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Determinants of post–fire regeneration demography in a subtropical monsoon–climate forest in Southwest China

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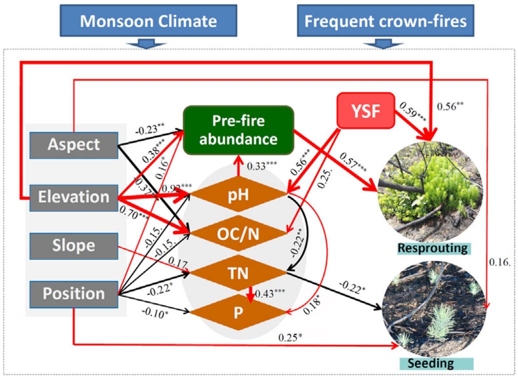
HIGHLIGHTS

- Exploring determinants of post-fire regeneration using structural equation models
- Resprouting dominates the rapid forest regeneration in Yunnan Central Plateau.
- Denser regeneration occurred with higher altitude and pre-fire abundance.
- Resprouts were widely distributed and more competitive in recovery.
- Reseeds were more successful on the infertile sites.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding the determinants of post–fire regeneration is critical for determining an appropriate restoration program following fire disturbances. However, studies addressing the drivers of post–fire regeneration of forests in monsoon climate are rare. This study explored the temporal and spatial variations of post–fire forest regeneration in the Central Yunnan Plateau of Southwest China, and disentangled the direct and indirect effects of the environmental factors via structural equation models (SEMs). We found that the overall post–fire regeneration density was generally greater for the habitat with higher values of elevation, pre–fire abundance, and soil pH. Post–fire regeneration was mainly composed of resprouts; seedlings were less relevant and appeared later. The SEM approach showed more variation of recruitment in resprouting ($R^2 = 0.66$) than seeding ($R^2 = 0.33$), and revealed different direct and indirect pathways. Resprouts were widely distributed, and significantly influenced by pre–fire abundance, elevation, soil pH, and years since the last fire. In contrast, seedlings preferentially occurred in infertile habitats, and were mainly influenced by topographic position and soil nutrients, showing distinct distribution from that of resprouts. Overall, forests under the subtropical monsoon climate in the Central Yunnan Plateau were resilient to fire mainly due to rapid post–fire resprouting. These findings indicate the complementary roles of resprouting and seeding in post- fire regeneration, and help to understand the mechanisms that regulate post-fire plant regeneration in a spatially heterogeneous landscape. Our results should contribute to improving the post–fire management of forest ecosystems under the influence of a semi–humid monsoon climate.

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1. Introduction

Post–fire plant regeneration has been a focal theme in community ecology and plant adaption studies for decades (Grubb, 1977; Bond and Midgley, 2001). This process critically relates to community assembly processes and long–term vegetation dynamics, species extinction risk, and ecosystem functions (Lawes and Clarke, 2011; Pausas and Keeley, 2014). From a management perspective, it is necessary to study the determinants of post–fire regeneration for developing appropriate management and restoration strategies after disturbances (Keeley et al., 2005; Greene et al., 2006).

Plants have evolved different regeneration strategies to respond to the disturbance of wildfires (Pausas et al., 2004): resprouting and seeding. Post–fire resprouting refers to generating new shoots from dormant buds located in burned remnants of branches, stems, lignotubers, rhizome, or roots, while post–fire seeding refers to the dispersal and recruitment from a fire–resistant seed bank stored either on the ground (i.e. soil seed bank), or in the crown (i.e. canopy seed bank, Pausas and Keeley, 2014). Resprouting is widely accepted as a fire–adaptive trait as it provides survival in recurrently burned environments (Bell and Ojeda, 1999; Bond and Midgley, 2001; Clarke et al., 2013; Pausas and Keeley, 2014; Paula et al., 2015; Pausas et al., 2016). In contrast, obligate seeders (those that only regenerate by seeding after fire) have shorter generation times and often they also have higher fecundity (Lamont and Wiens, 2003; Pausas and Keeley, 2014). Seeders allocate less resources to underground carbon storage than resprouters, and have higher aboveground growth rates (Bond and Midgley, 2003; Pausas et al., 2004). Therefore, these two regeneration strategies respond differently to environmental variations (Clemente et al., 1996; Pratt et al., 2014). Bellingham and Sparrow (2000) found that the predominance of multi–stemmed (from resprouting) architecture was primarily related to soil nutrient on tropical montane habitats, and mainly linked with elevation on temperate mountains; however, no difference was found in seeding. Seeder and resprouter species were found to have different feedback to drought and warming in Mediterranean regions (Prieto et al., 2009; Pausas et al., 2016; Parra and Moreno, 2018). Despite of these differences, species with different regeneration strategies are often coexist at local scales (Cardillo, 2012; Vilagrosa et al., 2014).

In recent decades, several studies have explored factors controlling post–fire regeneration, including fire severity and fire season (Konstantinidis et al., 2006; Wright and Clarke, 2007; Maia et al., 2012; Crotteau et al., 2013); fire frequency and pre–fire vegetation (Broncano and Retana, 2004; Mouillot et al., 2005; Lee et al., 2013); topography (Turner et al., 2003; Greene et al., 2006; Han et al., 2015) and soil properties (Certini, 2005; Wüest et al., 2016). However, no consensus has been attained on the relative importance of different environment factors and their interactions, owing to differences in studied units (community types or species), and environmental contexts. For example, post–fire recruitment of conifer and broadleaf tree species varied with topographic positions in temperate climate of Northeast China (Cai et al., 2013), but post-fire resprouting plays a key role in both tropical and temperate forests (Bellingham and Sparrow, 2000). The analytical tools can also reveal different causal links; for instance, structural equation models (SEMs) often detect indirect relationships that are missed by regression analyses (Spasojevic et al., 2016).

