has been demonstrated in relation to both old field successions (Riedel and Epstein 2005) and fire (Hill and Read 1984; Welch et al. 2016), as well as for forest types where fire is infrequent (Hooper et al. 2004). The recovery of tropical forests after fire is highly dependent on seed sources provided by trees from surrounding unburned forest (Swaine 1992; Miller and Kauffman 1998; Primack and Corlett 2005). Previous studies have shown that distance to the nearest undisturbed forest edge is often negatively correlated to plant species richness and diversity (Hooper et al. 2004; Balch et al. 2013; Stevens-Rumann and Morgan 2019).

Understanding post-fire regeneration patterns and the factors influencing post-fire recovery is important for forest management to effectively restore forest resources and reduce the negative consequences of wildfire. While there are some studies of post-fire regeneration in dry tropical forests where fires occur frequently (e.g., Verma and Jayakumar 2015; Mayke et al. 2017), the understanding of post-fire regeneration is more limited in tropical rainforests where fires are less frequent due to higher fuel moisture (Bowman et al. 2011). In the northern part of Vietnam, rainforests now occur mostly in nature reserves, national parks, and mountainous areas unsuitable for crop production (Averyanov et al. 2003; Phuong et al. 2012). The forests of this region have become a fire hotspot in recent decades, with fire now one of the key drivers of forest loss (Department of Forest Protection 2019; Doanh and Bao 2014; Le et al. 2014).

The objective of this study is to determine the effects of fire on forest attributes and recovery, with particular emphasis on time since fire (TSF), burn severity, and distance from unburned forest edges. We hypothesize that (i) burned forests will show increasing species richness with increasing time since fire, and increasing similarity to unburned forest, (ii) areas experiencing high burn severity will have lower tree species and total species richness and higher non-woody species richness (and therefore also strong compositional differences) than low severity burn areas, and (iii) areas far from unburned forest edges will have lower overall and tree species richness than areas close to forest edges. Since fires are generally infrequent in these tropical forests, it is not possible to fully explore the effects of short-interval repeat fire on forest regeneration. However, one short-interval repeat fire was available and is included in the analysis of time since fire patterns on species composition. The results of this study will help to build a knowledge-base for effective decision-making about tropical montane rainforest conservation and management.

Methods
Study sites
The study took place in and around 10 tropical montane forest fires across three northern Vietnam provinces over the period 2010–2016 (Fig. 1). The ten fires were located at elevations 1200–2400 m asl where the climate
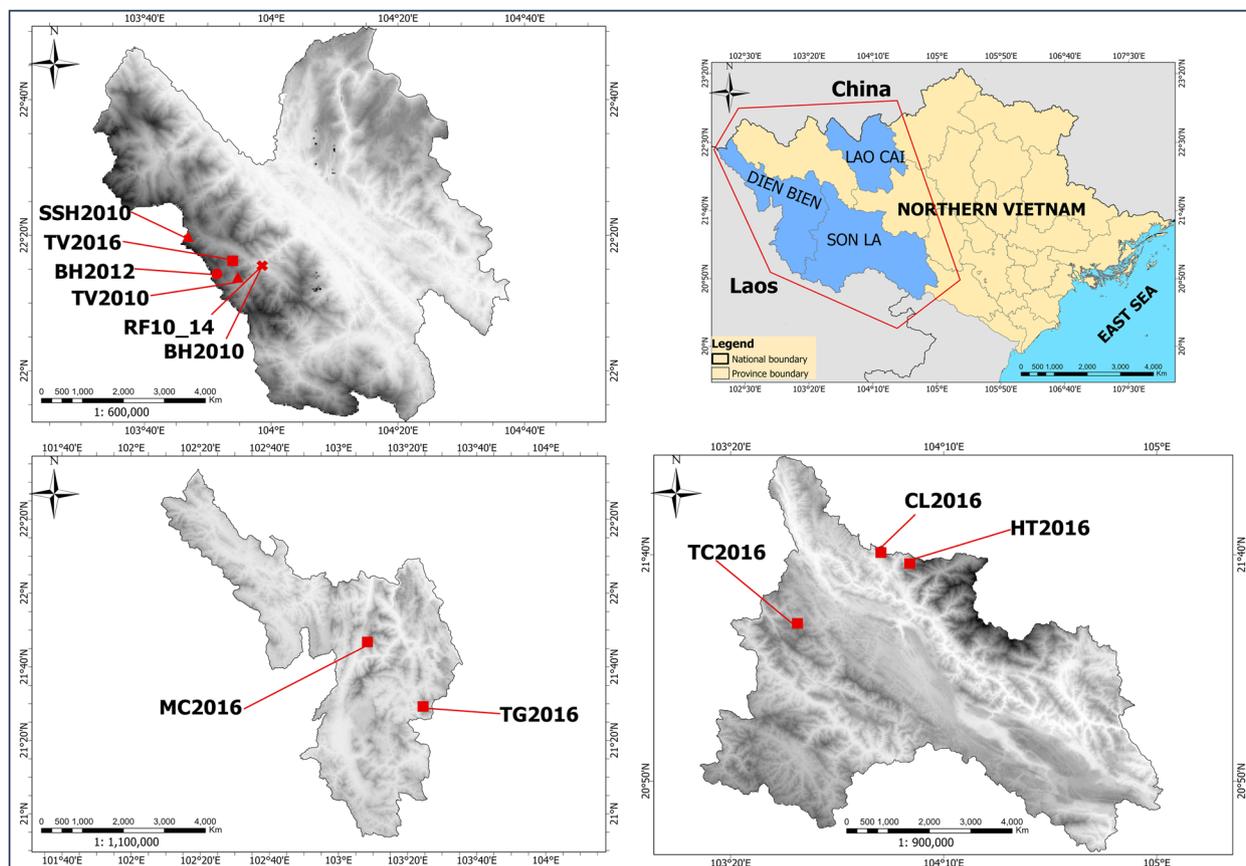
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Fig. 1 Location of the three study provinces in northern Vietnam, showing the locations of the ten fires (filled red symbols). Symbol shapes and site codes (see Table 1) indicate year of fire. The twice-burned location (burned in 2010 and again in 2014) is indicated by*

is montane monsoon tropical, with average temperatures from 20 to 23 °C, mean annual precipitation from 1500 to 2400 mm, a dry season of 2–5 months (from November to March, but decreasing in duration with elevation), and rainy season from April to September (Averyanov et al. 2003). Annually, this region experiences approximately 12 days of frost, and 40 days of Foehn winds (dry and hot winds) (Van 2015). The main soil types are acrisols and andosols (Sehgal 1989; Chuc et al. 2006). The region is characterized by mountains with very steep slopes. The main forest types are classified by Averyanov et al. (2003) as evergreen montane forests dominated by species from the families Illiciaceae, Lauraceae, Theaceae, Clusiaceae, Fabaceae, Fagaceae, and Magnoliaceae.

