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A shrubby resprouting pine with serotinous cones endemic to southwest China

Juli G. Pausas,[1] Wenhua Su,[2] Caifang Luo[3] and Zehao Shen[3,4]

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[1]CIDE-CSIC, Moncada, Valencia, 46113 Spain

[2]Institute of Ecology and Geobotany, Yunnan University, Kunming, 650091 China

[3]College of Urban and Environmental Science, MOE Laboratory for Earth Surface Processes, Peking University, Beijing, 100871 China

[4]Corresponding Author. E-mail: shzh@urban.pku.edu.cn

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Fig. 1. The shrubby form of *Pinus yunnanensis* (var. *pygmea*) generates extensive shrublands (top). It has serotinous cones (middle; tape reading = 57 cm) and resprouts after fire (bottom; 4 months postfire). Photos by C. Luo, W. Su, and J. G. Pausas, respectively, in the Yunnan Province of China.

The Yunnan Province of China is wet and warm enough to support magnificent forests. However, many mountains in the region are covered by a shrubland formation dominated by an unusual pine, the shrubby and multistemmed *Pinus yunnanensis* (Yunnan pine; Fig. 1). This formation is natural, and not the product of forest degradation; and fire appears to be a major factor explaining the features of this pine. This region has a subtropical monsoon climate influenced by both the Indian Ocean Monsoon from the west, and the Pacific Ocean Monsoon from the east. The climate has prominent seasonality in temperature and precipitation, alternating a warm dry season (December to May) with a hot wet season (June to November; Chen et al. 2019). The annual dry season creates conditions that can favor wildfires. Fires are currently common mainly between February and April (Zhao et al. 2009), with area burned depending on the variations in annual precipitation (Chen et al. 2014, Ying et al. 2017). The shrubby pines are found in the upper portions of the landscape, where it is drier and fires are more frequent. The Yunnan pine has several adaptations to frequent crown fires, which suggests that fires have long existed in the region and are not just a product of recent human activity (see Shao et al. 2012 for evidence of paleofires in the region). These fire adaptations include (Fig. 1) serotiny (Su et al. 2015), basal resprouting, and high precocity (<5 yr), a mix of traits that is relatively rare in pines (Keeley and Zedler 1995, Rodríguez-Trejo and Fulé 2003, Pausas 2015). *Pinus yunnanensis* often co-occurs with *Keteleeria evelyniana* (Pinaceae) which has a thick insulating bark (Li et al. 2017) and epicormic resprouting. All this

emphasizes the importance of fire in the ecology of the region (Su et al. 2015, Han et al. 2018).

In the Yunnan Province, *P. yunnanensis* occurs in two growth forms: as a tree and as a shrub. They are considered different varieties of the same species (var. *yunnanensis* and var. *pygmea*, respectively) with markedly different heights (up to 30 m and up to 2 m, respectively; eFloras 2008). A third variety, a tree (up to 30 m) is found in adjacent provinces (var. *tenuifolia*; in Guangxi and Guizhou provinces; eFloras 2008). The tree growth form dominates the lower slopes of Yunnan, and typically has a low serotiny level (i.e., many cones open at maturity) similar to the tree form in the adjacent province (var. *tenuifolia*). Previous research observed that trees (var. *yunnanensis*) in drier environments have more serotinous cones than those in wetter environments (Su et al. 2019), suggesting a possible higher crown-fire frequency in drier habitats (Hernández-Serrano et al. 2013). The shrub form is unusual among pines; it occurs mainly in upper slopes and ridges, where soils are poor and dry, and fires are likely. In such conditions, it forms extensive shrublands of this peculiar multistemmed pine (Fig. 1).

In order to determine the propensity for serotiny among the different varieties of *P. yunnanensis*, we studied 24 populations of *P. y. yunnanensis* (696 trees, Yunnan province), 13 populations of *P. y. pygmea* (371 individuals, Yunnan province), and 9 populations of *P. y. tenuifolia* (219 trees, in Guangxi province). The sampling was performed by Su et al. (2015; including unpublished sites available at Data S1). For each individual, we counted the number of open and closed cones in three main branches; then the level of serotiny was calculated as the percentage of closed cones in relation to total (open plus closed) cones. For *P. y. pygmea* we evaluated the resprouting capacity in the Lufeng County (Yunnan province). To do so, we counted the number of basal resprouts from 104 individuals distributed in different topographies, altitudes (ranging from 2,016 to 2,355 m asl), and postfire ages (from 2 to 11 yr; for more details see Luo et al. 2020). The results for both serotiny and resprouting are displayed in Fig. 2. Most of the individuals of the shrubby variety (*P. y. pygmea*) have a high proportion of serotiny cones (>80%; Figs. 1, 2a) and resprout from the base after fire (Fig. 2b). This shrub shows remarkably high precocity, with cones already appearing in the second or third year after germination (Fig. 1).