In this study, we investigated the post–fire regeneration of the mixed conifer and broadleaf forests in the Central Yunnan Plateau (CYP) of Southwest China. This vegetation type dominates under a subtropical semi–humid monsoon climate (Wu et al., 1987), which is characterized by a dry period through winter and spring and a wet summer with rainfall brought mainly by the Indian Ocean Monsoon (IOM, Li et al., 2015). In contrast to many studies of post–fire regeneration across the Mediterranean–climate regions (Keeley et al., 2005; Wright and Clarke, 2007; Power et al., 2011; Paula et al., 2015), the post–fire regeneration process is still unclear in regions affected by the IOM (Han et al., 2015; Verma and Jayakumar, 2015). Our study region neighbors the Indo–China Peninsula, a global hotspot of both biodiversity and wildfire activity (de Bruyn et al., 2014). Similar to its environmental context at a broader scale, the CYP region is a wildfire hotspot due to both the significant rainfall seasonality and intensive human activities that currently cause most of the fire events (Zhang et al., 1994; Su et al., 2015; Ying et al., 2019). Moreover, the strong monsoon rainfall following the fire season brings a huge risk of soil erosion and even landslides in the study area (Tao et al., 2009). Therefore, it is important to explore the determinants of post–fire regeneration and promote ecosystem recovery as soon as possible.

Based on the field investigation in sites that were burned in different years, this study aimed to quantify the post–fire regeneration of the dominant forest communities in the CYP region, and explored the controlling factors underlying the post–fire resprouting and seeding modes. Specifically, we addressed the following questions: (1) Does post–fire demographic patterns differ between regeneration strategies? (2) What is the relative contribution of each regeneration strategy to the post–fire dynamics in the study area? and (3) how does year since last fire (YSF), pre–fire abundance, and local habitat conditions influence regeneration demography, in relation to both direct and indirect pathways?

2. Materials and methods

2.1. Study region

The study area is located in Lufeng County (25°4′–25°10′N, 102°12′–102°20′E) in Yunnan Province of Southwest China. This area belongs to the CYP region that is a wildfire hotspot of Yunnan. The elevations range from 1780 m to 2615 m a.s.l. The climate is a subtropical semi–humid type, characterized by a prominent seasonality in precipitation dominated by IOM. The nearby meteorological station is Kunming national meteorological station (25°0′N, 102°23′24″E, 1888.1 m a. s. l), and the mean distance from the station to the study area is 15.92 km. According to the records of the meteorological station, mean annual temperature is 14.6 °C and mean annual precipitation is 912 mm. The subtropical monsoon climate is characterized by a relatively dry period from November to the following May with mean precipitation 229 mm (25.1% of annual precipitation), and a humid period during June–September with mean precipitation 683 mm (74.9% of annual precipitation, Chen et al., 2019). A mixed coniferous/broadleaf forest constitutes the dominant vegetation type and the typical landscape across the CYP region (Jin and Peng, 1998). The dominant species are *Pinus yunnanensis*, *P. yunnanensis* var. *pygmaea*, *Cyclobalanopsis delavayi, Lithocarpus mairei*, and *Lyonia villosa* (Su et al., 2015; Han et al., 2018).

Wildfires in this region are determined by both natural and anthropogenic factors, typically burning with relatively high severity (crown fires) (Chen et al., 2014; Ying et al., 2018). On one hand, the active plant growth during the wet (summer) season allows the buildup of a considerable amount of fuel that dries during the winter and the windy and warm spring (Han et al., 2015). On the other hand, the dense human population across the rural landscape of the CYP region acted as the direct cause of 99% of the 680 wildfires recorded in Lufeng County during 2003–2012 (Chen et al., 2019). The current fire frequency in this region is not well known but forests older than 50 years are very rare (Wu et al., 1987; Tang et al., 2010). Although there is a lack of detailed information for fire frequency distribution in this region, Si (2019) suggests the fire return interval of a natural secondary *Pinus yunnanensis* forests is 20– 30 years. In addition, Han et al. (2015) found that the spatial variability of fire severity in this region is dominated by topographical heterogeneity. Generally, both fire frequency and severity are higher at upper slope positions and south–facing slopes (Beaty and Taylor, 2001, 2008; Han et al., 2015).

In this study, we identified four post–fire sites in the typical mixed forest landscape. The distances between all of them are less than 10 km, but each site was burned separately in different fires (in 2005, 2010, 2013, and 2014, respectively; Fig. 1). The four sites burned in crown fires, across areas of 290, 413, 1240, and 235 ha, respectively; and there are no records of earlier forest fires in the four sites since 1990s, according to the local forestry department (Yunnan Forestry and Grassland Administration, http://lcj.yn.gov.cn/). This information was also confirmed by our visit to local people living nearby the studied sites. The post–fire vegetation types and dominant species were comparable across sites at similar topographic positions (Han et al., 2018), indicating the similarity of the fire regime features among the sites. Based on such observations, we used a space–for–time substitution approach (Legendre and Fortin, 1989) to explore the difference of post–fire plant regenerations in the sites of 2, 3, 6, and 11 YSF, and sampled post–fire regeneration in July 2015.

