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Title

Resilience of European larch (*Larix decidua* Mill.) forests to wildfires in the western Alps

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Abstract

European larch is a dominant species in the subalpine belt of the western Alps. Despite recent increases in wildfire activity in this region, fire ecology of European larch is poorly understood compared to other larch species around the world. This study aims to assess whether European larch forests are resilient to fires, and to find out the factors that drive such resilience. We assessed the recovery of larch forests along a gradient of fire severity (low, moderate, high) based on the abundance and dominance of post-fire larch regeneration. We established 200 plots distributed among burned larch forests in nine wildfires that occurred between 1973 and 2007 in the western Alps. We included variables regarding topography, climate, fire severity, fire legacies, ground cover, grazing intensity, and time since fire. To evaluate potential drivers of larch recruitment, we applied generalized linear mixed models (GLMM) and random forests (RF). Larch regeneration was much more abundant and dominant in the moderate- and high-severity fire classes than in the low-severity class. More than half of the plots in the moderate- and high-severity classes were classified as resilient, i.e., post-fire larch regeneration was enough to recover a larch stand. GLMM and RF produced complementary results: fire severity and legacies, such as snags, canopy cover and distance to seed source, were crucial factors explaining post-fire larch recruitment. This study shows that fire has a positive effect on larch regeneration, and we conclude that European larch forests are highly resilient to mixed-severity fires in the western Alps.

Keywords

Fire severity; fire resistance; fire legacies; post-fire regeneration; grazing intensity; subalpine fires.

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Introduction

Climate and land use changes are affecting forest fires in the European Alps. Land abandonment is increasing fuel biomass and forest connectivity, and extreme heat waves as well as frequent foehn winds are increasing the risk of forest fires (Valese et al. 2014). In fact, we expect larger and more intense fires in high elevation forests (Bebi et al. 2017). European larch (*Larix decidua* Mill.) forests are an extensive landscape component in the montane and subalpine belts of the western Alps, and provide diverse ecosystem services, such as timber, landscape scenery, recreation, protection from hydrogeomorphic hazards, and biodiversity (Garbarino et al. 2011). In this scenario of global change, where land abandonment interacts with climate warming, it is essential to know how European larch forests respond to wildfires.

The ecology of European larch is very similar to that of other larch species, such as Western larch (*Larix occidentalis*) in North America and Siberian larch (*Larix sibirica*) in Asia. These are considered fire-resistant species and share fire-related traits with European larch, including thick bark and self-pruning (Arno and Fisher 1995; Scher 2002; Wirth 2005; Schulze et al. 2012). In addition, fire is inherent and fundamental for the regeneration and dominance of natural populations of both Western (Schmidt and Shearer 1995; Scher 2002) and Siberian larch species (Kharuk et al. 2011; Schulze et al. 2012). Thus, we suspect that the common traits of these larch species may indicate a similar degree of resilience to fire in European larch forests.

The fire ecology of European larch forests is poorly understood. Larch forests have been continuously present in the western Alps for more than 11,000 years (Blarquez et al. 2010a, b). During the Holocene, fires were periodically frequent (Genries et al. 2009a), and may have selectively favored European larch over other tree species (Blarquez and Carcaillet 2010). Paleobotanical evidence shows that anthropic fire regimes had already replaced natural fire regimes in the western Alps by 4,000 years before present (Carcaillet et al. 2009; Leys and Carcaillet 2016). A combination of anthropic fires and agricultural land use resulted in open landscapes that could have favored larch forests (Gobet et al. 2003). Later, fire frequency decreased as a mosaic of pastures and woodlands dominated the cultural landscapes (Carcaillet 1998).

During the last few centuries, the fire regime in larch forests has consisted primarily of surface fires ignited by farmers to improve pasture quality and limit shrub encroachment (Genries et al. 2009b). Schulze et al. (2007) suggested that conditions in grazed larch forests are similar to the conditions created by fire (i.e., bare mineral soil, open canopies, seeds from live remnant trees), which are suitable for an early-successional species such as European larch. However, Genries et al. (2009b) assessed the effects of surface fires on *Larix decidua-Pinus cembra* stands, and concluded that this type of fires was not the main factor controlling forest structure and species composition. On the contrary, Wasem et al. (2010) observed that European larch was the main species regenerating naturally 25 years after a crown fire in a subalpine forest. The strict fire suppression policy of the 20th century (Valese et al. 2014) has decreased the occurrence and size of forest fires, thereby limiting the possibility to study fire ecology of European larch.