The study sites comprised both burned (time since fire 3–9 years) and adjacent unburned forest plots with sample plots in burned sites including contrasting burn severities (low, high) and distance from nearest unburned edge (near/far) (Table 1), as described below. The time since fire for unburned plots was unknown: Plots were chosen in areas of forest with a closed tree canopy layer comprised of individuals with stems of canopy trees

mostly > 20 cm DBH and with no fire scars evident, so that stands were assumed to be mature and with stand age > > 20 years.

Data collection

Fieldwork was carried out in 2019. In total, 133 plots were established. The number of burned/unburned, high/low severity, and near/far from unburned forest edge plots is shown in Table 2. One site burned twice within the study period (in 2010 and 2014; Table 2). The distance between plots ranged from 500 to 1000 m depending on the shape and size of each burn area. Plots were chosen randomly within the burn areas (burned plots) and within the immediate surroundings of the burned area but at a distance of at least 100 m from the disturbed forest edge (unburned plots) using the sample tool in TerrSet version 18.21 software (Eastman 2016). Plots were manually screened to exclude stream beds and cliffs.

Burn area and burn severity were estimated using remote sensing and digital maps provided by the Vietnam Ministry of Agriculture and Rural Development (2016) and the U.S. Geological Survey (USGS).

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Table 1 Study site code, location, fire year, elevation, total burned area, and area burned at high severity, for each fire included in the study

Site code	Location	Fire year	Elevation (m asl)	Burned area (ha)	High severity area (ha)
TV2010	Ta Van communes in Hoang Lien National park, Sapa, Lao Cai province	2010	1548	764	374
SSH2010	Sa Sa Ho communes in Hoang Lien National park, Sapa, Lao Cai province	2010	2321	151	103
BH2012	Ban Ho commune in Hoang Lien National park, Sapa, Lao Cai province	2012	1849	65	14
TV2016	Ta Van commune in Hoang Lien National park, Sapa, Lao Cai	2016	1906	27	1
MC2016	Hua Ngai commune, Muong Cha, Dien Bien province	2016	1531	1514	242
TG2016	Tenh Phong commune, Tuan Giao, Dien Bien province	2016	1587	1183	592
TC2016	Copia Nature Reserve Area, Thuan Chau, Son La province	2016	1502	278	100
CL2016	Chieng Lao commune, Muong La, Son La province	2016	1529	602	96
HT2016	Hua Trai commune, Muong La, Son La province	2016	1504	397	135
BH2010	Ban Ho commune in Hoang Lien National park, Sa Pa, Lao Cai province	2010	2156	338	113
RF2010_14	Ban Ho commune in Hoang Lien National Park, Sa Pa, Lao Cai province	2010 and 2014	2156	12[a]	12

[a] Area of overlap of fires in 2010 and 2014, no low severity burn area

Table 2 The number of burned and unburned plots in and around the ten fire locations, with burned plots also identified by fire severity level (high, low) and distance from unburned forest edge (near, far)

Site code	Time of fire occurrence	Number of plots			
		Burned			Unburned
		High severity[b]	Near edge, low severity	Far edge, low severity	
TV2010	2010	6	4	4	7
SSH2010	2010	4	3	3	6
BH2012	2012	2	1	1	4
TV2016	2016	1	1	1	2
MC2016	2016	4	3	3	5
TG2016	2016	5	3	3	5
TC2016	2016	5	3	2	5
CL2016	2016	4	3	3	5
HT2016	2016	4	3	3	6
BH2010	2010	1		1	2[a]
RF2010_14	2010, 2014	2			
Total		**38**	**24**	**24**	**47**

[a] These two unburned plots are common to both BH2010 and RF2010_14

[b] All high severity plots were far from unburned forest edges

Burn severity was mapped by calculating the relative differenced normalized burn ratio (RdNBR) from pre- and post-fire Landsat surface reflectance images (Landsat 5 Thematic Mapper (TM) and Landsat 8 Operational Land Imager (OLI)). Four levels of burn severity were identified: unburned (RdNBR < 249), low (RdNBR = 249–455), moderate (RdNBR = 456–798), and high (RdNBR ≥ 799), as detailed in (Trang PT, Enright NJ, Chu T, Andrew ME: Drivers of burn severity in the montane rainforests of Northern Vietnam, submitted) and following Miller et al. (2009). Moderate severity burn areas were excluded from the sample since our objective here, as stated in hypothesis ii, was to identify differences in measured variables between forest areas affected by high versus low severity fire.

Near plots were defined as those ≤ 100 m from the nearest unburned forest edge, while far plots ranged from 105 to 800 m from unburned forest. The distance from nearest unburned forest edge to each burned

forest plot was determined based on satellite imagery and confirmed on the ground when plots were surveyed.

Plots were navigated to in the field and elevations determined using a Garmin™ 78 s GPS, and slope and aspect recorded using clinometer and compass, respectively. Plots were 20×25 m in size, with 5×5 m sub-plots in each corner. In each plot, the diameter of individuals for all trees with a diameter at breast height (DBH)≥10 cm was measured and species identity recorded. In each subplot, species identity and DBH were recorded for all saplings (1–10 cm DBH), identity and total density for all tree species seedlings (<1 cm DBH), and identity and Braun-Blanquet cover-abundance score for other lifeforms (i.e., shrubs, herbs, grasses and sedges, ferns and fern allies).

All species were identified using the relevant floras and reference to herbarium specimens (Ban 2003, 2005; Ho 1999; Hoang Lien National Park 2020; WFO 2020).

Overview of analyses

Our hypotheses each set out expectations for the effects of fire regime characteristics on the species richness and composition of forest communities post-fire, which were evaluated by univariate statistical and ordination analyses, respectively. These analyses are described in the following sections. In both sets of analyses, the significance of time since fire (TSF, hypothesis i), burn severity (hypothesis ii), and distance to nearest unburned forest edge (hypothesis iii) on key forest attributes were tested.

Analysis of forest structure and diversity

Tree and total species (i.e., the pooled sample of all trees, shrubs, seedlings, saplings, and other life forms in both plots and sub-plots) data were described using a range of vegetation measures, including total, tree and non-woody species richness, Shannon diversity H′, tree density (D), and basal area ha^{-1} (BA).