2.2. Data sampling design

We used a stratified random sampling design to evaluate the effects of environmental factors and YSF on post–fire plant regeneration. For each burned site, we selected sampling plots across a topographic profile of the mountain from the sunny (south) to the shady (north) aspect, and at different topographic positions classified into five levels: valley, lower slope, middle slope, upper slope, and hilltop (Fig. 1c). At each position, we randomly sampled four replicate plots of 10 m × 10 m. Thus we surveyed $4 \times [(2 \times 4) + 1] = 36$ plots in each of the four burned sites, i.e., a total of 144 plots. In each sampling plot, we first counted all the stems of post–fire regeneration, and classified the regenerating stems into resprouts (multi-stemmed) and seedlings (single-stemmed). We included resprouts and seedlings of the four dominant woody species, i.e. *P. yunnanensis*, *C. delavayi*, *L. mairei,* and *Lyonia villosa*. Then we estimated the pre–fire abundance of the four dominant species through remnant stems, bark, and basal parts, using the method indicated by Han et al. (2015). We also counted the total species richness of woody and herbaceous plants in each plot.

We measured elevation and slope using a portable GPS and a compass, and recorded the topographic position. Aspect was classified as sunny (south) and shady (north), except those that at hilltop. Soil samples were collected in each plot ($n = 144$), at 0–10 cm depth below the litter layer. The samples were air–dried in laboratory for two weeks at room temperature about 22 °C. Roots and stones were removed, and the soil was crushed and sieved (2 mm mesh) before analyzing pH value, total nitrogen (TN), organic carbon (OC), and available phosphorus (P). The pH of each sample was measured in a 1:2.5 mixtures of soil and deionized water with a potentiometer (S20P–K). Then the samples were further sieved with a 0.15–mm mesh for analyzing soil total nitrogen and total carbon with an Elemental Analyzer (Model: vario Macro cube, Germany) using the Dry Combustion Method (Nelson, 1982). Inorganic carbon (IOC) was measured with a Carbonate Analyzer (Eijkelkamp 08.53) using the Gasometric Method (Jones and Kaiteris, 1983); OC was determined from total carbon minus IOC. Soil P was measured in a Continuous Flow Analyzer (SmartChem–140) by using the Molybdenum Blue Colorimetric Method (Zinzadze, 1935).

Due to technical problems in the data collection procedure, we were able to obtain plant regeneration data for only 138 of the total 144 plots, and soil samples of 120 plots. The data of these were used in the following analyses.

2.3. Statistical analysis

According to the results of Shapiro-Wilk test, the regeneration density values of both resprouts and seedlings did not follow a normal distribution. Therefore, we applied a non–parametric Kruskal–Wallis Test to determine the significance of differences in the regeneration density between resprouts and seedlings, and a Dunn Test (with Bonferroni correction) for multiple comparisons of resprouts vs. seedlings difference among different topographic positions and aspects. Then a partial correlation analysis was applied to test the relationship between resprouts and seedlings when controlling for environment factors. Both the pre–fire abundance and regeneration density values follow Poisson distribution, thus we log-transformed the regeneration values and fitted a linear regression models. The SEMs are widely used as powerful tools for

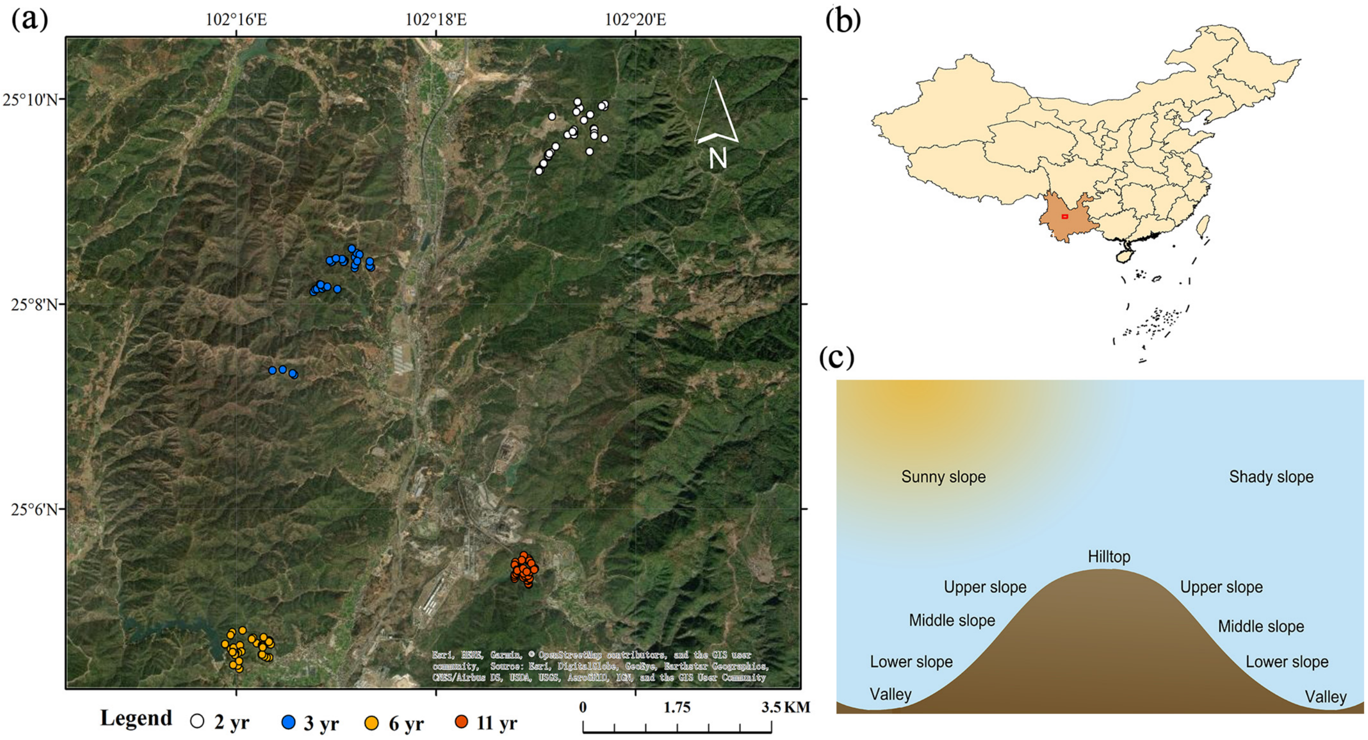


Fig. 1. (a) Locations of burned sites and sampling plots. (b) Geographical location of the study area. (c) Schematic diagram of the field sample design. Source: Esri, Digital Globe, Geoeye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community.