The objectives of this study were twofold. Firstly, we tested the hypothesis that European larch forests are resilient to wildfires because: first, they are resistant to fire, and second, they regenerate successfully after burning. Our second objective was to find out what factors drive the resilience of larch forests to fire. We expected that continental climate, high grazing intensity, bare soil, open canopy, and short distance to seed source would favor larch regeneration. Further understanding of the fire ecology of European larch forests will aid land managers in an era of climate and land use change.

Material and methods

Study area

The study area included the Italian regions of Piedmont and Aosta Valley, and the French department of Hautes-Alpes in the western European Alps (Fig. 1). Across the study sites, average annual temperature ranged from 2.2 to 5.8 ºC, and annual precipitation from 1155 to 1570 mm (Hijmans et al. 2005). Montane and subalpine forests are dominated by *Fagus sylvatica*, *Pinus sylvestris*, *Abies alba*, *Picea abies* and *Larix decidua*, and to a lesser extent by *Pinus uncinata*, *Pinus cembra* and broadleaved species (Camerano et al. 2008).

The fire regime in the western Alps is characterized by small fires (8-15 ha on average), while fires > 50 ha comprise < 5% of the fires, and very few reach > 500 ha (Valese et al. 2011). However, most of the burned area is due to few infrequent medium- and relatively large-size fires (> 100 ha). A high percentage of fires occurs in November-April, although the burned area in May-October can be higher. In larch forests, winter fires are usually human-induced surface fires, whereas summer fires can be crown fires caused by human activities or occasionally by lightning during drought periods (Valese et al. 2014).

We chose fire sites from three different databases: (1) Italian State Forestry Corp (Corpo Forestalle dallo Stato) fire database, (2) Aosta Valley forest disturbances database (Vacchiano et al. 2016), and (3) Prométhée French Mediterranean fire database (http://www.promethee.com). In summer 2014, we inspected fire sites to find areas that satisfied all of the following criteria: (1) burned area > 25 ha, (2) no salvage logging, (3) no artificial regeneration, (4) low, moderate, and high-severity fire classes present, and (5) larch was the pre-fire dominant species. In total, we selected 9 wildfires that occurred between 1973 and 2007 (Fig. 1, Table 1).

Field data collection

We randomly extracted 25 points in each fire site, with a minimum distance of 40 m between points to minimize spatial autocorrelation. In summer 2015, we established 12-m radius (horizontal distance) circular plots at locations that met all the following requirements: (1) clear evidence of having been burned, (2) presence of at least two pre-fire larch trees within the plot, (3) minimum distance of 20 m from plot center to fire perimeter to avoid edge effect, (4) absence of post-fire management (i.e., logging and planting). We established a balanced number of plots in each severity class (i.e., low, moderate, and high) within each fire site (Maringer et al. 2016). This preliminary severity stratification was based on a subjective in-field assessment of tree mortality inside the plot (Ascoli et al. 2015). When less than 20 plots satisfied the criteria, we checked an additional set of 25 random points in order of spatial proximity until at least 20 plots at each fire site were set up. We established 200 plots in total, between 20 and 25 plots at each site (Table 1, Appendix 2).

In each 12-m radius plot, we measured the diameter at 1.3 m height (dbh) of every living tree and snag, and recorded the species of every living stem, snag and stump. We used all available evidence to identify the species of snags and stumps, e.g., bark characteristics, crown architecture, fallen logs by the stumps, living trees in the proximity. If charring under bark was detected, we recorded the tree as dead at the time of fire (Larson and Franklin 2005; Belote et al. 2015), and excluded it from pre-fire density. We considered fire as the cause of all the dead trees, even if few trees might have died after the fire because of other agents. We measured every log on the ground that exceeded the minimum dimensions: large-end diameter ≥ 5 cm, small-end diameter ≥ 1 cm, and length ≥ 1 m. We also measured horizontal distance from the plot center to the nearest living adult larch tree. A hemispherical photograph was taken 1 m above ground at the plot center using a fisheye lens mounted on a digital single lens reflex camera.