Linear and mixed effect models were used to evaluate the effects of TSF, burn severity, and distance to unburned forest edge on species richness (total, non-woody, tree), diversity (H′), and forest structure (BA, D) response variables (results for H′ and D were similar to those for richness and BA, respectively, and are not presented). It was also necessary to include 2-way interactions with TSF in the models, to account for differences in recovery for high *vs* low severity and far *vs* near forest edge treatments. However, because a full factorial design was not possible, interactions were evaluated with a composite variable that indicated the combination of severity (unburned, low, high) or distance from edge (unburned, near, far) levels with TSF (unburned, 3 years, 9 years; twice-burned (*n*=2) and 7-year TSF plots (*n*=4) were not included due to small sample size). Because of

strong interactions, we could not evaluate our 3 hypotheses simply by testing the main effects of the corresponding terms. Instead, pairwise differences between levels of the severity-by-TSF or distance-by-TSF terms were evaluated with Tukey's tests. Further, since all burned areas near unburned forest edge experienced low burn severity, separate models were used to evaluate the severity-by-TSF and distance-by-TSF interactions. For each focal interaction term and each response variable, models were iteratively constructed with and without topographic covariates (elevation, slope, aspect—quantified as a southwestness index (see Trang et al. 2022)) and with and without random effects of location (province, site code), to account for confounding effects on forest composition and structure. Akaike's information criterion (AIC) was used to select the top model.

We repeated these analyses on subsets of the plots to attempt to separate the effects of burn severity and distance from unburned forest edge. The "controlled" effects of the severity-by-TSF interaction were evaluated within the set of plots that were far from unburned edge while the distance-by-TSF effect was tested for the plots that burned at low severity. These analyses identified patterns consistent with analyses on the full set of plots, so only the results from the analyses of all plots are presented in the text. All analyses were performed in R v4.2.2 using the packages "nlme" (Pinheiro et al. 2021) and "emmeans" (Lenth et al. 2019).

Analysis of forest community composition

Nonmetric multidimensional scaling (NMDS; PC-ORD v.7.08; Peck 2021) was used to explore patterns in species composition and their relationships to fire-related (i.e., TSF, burn severity, distance from nearest unburned forest edge) and other environmental drivers (elevation, slope, aspect, location) for (i) all (burned plus unburned) plots, and (ii) burned plots only. The all and burned forest plots only datasets were each described by two matrices: the main matrix containing species presence/absence data and a second matrix containing environmental variables (elevation, slope, southwestness), fire frequency (0=unburned, 1=once-burned, 2=twice-burned), TSF, burn severity (0=unburned, 1=low, 2=high), distance to the nearest unburned forest edge (0=unburned, 1=near, 2=far), and other derived vegetation variables (total, tree and non-woody species richness, Shannon diversity, density and basal area). Analyses using density and presence/absence were explored and the latter chosen since it allowed combined species data for all strata (trees, saplings, seedlings, and other life forms) to be used, and provided readily interpretable results with little loss in information.

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NMDS is a non-parametric ordination technique for analyzing ecological data which uses an iterative search for an ordination result with the lowest stress, as measured by the relationship between ranked distances in the original multidimensional space and the ranked distances for a specified number of dimensions in ordination space. It seeks a solution of sample unit ordination scores in which the paired interpoint distances have the same rank order as those calculated from the original data matrix. NMDS requires no assumptions of multivariate normality or linearity and is robust to the occurrence of large numbers of zero values (McCune and Grace 2002; Peck 2021). Sørensen (Bray–Curtis) distance was used to represent compositional dissimilarity. It is a robust measure of ecological distance (Faith et al. 1987) and is widely used with plant community data (Peck 2021).

The joint plot procedure was used to show the correlation of second matrix variables (as vectors) to the ordination axes of the samples (plots) in NMDS space. The significance of each vector was calculated using the Pearson's correlation (*r*) for continuous variables and Kendall's correlation (tau) for ordinal variables (Peck 2021).

Multi-response permutation procedure (MRPP) was used to evaluate the significance of difference in species composition between groups based on TSF (3, 5 [note that the 5 year TSF samples are the twice-burned plots], 7, 9, and > 20 years [unburned]), burn severity (high/low), distance to nearest unburned forest edge (near/far), and elevation (> 1750 m asl/ < 1750 m asl). MRPP is a non-parametric procedure for testing the hypothesis of no difference between two or more groups (Peck 2021). Sørensen (Bray–Curtis) distance was used for all MRPP tests. MRPP calculates two key statistics; *T*, describing the separation between communities, and *A*, the chance-corrected within-community agreement: $A = 1$ when there is complete within-group homogeneity, $A = 0$ if the heterogeneity within groups is equal to the random expectation, and $A < 0$ where there is less agreement within groups than expected by chance (McCune and Grace 2002; Peck 2021).

To better understand species associations with TSF, burn severity, distance from unburned forest edge, and elevation, indicator species analysis (ISA) for binary data was used, following McCune and Mefford (1999) and De Caceres and Legendre (2009). Species with high indicator values suggest high frequency of occurrence within a given group of plots relative to other comparison groups (De Caceres and Legendre 2009).

Results

General forest attributes

Across all (*n* = 133) burned and unburned plots, 293 species belonging to 94 families were recorded. This included 192 tree species from 55 families, plus 101 species from 52 families of other lifeforms (13 families common to both). The most frequently encountered species were the canopy tree *Schima wallichii* (Theaceae), the grass *Cyrtococcum patens* (Poaceae), and the small early successional tree *Eurya ciliata* (Pentaphylacaceae). Fagaceae was the most species-rich family (23 species), followed by Lauraceae (19), Fabaceae (14), Moraceae (11), and Ericaceae (10). The number of species occurring in burned only, unburned only, and both burned and unburned plots was 112, 80, and 101 species, respectively.

In unburned forest, 181 species from 73 families (130 tree species from 43 families and 51 other life-form species from 33 families) were recorded in 47 plots. Mean ($\pm$ s.e.) basal area was 35.5 ± 6.5 m^2 ha^{-1} (range 14–107) and mean density was 450 ± 41 ha^{-1} (range 220–800). Mean total species richness per plot was 22.6 ± 1.9 (range 9–32) and mean tree species richness was 10.0 ± 1.0 (range 5–17).