exploring causal links among variables, with regard to both direct and indirect effects (Lefcheck and Freckleton, 2016). We first considered a full model including pre–fire abundance, YSF, topography, and soil properties linked to the post–fire regeneration density. The full model contained all possible pathways, and then eliminated non–significant pathways until we attained the best fit. The SEMs were also fitted separately for total, resprouts and seedlings density of the plots. We first fitted the component models of the piecewise SEM as linear models, with data of 120 plots data. The path coefficients of each path as strength of the relationship were reported. We calculated the R square to evaluate of the fit of component models, and used *P*–value, χ^2 test and Akaike information criteria (AIC) were to evaluate the fitness of the SEM models. We also extracted the hotspots from the satellites Terra and Aqua (MODIS) around those plot (radius = 2 km), from 2002 to 2015. Putting the fire frequency and fire intensity data into the previous full model of SEMs to test the effect of fire on post-fire regeneration.

All statistical analyses were conducted using R version 3.4.3 (R Foundation for Statistical Computing, Vienna, Austria, 2017). The 'dunn.test' package was used for the Kruskal–Wallis test and Dunn test (Dinno, 2017), the 'psych' and 'ggm' packages for partial correlation analysis (Marchetti et al., 2015; Revelle, 2018), the 'ggplot2' package for plotting all histograms and regression figures (Wickham, 2016), and the 'piecewiseSEM' package for SEM (Lefcheck and Freckleton, 2016).

3. Results

3.1. Post–fire regeneration demography

The value ranges of post-fire regeneration and habitat factors on four fire sites were summarized in Table S1. The four dominant woody species including *P. yunnanensis*, *C. delavayi*, *L. mairei,* and *Lyonia villosa* comprised over 75% of total post–fire regeneration in all communities of four sites burned in different years (Fig. S1). Regeneration density values (including resprouts and seedlings) of the four species ranged from 0.01 to 27.68 trees/m^2, with the highest value of 14.13 ± 0.64 trees/m^2 in plots of two years post–fire (Fig. S2). For the total regeneration density of four dominant species, respouts comprised 82.5% and seedlings 17.5%, and each species had different composition of the two regeneration types. For the conifer species *P. yunnanensis,* resprouts and seedlings contributed equally (resprouts/seedlings density ratio of ca. 1) to the early post–fire regeneration (Fig. 2a). Broadleaf species (*L. mairei*, *Lyonia villosa,* and *C. delavayi)* regenerated mainly by resprouting from a basal burl, until 3 years after fire when seedlings started to appear (Fig. 2b and c). Their mean percentage of seedlings was 8%, 6%, and 4%, respectively, with seedlings density increasing gradually with YSF (Fig. 2b).

The Kruskal–Wallis test did not show a significant effect of slope aspect on the post-fire regeneration density ($P = 0.588$, Table S2), while topographic position had a significant effect ($P = 0.001$, Table S3). The highest and the lowest density values were observed at the hilltop and bottom valley, respectively (Fig. 3b). Resprouts density was not significantly different between sunny and shady slopes ($P = 0.550$, Table S2), but seedlings had a significantly higher density on sunny slopes ($P = 0.082$, Fig. 3a). Furthermore, resprouts density increased with topographic position (from bottom valley to hilltop) and elevation, while seedlings density decreased with elevation although they preferred higher topographic positions (Fig. 3b and c).

As expected, there were significantly negative correlations between resprouts and seedlings in the partial correlation analysis after controlling for all environmental factors ($r = -0.17$, $P < 0.001$), suggesting a possible trade–off between the two regeneration modes (see also Fig. 3c and d). Specifically, resprouts density increased with elevation ($R^2 = 0.169$, $P < 0.001$), while seedlings density decreased along the elevation gradient ($R^2 = 0.085$, $P < 0.001$). Pre-fire abundance also showed contrasted patterns by enhancing resprouting ($R^2 = 0.518$, $P < 0.001$), but limiting seedlings regeneration ($R^2 = 0.106$, $P < 0.001$). These contrasting relationships indicated the possible existence of a trade—off between resprouts and seedlings in the post—fire community regeneration.

3.2. Effects of environmental factors on regeneration density

The SEMs explained a considerable percentage of variance in total regeneration density ($R^2 = 0.53$, Fig. 4a), which showed a significant and positive relationship with YSF (standardized coefficient $\beta = 0.60$), pre–fire abundance ($\beta = 0.46$), and elevation ($\beta = 0.48$); while soil TN only had a weak negative relationship with regeneration ($\beta = -0.13$). Moreover, topographic factors exerted strong indirect effects on regeneration density through positive correlations with pre–fire abundance. Similarly, soil pH had an indirect effect on regeneration density by negatively affecting TN (Fig. 4a). Taking direct and indirect effects together, elevation and YSF were the most important predictors of post—fire regeneration, followed by pre-fire abundance and soil pH (Fig. S3a). We also added the fire regime data including fire frequency and fire intensity into the full model (Table S4). The R-square of models had no significant change except total regeneration density whose R-square increased from 0.53 to 0.69. We found that fire intensity had positive effect on total regeneration density ($P < 0.05$). However, fire frequency and intensity usually affected soil properties while had no effect on regeneration density (($P > 0.05$).