Within a 6-m radius circular subplot at the plot center, we estimated visually the percent of ground covered by rocks, mineral soil, litter, coarse wood debris (CWD) and vegetation to the nearest 5%. Additionally, relative abundance (i.e., percent ground cover) of vascular plant species was visually assessed in the understory layer (0-1.8 m height) of each subplot (Iussig et al. 2015). Vegetation surveys were limited to species with relative abundance ≥ 1%. Finally, we counted every sapling and seedling (≥ 10 cm height) by tree species. We did not apply any dbh or height threshold to separate pre-fire trees from post-fire regeneration, and therefore all the young trees that appeared after the fire were considered as post-fire regeneration. When needed, we took tree core samples as close as possible to the root collar and counted visible tree rings to make sure that all the regeneration was post-fire.

Predictor variables

We derived 20 variables grouped into 8 categories: larch regeneration, topography, climate, fire severity, fire legacies, ground cover, grazing intensity, and site variables (Table 2). We obtained topographic and climatic variables from digital elevation models (DEM) and global climate data (Hijmans et al. 2005) respectively. Climate continentality was assessed with the hygric Gams index, and the thermal compensated continentality index (Icc) (Caccianiga et al. 2008).

Fire severity was quantified as tree mortality caused by fire, i.e., the percent of pre-fire trees killed by fire (Keeley et al. 2009; Morgan et al. 2014). Therefore, tree mortality will be used hereafter as the fire effect that describes fire severity. Plots were grouped into three fire severity classes: low (0-40% tree mortality), moderate (41-80%) and high (81-100%). We calculated basal area of living trees and snags separately, as well as total volume of logs by approximating them to a truncated cone. Percent of canopy cover was calculated from the hemispherical photograph using CanopyDigi (Goodenough and Goodenough 2012). To account for time since fire, fire sites were grouped into three time classes: “old” (before 1990), “mid” (1990-1999), and “new” (2000 and later).

Grazing intensity was assessed indirectly using the following vegetation-based indicators, each of them weighted by species relative abundance in the subplot: (1) Nutrient indicator value (N_L) (Landolt et al. 2010), (2) Mowing tolerance value (MV_L) (Landolt et al. 2010), and (3) Pastoral Value (PV) (Daget and Poissonet 1971; Ravetto Enri et al. 2017). We assumed that these indicators describe a land use gradient (Strebel and Bühler 2015), and are representative of the grazing regime in the previous 10-30 years, since vegetation dynamics are slow in this high elevation ecosystem (Körner et al. 2003). We additionally described grazing intensity by considering the relative abundance of plant species indicative of different grazing regimes (Strebel and Bühler 2015). Every plant species was allocated to its phytosociological optimum chosen among six vegetation units defined according to a gradient from ungrazed to regularly grazed land (Theurillat et al. 1995; Aeschimann et al. 2004): woodlands (WOOD), shrubs and thickets communities (SHRUB), fringes and tall herbs communities (FRINGE), dry nutrient-poor grasslands (DPGRASS), mesophilous nutrient-poor grasslands (MPGRASS), and mesophilous nutrient-rich grasslands (MRGRASS). Relative abundance of each vegetation unit was calculated in every subplot. Further description of the indicators and vegetation units is found in Fig. S1.

In order to reduce the number of variables of grazing intensity, we performed a principal component analysis (PCA) on the three indicators (N_L, MV_L, PV) and relative abundances of the six vegetation units (WOOD, SCHRUB, FRINGE, DPGRASS, MPGRASS, MRGRASS). Two main components (PCA_1 and PCA_2) were extracted and used as proxies of grazing intensity (Table 2, Fig. S1). The first component reflected a short-term abandonment gradient, from extensively grazed fringe communities to recently grazed pastures. The second component represented a long-term abandonment gradient, from abandoned woody areas to semi-abandoned shrub communities.