In burned forest, a total of 213 plant species from 81 families were recorded in 86 plots (142 tree species from 52 families and 71 other lifeform species from 41 families). Mean basal area was 4.8 ± 1.1 m^2 ha^{-1} (range 0–22.3) and mean density was 180 ± 28 ha^{-1} (range 0–600), the wide ranges reflecting differences in burn severity impacts, with no trees > 10 cm dbh in some high severity burn plots. Mean total species richness per plot was 17.6 ± 1.7 (range 7–46) and mean tree species richness was 5.0 ± 0.8 (range 0–13). Mean elevation (1626 ± 32 m *vs* 1681 ± 45 m), slope ($29 \pm 1°$ *vs* $31 \pm 1°$), and aspect (southwestness index 0.05 ± 0.07 *vs* 0.00 ± 0.11) were similar for burned and unburned plots, respectively.

Forest recovery was significantly affected by burn severity, as revealed by strong severity-by-TSF effects on BA ($F_{4,121} = 209.31$; $p < 0.0001$), tree species richness ($F_{4,113} = 62.81$; $p < 0.0001$), and total species richness ($F_{4,112} = 20.18$; $p < 0.0001$) (see Supplementary Table 1 for full model results, including covariates and grouping terms used). The lowest values for each of these variables occurred in the high severity burn plots and did not improve with TSF (Fig. 2a, b, d). In contrast, in low severity burn plots, basal area (Fig. 2a), tree richness (Fig. 2b), and total richness (Fig. 2d) were all lower in the 3-year TSF plots relative to values in unburned forests (though significantly higher than in the high severity burn plots of this age), but increased significantly with TSF (all pairwise comparisons noted in this text were significant at Tukey $p < 0.05$; Fig. 2). Nine years post-fire, basal area remained significantly lower than in unburned forests, while tree species richness had recovered to unburned levels and total species richness exceeded that in unburned plots (Fig. 2a, b, d). This increase in total species richness can be attributed
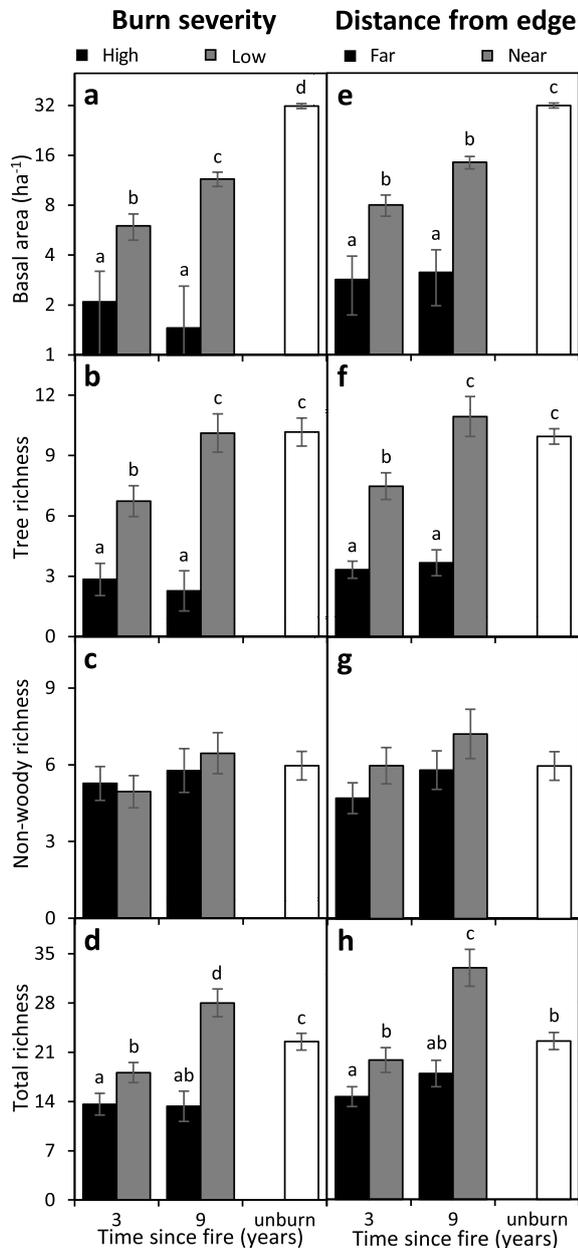
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Fig. 2 Plot-scale patterns of **a**, **e** basal area (m^2 ha^{-1}), **b**, **f** tree species richness, **c**, **g** non-woody species richness, and **d**, **h** total species richness, by interactions of time since fire with **a–d** burn severity and **e–h** distance from unburned forest edge. Non-woody species richness includes ferns, grasses, sedges, and herbs. Significant pairwise comparisons (Tukey $p < 0.05$) are indicated by different letters (**a–d**). Values are means ± standard error

partly to the increase in tree species richness, but also to greater richness of small woody species (seedlings, saplings, and shrubs), as non-woody species richness did not vary with burn severity or TSF ($F_{4,113} = 1.31$; $p = 0.27$; Fig. 2c).

The effects of distance from the unburned forest edge broadly paralleled those of burn severity on forest recovery for BA ($F_{4,121} = 105.37$; $p < 0.0001$; Fig. 2e), tree species richness ($F_{4,119} = 27.04$; $p < 0.0001$; Fig. 2f), and total species richness ($F_{4,112} = 17.23$; $p < 0.0001$; Fig. 2h), with more severe reductions in BA and richness, and no significant recovery with TSF, in plots far from the unburned forest edge. Distance tended to have slightly weaker effects than burn severity based on comparisons of F values. The exception was non-woody richness, which was significantly affected by the distance-by-TSF term ($F_{4,113} = 3.03$; $p = 0.02$), though it was not affected by burn severity. Non-woody richness was marginally lower (Tukey $p < 0.1$) 3 years post-fire in plots far from the unburned forest edge than in unburned plots, while all other combinations of edge distance and TSF were indistinguishable from unburned plots and from each other (Fig. 2g).

MRRP analyses confirmed the significance of differences in species composition between groups for burned vs unburned, high vs low burn severity, near vs far from forest edge, and all TSF age groups (i.e., including twice-burned and 7-year TSF groups which were removed from the univariate statistical analyses due to small sample size) (Supplementary Table 2). In relation to TSF, unburned vs 3 years TSF was the least similar ($T = -39.13$), and 9 vs 7 ($T = -2.14$) and 7 vs 5 years TSF ($T = -1.89$) the most similar.