Besides, the full model of SEMs for resprouts density showed a better fit and explained more variance ($R^2 = 0.66$, Fig. 4b) than the SEMs for seedlings density ($R^2 = 0.33$, Fig. 4c). In addition, resprouts density was strongly (and positively) correlated with YSF ($\beta = 0.59$), Pre-fire abundance ($\beta = 0.57$), and elevation ($\beta = 0.56$), while seedlings density was positively related with topographic positions ($\beta = 0.25$) and aspect ($\beta = 0.16$), and was negatively with soil TN ($\beta = -0.22$). There was no correlation between pre–fire abundance and seedlings density. Moreover, elevation and soil pH had indirect effects on resprouts density by affecting pre–fire abundance. Similarly, topographic positions and slope affected seedlings density via soil TN (Fig. 4b and Fig. 4c). Taken together, elevation, YSF, and pre–fire abundance were the important factors determining resprouts density, while topographic positions and soil TN were the most determinant factors for seedlings density (Fig. S3b and c).

4. Discussion

Determinants of post–fire regeneration are complex and related with environmental context (Keeley et al., 2005). The demography of post–fire regeneration in monsoon–climate forests was found to be mainly affected by elevation, post–fire age (YSF), Pre-fire abundance, and soil pH. SEMs also indicated an indirect effect of elevation on regeneration density by influencing soil nutrients, especially TN. In the early years after fire, regeneration is an obvious accumulative process, and thus increases with YSF. Elevation has a strong relation with temperature, precipitation (Dodson and Root, 2013), and also topographic position. The enhanced post–fire regeneration with elevation is consistent with previous studies (Hanes, 1971; Buscardo et al., 2011), and can be interpreted primarily as the effects of higher precipitation and fire released canopy gap that favored regeneration (Lippok et al., 2013; Chen et al., 2019). Pre-fire abundance was significantly associated with resprouts regeneration, through providing bud bank and carbohydrate resources (Drewa et al., 2002; Paula et al., 2015). Therefore, the sites with higher Pre-fire vegetation had higher post–fire regeneration density. Post-fire soil nutrients are an important precursor to post-fire regeneration (Bloom and Mallik, 2006; Wüest et al., 2016). Fire can strongly affect soil properties with ash deposition and nutrient release from vegetation burning, while the subsequent nutrient change as a result of erosion, percolation, and plant consumption (Certini, 2005; Cui et al., 2014). However, the influence of fire on the spatial variations of

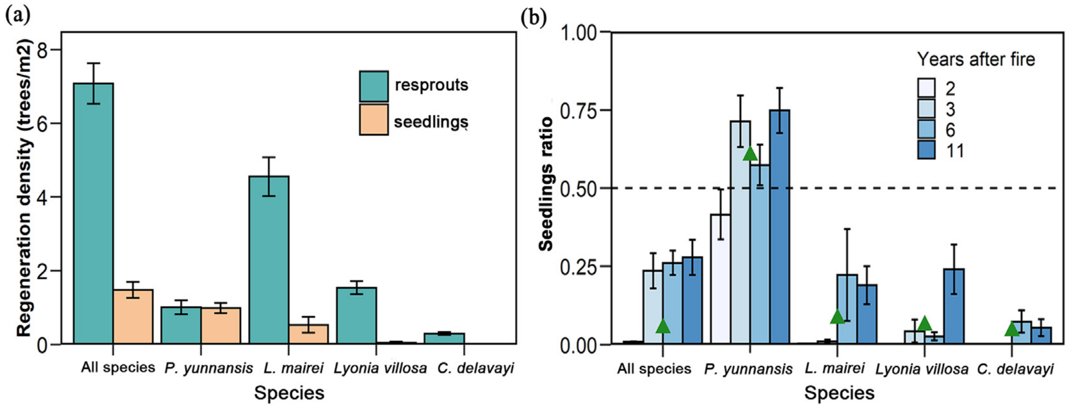


Fig. 2. (a) Two regeneration modes distributions of different species (mean ± se). (b) Relative proportions of seedlings along with YSF by species (mean ± se). Percentage of seedlings (%) = Seedlings density/Total regeneration density. Green triangles represent the mean percentage of seedlings across different YSF sites. The horizontal dotted line indicates the seedlings account for 50% regeneration density, that is, when seedlings and resprouts have the same density; below that line, resprouts are dominant and, above, seedlings are dominant.

soil nutrients gradually surpassed by topography in the long term (Kong et al., 2015, 2019). Surprisingly, soil pH and soil nutrients (including TN, P and OC/N) generally showed weak links with regeneration density in our study. The experiment of Hanley and Fenner (1997) discussed that each species seeds with internal nutrient supplies complement the early external supplies, especially *Pinus brutia*. Therefore, it is possible that the source of nutrients for post−fire regeneration was provided by that stored in seeds and the underground parts of resprouting plants in the early stage (Stock et al., 1990; Paula et al., 2015). The requirement of soil nutrients in the early post−fire regeneration might be inconsistent across space and time. SEMs also revealed indirect effects of soil pH on regeneration density via a positive relationship with Pre-fire abundance, and a barely significant negative relationship with TN. Obviously, soil pH alters nutrient availability through its effect on soil microbial community composition and soil biogeochemical processes (Falkengren-Grerup et al., 2006; Lambkin et al., 2011; Cheng et al., 2013). However, in the post−fire sites, soil pH itself is an indicator of habitat conditions that is regulated by topographical heterogeneity and the vegetation restoration process (YSF), as shown in Fig. 4a.