Resilient space

Following the approach of Nimmo et al. (2015) and Hodgson et al. (2015), we defined a resilient space to decide which plots were resilient to fire (Fig. 2). We included two types of variables to build such a space. First, fire severity, which is inversely related to resistance to fire. Second, larch regeneration, which describes post-fire recovery. We used two larch regeneration variables

(Table 2), larch_density and larch_percent, to characterize post-fire recovery. We applied a simple rule to define the larch resilient space. If larch_density ≥ minimum larch regeneration density or larch_percent > 50%, plots were considered resilient. On the contrary, if larch_density < minimum density and larch_percent ≤ 50%, then plots were labeled as non-resilient. Minimum larch regeneration density was a function of fire severity. In the low-severity class, minimum density was set to 0 (i.e., no larch regeneration is required) to reflect that the short-term persistence of larch stands is not compromised by low-severity fires. In the moderate-severity class, minimum density grows linearly from 0 to 600 trees ha^{-1}, and also linearly from 600 to 2,000 trees ha^{-1} in the high-severity class (Fig. 2). Indeed, 600 trees ha^{-1} is a common target for forest managers when European larch regeneration has reached a few meters in height (Bernetti 1995). In European larch forests affected by small clearcuts, 2,000 trees ha^{-1} is a typical initial density for artificial regeneration (Bernetti 1995).

Data analysis

We performed four types of analyses: effect size estimation, resilient space assessment, generalized linear mixed models (GLMM), and random forests (RF). For each severity class (i.e., low, moderate, high), we calculated the mean and 95% confidence interval (CI) of both variables of larch regeneration. CIs of larch_density and larch_percent were computed using a Poisson and binomial distribution respectively. Effect size was defined as the difference between means of fire severity classes. We did not perform any statistical test to compare means because we were more interested in the ecological differences in larch regeneration, which are sufficiently described by the unstandardized mean difference together with CIs.

To evaluate the influence of the predictor variables (Table 2) on post-fire larch recruitment, we fitted two GLMM, one for each response variable (i.e., larch_density and larch_percent). We examined the spatial autocorrelation of the response variables in each fire site with Mantel tests (van Mantgem and Schwilk 2009) and Mantel correlograms (Borcard and Legendre 2012), and we found no evidence of significant spatial dependence among plots. To avoid collinearity, we excluded from modeling: elevation (r = 0.90 with icc), gams (r = 0.75 with icc), severity (r = -0.74 with canopy), ba (r = 0.72 with canopy) and vegetation (r = -0.71 with soil). No additional variable-selection was performed because the models were not intended for prediction. Continuous predictor variables were standardized and fire site was used as random effect in both models. We applied a log-link function (negative binomial error distribution) and logit-link function (binomial error distribution) to model larch_density and larch_percent respectively. Overdispersion was estimated with Pearson residuals (Zuur et al. 2009). We checked zero inflation models, interactions by adding bivariate interaction terms between continuous variables (soil, PCA_1, PCA_2) and time (categorical), and non-linear relationships by fitting smoothing curves to Pearson residuals (Zuur et al. 2009). We also checked model assumptions (i.e., homogeneity, normality, independence) graphically using Pearson residuals (Zuur et al. 2009). We calculated marginal and conditional R^2_{GLMM} to estimate the variance explained by the models (Nakagawa and Schielzeth 2013). Modeling was carried out using the function *glmmadmb* from the R package *glmmADMB* (Fournier et al. 2012).

We applied RF to complement GLMM for the following reasons (Cutler at al. 2007; De'ath et al. 2007): (1) RF are more robust to collinearity and thus we can include all the predictor variables, (2) we can estimate the importance of the predictor variables, and (3) we can easily visualize the effect of predictors on the response variable. All the predictors were added to two RF, one for each response variable, and we applied default parameters: number of trees = 1000, minimum terminal node size = 5, and number of variables tried at each split = 6. We used variable importance (VIMP) to rank predictor variables (Ehrlinger 2015). Partial dependence plots were produced to interpret the effect of each predictor on the response variables (Ehrlinger 2015). To evaluate model performance, we used total variance explained by RF and R^2 between predicted and observed response values. Modelling was carried out using the function *rfsrc* from the R package *randomForestSRC* (Ehrlinger 2015). We performed all the analyses within the R statistical framework (R Core Team 2014). The dataset and R scripts are available in Appendix 3.