Forest community composition: all plots

NMDS ordination of the all-plot data captured three dominant gradients (axes) in species composition space (Fig. 3). The ordination had a final stress of 15.6, with the three-axis solution explaining 70% of the variance in species composition (40.2, 13.5, and 16.2% for axes 1–3, respectively). Most burned plots had low scores on axis 1, while unburned plots had high scores on this axis, reflecting a strong difference in plant species composition between burned and unburned forest (Fig. 3). The two repeat fire plots had the lowest scores on this axis. Axis 2 separated plots burned 3 years ago (low scores) from those burned 9 years ago (high scores), with unburned plots also widely distributed along this axis. Axis 3 showed no clear patterns of plot distribution and is not further interpreted.

The joint plot showed strong correlation with a number of measured environmental, vegetation and fire variables (Fig. 3, Table 3). TSF, BA, density, and richness were strongly positively correlated with the first axis, and burn frequency, severity, and distance to unburned forest negatively with this axis. Elevation was positively correlated with the second axis, with both burned and unburned
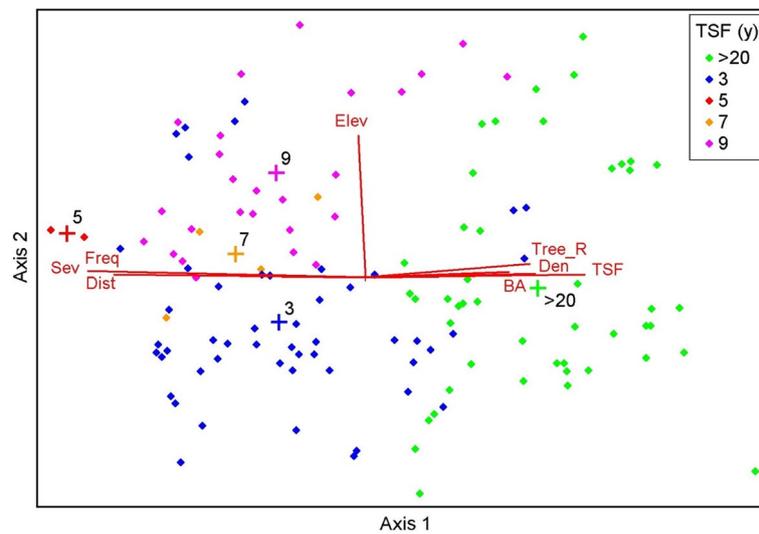
Fig. 3 Distribution of plots on the first two axes of the NMDS ordination for all plots. Plots are coded by TSF (years). TSF centroids are shown, along with biplot variables significant at $p < 0.01$: TSF—Time since fire; Sev—Burn severity; Elev—Elevation; Den—Density ha^{-1} of trees > 10 cm dbh; Tree R—Tree species richness; Freq—Number of times burned; BA—Basal area ha^{-1}

Table 3 Relationship between nonmetric multidimensional scaling (NMDS) axis values and environmental variables for all plots (presence/absence, all strata, $n = 133$). Values shown are Pearson correlation coefficient "r" for continuous variables, and Kendall's "tau" for ordinal/ranked variables. Values significant at $P < 0.001$ are bolded

	NMDS axis					
	1		**2**		**3**	
Variable	r	tau	r	tau	r	tau
Fire frequency		**− 0.65**		0.07		− 0.25
Time since fire		**0.52**		0.15		**0.33**
Burn severity		**− 0.73**		0.11		− 0.24
Distance from forest edge		**− 0.7**		0.06		− 0.29
Elevation	− 0.14		**0.61**		0.27	
Slope	0.23		− 0.13		− 0.10	
Southwestness	− 0.15		0.00		0.05	
Total species richness	**0.53**		0.27		0.13	
Basal area ha^{-1}	**0.61**		0.12		**0.34**	
Shannon diversity, H'	**0.51**		0.27		0.12	
Tree density ha^{-1}	**0.66**		0.10		**0.40**	
Tree species richness	**0.65**		0.19		**0.45**	

plots at elevations > 1750 m asl showing high scores on this axis (Table 3).

Indicator species analysis clearly identified key species characteristic of unburned forest, including the trees *Eberhardtia tonkinensis* and *Gironniera subaequalis*, understorey shrubs *Loxostigma griffithii* and *Psychotria prainii*, the tree fern *Cyathea contaminans* and lesser club-moss *Selaginella chrysocaulos* (Table 4). Plots most strongly impacted by fire, i.e.,

burned at high severity, far from the unburned forest edge and/or burned twice, were characterized by strong presence of the early successional tree species *Eurya ciliata*, invasive weed *Chromolaena odorata* (Siam weed: Asteraceae), invasive sedge *Kyllinga brevifolia*, and climbing fern *Dicranopteris linearis* (Gleicheniaceae). While there were a large number of indicator species (especially trees) for forest plots at elevations > 1800 m, there were few for lower elevation

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Table 4 Indicator species analysis (ISA) results, showing species (and their life forms) strongly significantly associated (*P*<0.005) with groups based on burn severity, distance from nearest unburned forest edge, elevation, and time since last fire. Unburned forest plots are shown as ">20 years (unburned)." Values are Indicator value (IV). Indicator species present in the twice-burned plots are shown (*) to highlight the dominance of fire indicator species in these plots.Columns are color-coded based on hypothesized fire severity impact on species composition (green—no fire impact, yellow—low fire impact, orange—high fire impact). # indicates invasive species

Species	Life-form	Severity		Distance from edge		Elevation		Time since fire (yrs)			Twice burned
		High (n=38)	Low (n=48)	Near (n=24)	Far (n=62)	High (n=37)	Low (n=96)	3 (n=54)	9 (n=26)	>20 (unburned) (n=47)	(n=2)
Cyathea contaminans	Fern ally			47.9						44.6	
Dicranopteris linearis	Fern ally	47.6			55				35.8		*
Selaginella chrysocaulos	Fern ally									57.6	
Imperata cylindrica	Grass/sedge	22.5									
Kyllinga brevifolia#	Grass/sedge	21.4		31					47.8		*
Alpinia calcarata	Herb									35.2	
Aspidistra typica Baill.	Herb	18.4									
Chromolaena odorata#	Herb	29.6			34.7				45.3		
Didymocarpus purpureobracteatus	Herb									46.8	
Impatiens siculifer	Herb					18.9					
Urena lobata	Herb	20.1									*
Loxostigma griffithii	Shrub									23.4	
Melastoma malabathricum	Shrub	38.2		35.6					32.3		*
Psychotria prainii	Shrub									23.4	
Thespis tonkinensis	Shrub	16.1							32.4		
Adinandra megaphylla	Tree					40.4					*
Alnus nepalensis	Tree								34.6		
Aralia chapaensis	Tree		16.7	22.1							
Archidendron chevalieri	Tree						24				
Betula alnoides	Tree					37.8					
Castanopsis acuminatissima	Tree					35					
Choerospondias axillaris	Tree		25.2				32.8				
Cratoxylum cochinchinense	Tree	36.8			22.6			25.9			
Eberhardtia tonkinensis	Tree									39.7	
Eurya ciliata	Tree	27.5			29.9			34.2			*
Eurya laotica	Tree	21.3									
Gironniera subaequalis	Tree									23.4	
Gordonia axillaris	Tree					48.6					
Ilex triflora	Tree								40.7		
Illicium ternstroemioides	Tree					21.6					
Iteadaphne caudata	Tree		28	32.1					46.8		*
Litsea cubeba	Tree		25.8	33.7							
Macaranga denticulata	Tree		19.5		22.7			28.2			
Magnolia cathcartii	Tree					24.3					
Myrica esculenta	Tree							21.8			
Nyssa sinensis	Tree					26.5			33.4		*
Persea odoratissima	Tree					45.9					
Premna serratifolia	Tree					27.8					
Rhododendron arborium sub sp. Cinnamomum	Tree									27.7	
Rhododendron tanastylum	Tree					27					
Rhodoleia championii	Tree					37.6					
Saurauia napaulensis	Tree		27.1	32				24.1			
Tetradium ruticarpum	Tree						18.8	29.5			
Rubus phoenicolasius	Vine		26.6								
Number of indicator species		11	7	7	5	12	3	6	9	9	8