Huston and Smith (1987) suggested that one of the important determinants of succession was competitive displacement and trade–off of different life forms by preempting resources. A trade−off is generally recognized between the regeneration strategies of resprouting and seeding, caused by their complementary habitat preferences (Bellingham et al., 1994; Clemente et al., 1996; Kruger et al., 1997). Bellingham and Sparrow (2000) overviewed that the trade−off

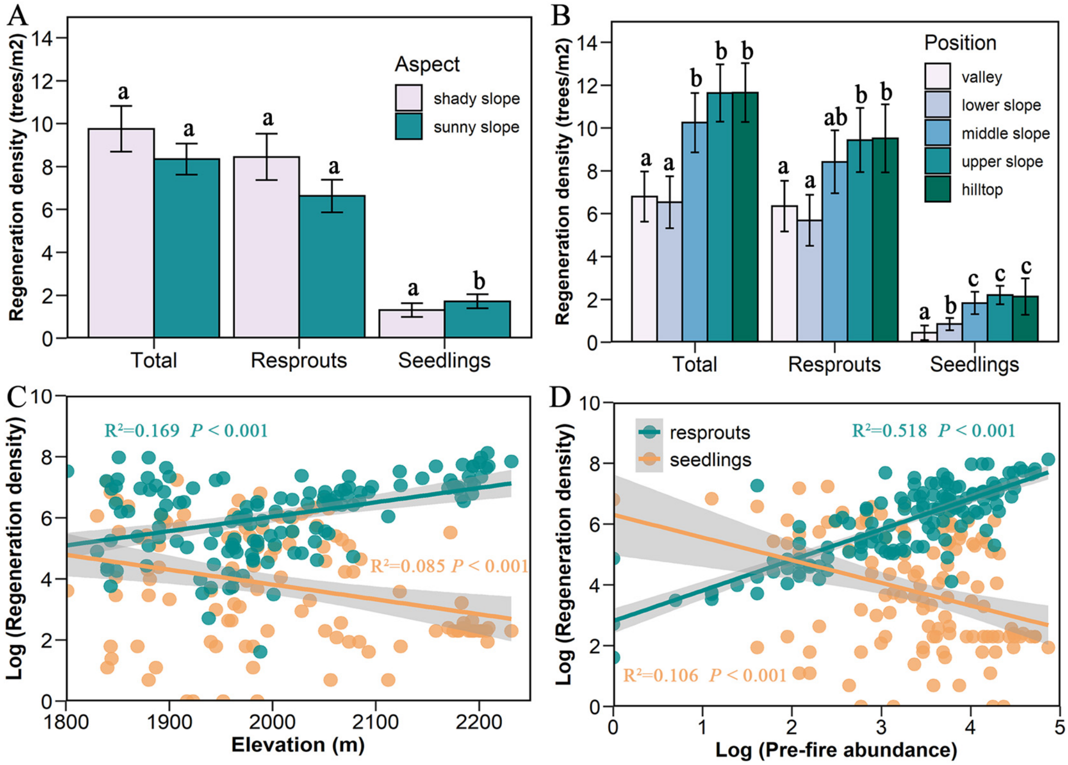
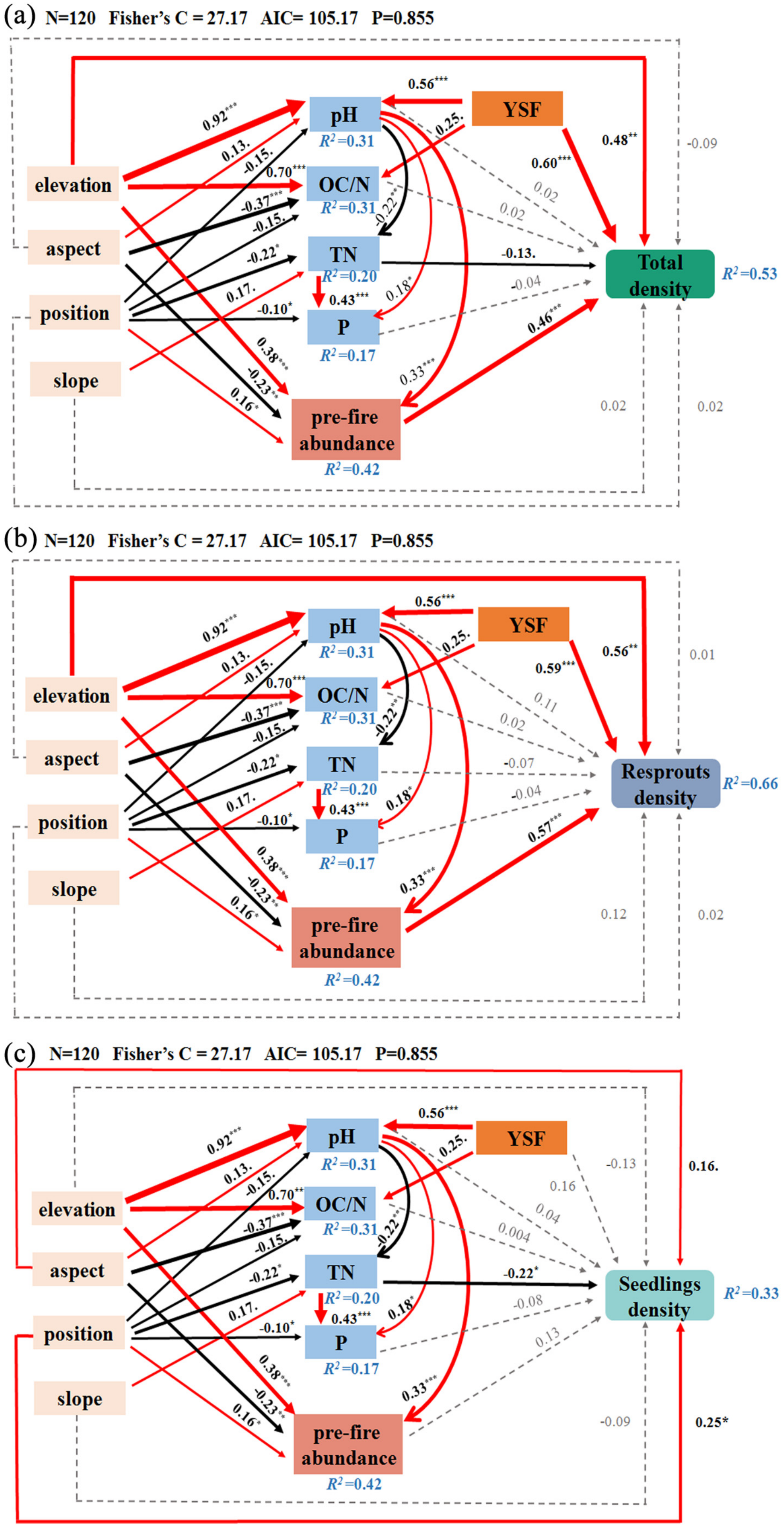