Serotiny is common among pines (He et al. 2012, Lamont et al. 2020) while resprouting is rare, so pines with both serotiny and resprouting are even rarer (Keeley and Zedler 1998, Rodríguez-Trejo and Fulé 2003, Pausas 2015). In fact, postfire resprouting capacity in pines (either from epicormic or from basal buds) typically only occurs when individuals are young, with the extraordinary exception of *Pinus canariensis* that has a strong epicormic resprouting capacity at any age (Pausas and Keeley 2017) in addition to some serotiny (Climent et al. 2004). When resprouting from epicormic buds, the main stem of this pine survives (i.e., it remains as a tree); when resprouting from basal buds, pines may develop more than one stem, so with time they may appear as several trees together (or one of the stems dominates); but in any case, they mostly remain as trees. However, *P. yunnanensis* can acquire the physiognomy of a multistemmed shrub with high resprouting and high serotiny,

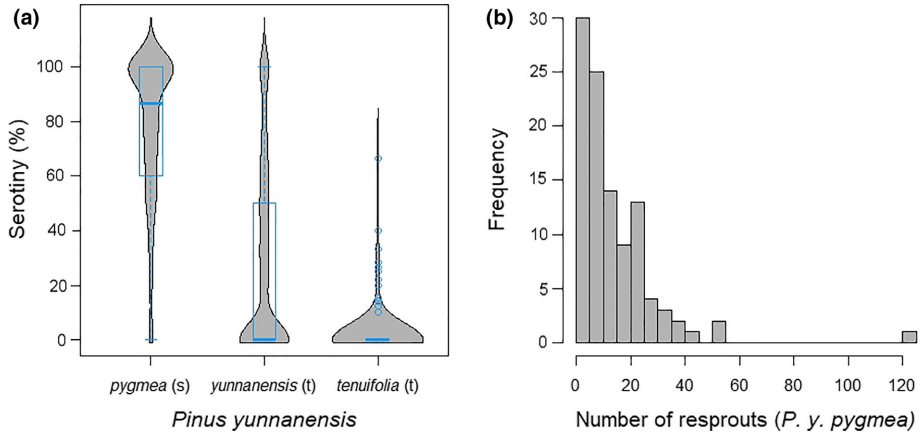

FIG. 2. Variability of serotiny (proportion of closed cones) in the three varieties of *Pinus yunnanensis* (a) and variability in the number of basal resprouts in *P. y. pygmea* (b). Resprouting data refers to the number of resprouts observed among 104 *P. y. pygmea* plants with postfire age ranging from 2 to 11 yr. Variability in serotiny is shown as bean plots (with density shape in gray) and boxplots (in blue; with the horizontal line representing the median). Elaborated from data in Su et al. (2015, 2019), Luo et al. (2020), and Data S1.

and forms extensive shrublands where fires are frequent (var. *pygmea*; Fig. 1). Other shrubs with these traits are found in the family Proteaceae (Pausas and Lamont 2018, Lamont et al. 2020). In *P. yunnanensis*, the spatial variability in fire regime, generates mosaics of alternative vegetation types (forest vs. shrubland) without changing the dominant species. This species is a good example of population divergence driven by different fire regimes (Pausas and Schwilk 2012, Pausas et al. 2012, Hernández-Serrano et al. 2013), or more specifically, a case of sympatric speciation driven by variability in fire regime at the landscape scale.

The variable response of fire traits within species is of increasing interest, as it provides insights on the role of fire in plant evolution (Pausas and Schwilk 2012). For instance, to what extent are these traits genetically fixed in each variety? Are forward and backward evolutionary transitions possible with changes in fire regime? Within species (population-level) variability in serotiny linked to different fire regimes is known in pines (Hernández-Serrano et al. 2012) and has a genetic basis (Castellanos et al. 2015); but little is known about variability in the resprouting and growth form. There is evidence of within-species variability for those two traits in *Eucalyptus*, for instance. Some *Eucalyptus* species resprout from the base (from a lignotuber) when young, forming a multistemmed shrub, but if they are not disturbed they can develop a main trunk, and the trees lose their lignotubers (Abbott and Loneragan 1984, Burrows 2013). Research is needed to understand the variability in growth forms and fire response in the Yunnan pine fully. Common garden experiments, including perturbation, could help to disentangle the genetic and environmental role of resprouting and growth form. In addition, combining field studies and genetic studies in the field may contribute to understanding selection gradients at landscape scale. In any case, *P. yunnanensis* is a key species for further improving our understanding of fire-driven evolution in pines, and adds to the diversity of fire strategies of pines worldwide.

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Supporting Information

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