plots (Table 4). The most frequently occurring species across all plots, the tree *Schima wallichii* and grass *Cyrtococcum patens*, were not associated with any tested grouping, reflecting their occurrence across a range of both burned and unburned (but not twice-burned) plots and elevations.

Table 5 Relationship between nonmetric multidimensional scaling (NMDS) axis values and environmental variables for burned plots (presence/absence, all strata, $n=86$). Values shown are Pearson correlation coefficient "*r*" for continuous variables, and Kendall's "tau" for ordinal/ranked variables. Values significant at $P<0.001$ are bolded, and $P<0.01$ in italics

| | NMDS axis | | | | | |
| | 1 | | 2 | | 3 | |
Variable	*r*	tau	*r*	tau	*r*	tau
Fire frequency		0.215		0.11		−0.133
Time since fire		0.025		*0.307*		*−0.345*
Burn severity		0.256		*0.329*		−0.063
Distance from forest edge		0.127		0.027		−0.191
Elevation	−0.009		**0.473**		−0.135	
Slope	0.038		−0.15		0.104	
Southwestness	0.155		0.015		−0.286	
Density, ha^{-1}	**−0.455**		−0.23		−0.121	
Total species richness	**−0.404**		−0.19		−0.257	
Basal area ha^{-1}	−0.263		−0.023		−0.173	
Shannon diversity, H'	**−0.46**		−0.209		−0.198	
Tree species richness	−0.157		−0.039		0.019	
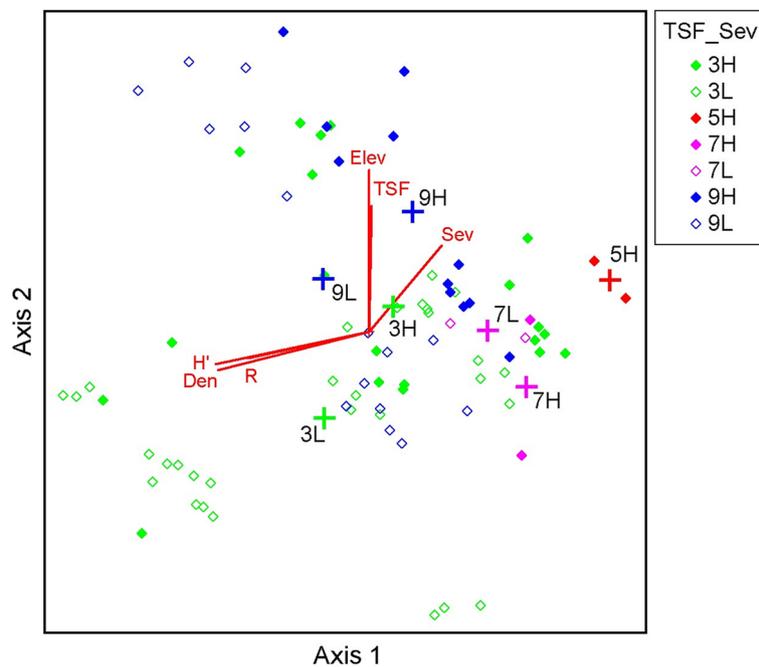
Fig. 4 Distribution of plots on the first two axes of the NMDS ordination for burned plots. Plots are coded by TSF (years) and burn severity (Sev: H—High, L—Low).Group centroids (+) are shown along with biplot variables significant at $p<0.01$: TSF—Time since fire; Sev—Burn severity; Den—Density ha^{-1} of trees > 10 cm dbh; Elev—Elevation; R—Total species richness; H'—Shannon diversity

Forest community composition: burned plots

The optimal NMDS solution for the burned plots data had three dimensions with final stress of 16.8 and axes 1–3 explaining 31.7, 25, and 15.8% of the variation in species composition respectively (72.5% overall). Twice-burned forest plots had the highest scores on axis 1 (Fig. 4). Most other high severity burn plots were located with positive scores on this axis, while low severity burn plots had negative scores. The joint plot showed a significant positive correlation primarily along axis 1 for burn severity,

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and negative correlations for species diversity, total species richness, and tree density (Fig. 4, Table 5). Elevation and TSF (along with burn severity) were positively associated with axis 2.

A number of tree species including *Aralia chapaensis*, *Iteadaphne caudata*, and *Litsea cubeba*, and the vine *Rubus phoenicolasius* were indicator species of low severity and near forest edge burn plots, while few fern, herb, or shrub species were significantly associated with them (Table 4). In contrast (as noted above) a number of such species characterized high severity burn plots, twice-burned plots, and plots 9 years TSF. Many of the same tree species present as indicators of high severity burn areas were also indicators of TSF plots, including early successional trees *Eurya ciliata* and *Macaranga denticulata,* and *Cratoxylum cochinchinense* (Table 4).

Discussion

Fire is normally infrequent in tropical forests, typically leaving ample time for forests to return to pre-fire forest composition and structure (Slik et al. 2008). However, in recent decades, tropical forest fires have occurred more frequently and at larger spatial scales, primarily due to on-going anthropogenic global change drivers (Cochrane 2003; Slik et al. 2008), resulting in increasingly large areas of secondary, regenerating forest, and potential ecosystem state changes (Balch et al. 2013; Mayke et al. 2017; Numata et al. 2017, 2022), and raising concerns for forest conservation and recovery in relation to fire. Here, we address in turn the hypotheses proposed of how time since fire (TSF), burn severity, and distance to nearest unburned forest edge, influence forest structure, composition, and recovery in the tropical montane forests of NW Vietnam.