Fig. 3. Variation of regeneration density with aspect (A) and topographic positions (B) between different regeneration types (total, resprouts, and seedlings). Each bar represents regeneration density: mean ± se. Multiple comparisons were corrected using the Dunn test (method = Bonferroni) and tested for significance at the 95% confidence level ($\alpha = 0.05$). Different letters denote statistical difference of multiple comparisons. Relationships of post–fire regeneration density with elevation (C) and pre–fire abundance (D). Colored lines represent regression plots for each regeneration type. The shaded areas surrounding the solid lines represent the 95% confidence intervals of regeneration density estimations ($\alpha = 0.05$).


(a) N=120 Fisher's C = 27.17 AIC= 105.17 P=0.855
pH
R^2=0.31
OC/N
R^2=0.31
TN
R^2=0.20
P
R^2=0.17
pre-fire abundance
R^2=0.42
YSF
Total density
R^2=0.53
elevation
aspect
position
slope
0.56***
0.92***
0.13.
-0.15.
0.70***
-0.37***
-0.15.
-0.22*
0.17.
-0.10*
0.43***
0.25.
0.60***
0.48**
-0.09
0.02
0.02
-0.22**
-0.13.
-0.04
0.18*
0.46***
0.33***
0.38***
-0.23**
0.16*
0.02
0.02
(b) N=120 Fisher's C = 27.17 AIC= 105.17 P=0.855
pH
R^2=0.31
OC/N
R^2=0.31
TN
R^2=0.20
P
R^2=0.17
pre-fire abundance
R^2=0.42
YSF
Resprouts density
R^2=0.66
elevation
aspect
position
slope
0.56***
0.92***
0.13.
-0.15.
0.70***
-0.37***
-0.15.
-0.22*
0.17.
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0.38***
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0.12
0.02
(c) N=120 Fisher's C = 27.17 AIC= 105.17 P=0.855
pH
R^2=0.31
OC/N
R^2=0.31
TN
R^2=0.20
P
R^2=0.17
pre-fire abundance
R^2=0.42
YSF
Seedlings density
R^2=0.33
elevation
aspect
position
slope
0.56***
0.92***
0.13.
-0.15.
0.70**
-0.37***
-0.15.
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-0.09
0.25*

also regulated by the frequency and severity in many disturbance regimes including wildfires, and disturbances of high frequency and low severity were in favor of resprouting. In this study, the temporal displacement (Fig. 2b) and trade–off along environmental gradients (Fig. 3c and d) were both observed between the two regeneration strategies. While resprouts were widely distributed across different habitats, seedlings distribution was significantly limited by soil nutrients and topographical position. This is consistent with the studies in moisture—or nutrient–limited shrubland and grassland (Clarke et al., 2005; Pausas and Bradstock, 2007). The SEM results showed that pre–fire abundance, elevation, and YSF were the primary determinants of resprouts density. Obviously, resprouting occur at the pre — occupied habitats without additional requirement for new habitat adaption, they grow quickly from the bud bank and have a much more stable and abundant source of carbohydrate storage from the unburned underground part, compared with seeding (Bowen and Pate, 1993; Pausas et al., 2004; Lawes and Clarke, 2011). Thus, resprouting is a generally more efficient and reliable strategy for a quick occupy of the fire—released canopy space (Bond and Midgley, 2001). In contrast, the percentage of seedlings in post—fire regenerations was very low in the beginning (except *P. yunnanensis* that accumulates a serotinous canopy seed bank), and increased with YSF for all four dominant species (Fig. 2b). Seedlings had prominently higher densities at hilltop and sunny slope habitats (Fig. 3a and b), where the sites generally suffered high fire severity and generated larger canopy gaps (Bradstock et al., 2010; Han et al., 2015; Lacki et al., 2016). These facts indicated that, although resprouting is superior in competing for space with its efficiency, seeding as an alternative strategy of regeneration showed its advantage in filling larger empty habitats in space and time that cannot be reached by resprouting. Therefore, the two regeneration strategies showed complementary rather than direct competing relationship in the post—fire community restoration process. Indeed, fecundity was commonly observed on the resprouts of L. *mairei* and *C. delavayi* since the second year after fire and became very intensive in the following years, although seedlings of these species are generally rare under a closed forest canopy (Wang et al., 2007; Tang et al., 2010).

It is noteworthy that there is a different proportional composition of post–fire regeneration strategies (PFRSs) in Mediterranean–climate region responses to different fire regimes and climates (Lamont and Markey, 1995; Cowan, 2010; Rogers et al., 2015). Pausas et al. (2004) proposed a hierarchical classification of PFRSs that comprised four types: obligate resprouters (OR), obligate seeders (OS), facultative seeders (FS), and opportunists (OP). The OR species are widely distributed and account for more than 50% of the plant species in the Mediterranean basin and California which suffered more frequent fire regimes, while OS and FS species represent more than 80% in Australia and South Africa (Cowan, 2010; Russell-Smith et al., 2012). In our study region, most of the dominant species were identified as OR species and only conifer species *P. yunnanensis* was a FS species. Su et al. (2015) found that over 90% of common woody species were resprouters in the central Yunnan Plateau region. The dominance of resprouters was consistent with other studies in the monsoon region of East China, Thailand and India (Wang et al., 2007; Baker et al., 2008; Mondal and Sukumar, 2015). Collectively, resprouting is the dominant pathway of regeneration under a monsoon climate, with its role in post—fire plant community assembly enhanced by the efficiency for community recovery in response to the monsoon precipitation, which normally arrive several weeks after the wildfires.

Although the SEMs revealed YSF as a critical determinant of post–fire plant regeneration, the space–for–time substitution approach we used may have affected the estimation accuracy of the effect of YSF, and resulted in insufficient information for a general conclusion. Further efforts on a longer post-fire chronosequence of burned sites would be critical for a full understanding of the process. Additionally, SEMs explained a smaller amount of variance for seedlings than for resprouts density. The unexplained variability, especially that of seedlings, may be partly due to other factors not considered in this study, such as spatial variability of fire severity, fire frequency and characteristics of the soil seed bank. Earlier studies have demonstrated the effects of topographical features on spatiotemporal patterns of fire frequency (Tang et al., 2010; Matson and Bart, 2013; Kim et al., 2016) and fire severity (Beaty and Taylor, 2001, 2008) at small scale. Besides, it is known that repeated fire disturbances at a particular frequency might have a distinct accumulative effect on plants (e.g., exhaustion of buds or carbohydrates in resprouters; Moreira et al., 2012) and on the structure and composition of communities. Therefore, lack of long-term fire history information may also be a critical source of uncertainty about the roles of determinants on post–fire regeneration. However, some studies found that fire severity did not limit the resprout ability of forest (Knox and Clarke, 2005), and the impact of fire severity on regeneration density was found low (Han et al., 2015). Our study is also in line with the result of other study in this region (Han et al., 2015). This might be caused by the accuracy of remote sensing data on such local small scale, or insensitivity due to the rapid regeneration in CYP region. For better understanding of the effects of fire on post-fire regeneration, we may defined the average ratio of flame height to total height of burned trunks as fire severity (Maia et al., 2012) to increase the reliability of fire data at small scale. Otherwise, we also can use the remote sensing data by enlarging our study area into large scale in the future. Nevertheless, our results showed that monsoon—climate forests in the CYP region have evolved post-fire adaptive strategies and regenerate profusely after fire. Our results suggest that in most cases, there is no need to plant trees for vegetation recovery and soil erosion preventing.

5. Conclusions

Our study showed that forests in a subtropical monsoon climate were resilient to fire due to rapid regeneration, mainly by resprouting. Community regeneration density was higher for sites with higher elevation (more mesic) and higher pre–fire vegetation abundance, which was consistent across studied post–fire periods. Pre–fire abundance, post–fire age, elevation, and soil pH strongly affected post–fire regeneration density, but the magnitude of the effects was variable between resprouts and seedlings. The SEMs revealed the direct and indirect pathways and effects of environmental factors on the distribution of resprouts and seedlings. Resprouts were widely distributed and were significantly influenced by pre–fire abundance, elevation, and soil pH. In contrast, seedlings dominated the infertile sites and were mainly influenced by soil nutrients and competition pressure from resprouts. Our results suggest a complementary relationship behind the trade–off distribution patterns of resprouts and seedlings, which have important implications for post-fire restoration, and for sustainable forest ecosystem management.

Fig. 4. Structural equation models of pre–fire abundance, YSF, and environmental factors as predictors for (a) post–fire total regeneration density, (b) post–fire resprouts density, and (c) post–fire seedlings density. We report the path coefficients as standardized effect sizes which are adjacent to arrows, and arrow width is proportional to strength of the relationship. Solid red and black arrows represent significant positive and negative paths ($P < 0.10$, piecewise SEM), respectively; dotted gray arrows represent non–significant paths ($P > 0.10$, piecewise SEM). R^2 represents the proportion of variance explained. Overall fit of piecewise SEM was evaluated by Fisher's C statistic ($P > 0.05$ means the model is a good fit) and Akaike information criterion (AIC). Significant relationships: $P < 0.10$, $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

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CRediT authorship contribution statement

Caifang Luo: Formal analysis, Writing - original draft. **Zehao Shen:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Yiying Li:** Investigation, Software. **Jie Han:** Investigation, Methodology. **Juli G. Pausas:** Writing - review & editing. **Qian Xu:** Investigation. **Zhiming Zhang:** Investigation. **Youxu Jiang:** Conceptualization.

Declaration of competing interest

The authors declare that they have no competing financial interests or personal relationships that could influence the work reported in this paper.

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