Time since fire

We proposed (hypothesis i) that burned forests should show increasing species richness with increasing time since fire, and increasing similarity to unburned forest. Rapid forest recovery was found in most measured variables following fire in plots experiencing low severity fire, and/or that were near unburned forest edges (*nb.* there were no high severity burn plots near to unburned forest edges), where total species richness quickly approached unburned forest values after 9 years. Tree species richness increased rapidly over the first 9 years after fire, suggesting arrival of new species propagules from nearby unburned forest. In contrast, non-woody species richness remained approximately constant over time, but with species turnover from early successional (including some invasive) species to more shade-tolerant species (Table 4). Total species richness was highest at 9 years, likely reflecting the presence of both early and later successional species at this stage of forest recovery. However, mature tree density (not shown) and basal area showed slower trends of recovery. High severity burn plots showed the strongest negative impacts of fire (reduced richness, density, basal area) with no clear trend of recovery towards the characteristics of unburned forest over the first 9 years TSF. Thus, there was partial support for hypothesis i, with a clear pattern of increasing species richness and diversity with time since fire and increasing similarity to unburned forest overall, although this was contingent on both burn severity and proximity to unburned forest. Species composition was also different between unburned and burned forests at all fire ages (MRRP analysis; Supplementary Table 1), suggesting successional changes and continued large differences in species composition between forest stands at 9 years of age and mature forest.

Plots 3 years TSF showed strong presence of pioneer tree species *Eurya ciliata, Macaranga denticulata* and *Cratoxylum cochinchinense*, while at 9 years a mix of ground layer species (also strong indicators of high severity fire; Table 4) were more frequent, including the invasives *Chromolaena odorata* (Siam weed) and *Kyllinga brevifolia*, *Dicranopteris linearis*, and shrub *Melastoma malabathricum*, along with an increasing number of tree species. As noted above, while understorey (non-woody) species richness remains approximately constant, there is a shift in composition, from these early successional species to understorey shrubs *Loxostigma griffithii* and *Psychotria prainii*, the tree fern *Cyathea contaminans* and lesser club-moss *Selaginella chrysocaulos*, along with the appearance of *Eberhardtia tonkinensis* as a common canopy layer tree (Table 4*).* The trends in species richness and composition with time since fire revealed here suggest that woody species are increasing over time as propagules are dispersed in from surrounding unburned forest (i.e., are not all there from the start as found in some forests which follow an initial floristic composition successional pathway (van Breugel et al. 2007)), while non-woody species composition changes, reflecting a replacement of early seral light-demanding species by later seral, shade-tolerant understorey species. *Schima wallichii* was the most frequently encountered tree species in this study, occurring across most stand ages and elevations. It is widely distributed in SE Asia and has been described elsewhere as a light-demanding pioneer tree species able to persist as a large tree in mature forest due to its longevity (Do et al. 2011), explaining its widespread presence here.

Burn severity

In relation to burn severity, we proposed (hypothesis ii) that areas experiencing high burn severity will have

lower tree species and total species richness and higher non-woody species richness (and therefore also stronger compositional differences) than low severity burn areas. In agreement with this hypothesis, total and tree species richness were significantly lower in high (vs. low) severity burned plots (Fig. 2). Basal area was also lower for high compared to low severity burn areas. However, contrary to the hypothesized trend, non-woody species richness showed no difference between severity levels. High severity fire can increase stand-level tree mortality, reduce seedbanks (Ghermandi et al. 2013), and negatively impact a range of soil properties (Hart et al. 2005; López-Poma and Bautista 2014). High soil temperatures in high severity fires can reduce densities of viable seeds and other underground regenerative plant tissues (Holl et al. 2000; Kennard et al. 2002), slowing post-fire recovery in species richness and composition. In contrast, higher species richness after low severity fire may reflect survival of a greater proportion of mature trees, seed and seedling banks, and vegetative buds (e.g., de Oliveira et al. 2014).

Results of ISA showed that pioneer non-woody (e.g., *Cyrtococcum patens*, *Dicranopteris linearis*) and woody species (*Schima wallichii*, *Cratoxylum cochinchinense*) were prominent in high burn severity plots (Table 4), likely benefiting from the more open growing conditions (Balch et al. 2013, 2015; Cury et al. 2020). Later successional tree species, including *Quercus lineata* and *Lithocarpus truncatus*, only occurred in low severity burn plots (Table 4). Here, remnant surviving trees become seed sources for regeneration (Brando et al. 2012; Cury et al. 2020) and provide shade which may limit competition from herbs and grasses, permitting high densities of tree species seedlings to establish (Smith and Ashton 1997; Crotteau et al. 2013). Additionally, they act as nuclei for forest species regeneration, providing perch sites for birds which may disperse the seeds of a range of forest species. We observed rapidly increasing basal area and tree species richness from 3 to 9 years TSF in low severity burn plots, but not in high severity burn plots (Figs. 2 and 3). Total and tree species richness in unburned forest areas were higher and more similar to those in low severity than in high severity burned forest areas suggesting that forest recovery in low severity burned areas may be more rapid, as noted elsewhere (Numata et al. 2011; Martins et al. 2012; Welch et al. 2016; Strand et al. 2019).

Distance to unburned forest edge
According to hypothesis iii, we expected lower total and woody species richness, and higher non-woody species richness, in areas far from unburned forest edges. Results support this hypothesis for total and woody, but not for non-woody species (Figs. 2 and 3). The lack of a relationship for non-woody species richness may be due to overlap of the presence of both forest understorey non-woody species that have survived the disturbance, and growth of additional early successional species that have invaded after disturbance. The highest total species richness (and significantly higher than for unburned plots; Fig. 2, Supplementary Table 1) occurred for near-edge plots 9 years TSF, reflecting a marked peak in both tree and shrub (not shown) species suggestive of ready colonization of these locations by species from adjacent undisturbed forest. Recovery of the near-edge plots may also have been facilitated by the fact that all of these sites burned at low severity, while high burn severity occurred closer to the middle of burned areas. However, analyses restricted to only low burn severity plots to assess the controlled effects of distance from forest edge yielded similar results (not shown) to those presented for the set of all plots (Fig. 2).

A high abundance of mature woody species in unburned forest close to the forest edge leads to an increase in seed dispersal (propagule availability) in these near-edge areas (Cubiña and Aide 2001; Bueno and Llambí, 2015). In tropical forests, and forests more generally, most previous studies of edge effects have focused on anthropogenic activities such as land clearance and abandonment (Mesquita et al. 2001; Ribeiro et al. 2010), while forest edges in relation to post-fire recovery have rarely been evaluated. Hooper et al. (2004) found that proximity to seed sources is linked with increased seed dispersal and plant establishment near the edge compared to far from the edge in tropical forests in Panama. Similarly, Turner et al. (1997), Gill et al. (2021), and Hoecker and Turner (2022) found that distance to the unburned forest edge negatively impacted herb and shrub cover, seedling density, and total seed rain in northern USA. Falk et al. (2022) reported a rapid decline in forest species propagules at distances > 75 m from nearest forest edge for forests in western USA, while Donaldson et al. (2002) showed that abundance of pollinators was also closely related to distance from the forest edge, so that even surviving trees in low severity burn areas far from forest edges may show reduced seed set as a result of pollinator limitation, further impacting rate of recovery of burned areas far from intact forest edges.

Indicator species analysis results here showed that non-pioneer species including *Iteadaphne caudata*, *Litsea cubeba*, *Aralia chapaensis*, and *Saurauia napaulensis* were more common in burned forest plots close to unburned forest edges, likely explained primarily by ready seed dispersal from adjacent unburned forest. Conversely, pioneer species such as *Dicranopteris linearis*, *Chromolaena odorata*, *Eurya ciliata*, *Macaranga denticulata*, and *Schima wallichii* were widespread in

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burned forest plots far from unburned forest edges (Table 4). A strong negative relationship between tree seedling density and distance to the nearest surviving reproductive tree has been reported in other studies (Owen et al. 2017; Stevens-Rumann and Morgan 2019). Most seeds of tropical montane forest tree species are dispersed by wind (Rother and Veblen 2016; Halpern and Antos 2021), but animals may be important for dispersal of some tree and other plant species (Rueangket et al. 2021): Birds may be effective dispersers over longer distances, with the use of perch sites in remnant trees within burned areas acting as nuclei for forest species invasion, making low severity burn areas with surviving trees very important to patterns of recovery far from forest edges (Primack and Corlett 2005; Carpenter et al. 2019). Forest mammals may be less effective as long-distance dispersers, being reticent to move across areas of land without suitable tree cover (Primack and Corlett 2005; Naniwadekar et al. 2019). Thus, specific forest species may show very different rates of recovery in relation to distance from unburned forest edges depending on their dispersal vectors.

Short interval fire

While based on only a small sample size, species composition, richness, diversity, and density were lowest (Figs. 3 and 4) in the two (5 years TSF) forest plots which experienced two fires in 4 years (burned in 2010 and 2014). The short period between successive fires is likely to have increased tree mortality and reduced woody species richness relative to once-burned forests at a similar time since last fire (Balch et al. 2013, 2015; Cury et al. 2020). Elsewhere, short time intervals between consecutive fires have been shown to result in more open forest canopy, increased susceptibility of the forest understorey to drought, and larger near-surface and fine fuel load (Uhl and Kauffman 1990; Cochrane and Schulze 1999; Slik et al. 2008), facilitating colonization and establishment of invasive grasses, and killing regenerating tree seedlings (Hoffmann et al. 2004; Brando et al. 2014). Pioneer species dominated the twice-burned sites in this study (including *Eurya ciliata*, *Urena lobata*, *Kyllinga brevifolia*, *Melastoma malabathricum*, and *Dicranopteris linearis*) and these twice-burned areas appear to be at risk of transition to an alternative structural/compositional state of non-woody seral species dominance, potentially more prone to repeat, short interval fire. Although the small sample of just two repeat burned forest plots is insufficient to confirm this trend in the present study, results provide a preliminary picture of the effect of repeat fire on species diversity and composition. Fires at low frequency of occurrence provide good regeneration opportunities, maintain more woody species, and take less

time to return to the unburned forest composition, while repeat fires over short time intervals can delay recovery or may shift vegetation towards a different state (Barlow and Peres 2008; Oakman et al. 2021). Overall, these TSF results are consistent with those for a range of other studies from tropical forest ecosystems (Veldman and Putz 2011; Teegalapalli et al. 2016).

Conclusions

Fires are occurring more frequently in tropical rainforests, raising concerns for forest recovery following fire since generally they lack adaptations to this historically rare disturbance. We evaluated those concerns by studying patterns of tropical montane forest community structure and composition in burned and unburned forests, and among burned areas that experienced different fire characteristics in northern Vietnam. Analyses of unburned and burned forest plots, and among burned forest plots, found that fire characteristics, including time since fire, fire severity, and distance from the unburned forest edge, were important drivers of the measured forest attributes, and these results were verified by statistical analyses which supported the three hypotheses proposed: higher total species richness, tree species richness, tree density and basal area were found in (1) longer (*vs.* shorter) time since last fire, (2) low (*vs.* high) severity burn areas, and (3) near to (*vs.* far from) unburned forest edges. Maximum species richness, both total and for trees, was associated with plots at an early-intermediate stage (9 years TSF) of recovery after fire, reflecting presence of a mix of both early and later successional species, and conforming with the intermediate disturbance hypothesis (Molino and Sabatier 2001). While forests burned at low severity and close to unburned forest edges are recovering rapidly on a trajectory towards unburned forest composition, recovery appears markedly slower where fires are of high severity and distance from edge is large, and forests may shift towards a different state where more than one fire affects the same area over a short time interval.

Supplementary Information

Additional file 1: Table S1. Specification of the top models and fixed effects parameter estimates for the linear mixed effects models evaluating the univariate effects of burn severity (a-e) and distance to unburned forest edge (e-h) by TSF on forest structure (basal area) and diversity (Tree species richness, Non-woody richness, Total richness) measures. **Table S2.** Test statistics (T, A) and significance of difference among groups for multi–response permutation procedure (MRPP) analysis of unburned vs burned, high vs low burn severity, near vs far from forest edge and time since fire. **Table S3.** List of species, their abbreviations and families recorded from burned and unburned plots in northern Vietnam.

Availability of data and materials
The data that support this study will be shared upon reasonable request to the lead author.

Declarations

Ethics approval and consent to participate
PTT obtained all necessary permissions to conduct field research in Vietnam.

Consent for publication
All authors consent to publication.

Competing interests
The authors declare they have no competing interests.

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