Results

Effect size and resilient space

Effect sizes in larch regeneration between moderate- and high-severity fire classes were very small: 142 trees ha^{-1} and 4% (Fig. 3). In contrast, effect sizes between low and moderate-high classes were broad (Fig. 3). As expected, abundance and dominance of larch regeneration were much lower in the low-severity class.

Larch was the most abundant post-fire species, although its density was highly variable, from 0 to > 20,000 seedlings and saplings ha^{-1} (Fig. 4). Plots in the low-severity class were considered resilient by definition. In the moderate class 51% of the plots were labeled as resilient, as well as 52% in the high class (Table 3). Therefore, approximately half of the plots in the moderate and high classes showed enough regeneration to recover a stand dominated by larch. In the high-severity class 20% of the plots had no larch regeneration, and only 7% had no tree regeneration (Table 3).

GLMM

Mixed models showed that several drivers were associated with post-fire larch regeneration (Table 4). Larch_density was negatively related to the continentality index (icc), but the relationship was not significant with larch_percent. The relationships of the remaining predictors were consistent across both models: positive for slope and snag basal area, and negative for canopy cover, distance to seed source, and grazing intensity (PCA_1 and PCA_2). Post-fire larch establishment was not significantly related to southness, logs volume, soil cover and time since fire in any of the models (Table 4). Odds ratios (OR) represented the effect of a change of one standard deviation holding fixed the rest of predictors and the random effect. For example, an increase of about 30 m in the distance to seed source would reduce approximately in half the density of larch regeneration (Table 4). Variance explained by fixed and random factors was > 60% in both models (Table 4).

RF

Due to the stochastic component, each time a RF is run, the rankings of variable importance can vary to some extent. Nevertheless, the two most important predictors did not change: snags and fire in the larch_density RF, and fire and canopy in the larch_percent RF (Fig. 5). This confirmed the great influence of the different study sites on larch regeneration. Icc and slope also ranked high in the larch_density and larch_percent RF. Low values of VIMP indicated that those variables contributed little to predictive accuracy (Fig. 5). The larch_density RF explained 32% of the variance, and the larch_percent RF 52%. R^2 between predicted and observed values were 0.81 and 0.87 respectively.

Non-linear relationships were common in both RF. Larch_density did not increase after 12 m^2 ha^{-1} of snag basal area was reached, and maximum establishment of larch took place with severity about 80% (Fig. 6, 7). Shapes of larch_percent responses were similar to those of larch_density, with the exceptions of elevation, southness and continentality (icc and gams) (Fig. 6, 7). RF predicted peaks of larch regeneration when distance to seed source was around 12 m and living basal area was around 9 m^2 ha^{-1} (Fig. 6, 7). As expected, both models predicted higher levels of larch regeneration when canopy cover was low and bare soil cover was high. Negative relationships between larch_density and grazing intensity (PCA_1 and PCA_2) were expected, but surprisingly similar patterns were also found in larch_percent (Fig. 6 , 7).

Discussion

Our results are consistent with the hypothesis that European larch forests are resilient to fire across a range of severity. Successful post-fire larch recruitment was common throughout the study sites, but varied depending on climate continentality, terrain slope, grazing pressure, and severity, especially through the effect of fire legacies. Our results are in line with the heterogeneous post-fire regeneration found in Asia, where boreal larch forests not only self-replace after burning (Furyaev et al. 2001; Kharuk et al. 2011), but also experience diverse successional trajectories (Cai et al. 2013; Otada et al. 2013).

Resilient space

Post-fire larch regeneration was much more abundant and dominant in the moderate- and high-severity fire classes than in the low-severity class (Fig. 3). We did not establish control plots outside the fire perimeters, but natural regeneration of non-disturbed larch forests in the western Alps is dominated by other tree species such as *Pinus cembra*, *Abies alba* and *Picea abies* (Motta and Dotta 1995; Bonnassieux 2001). Our results suggest a positive effect of fire on larch recruitment, and a minor effect of low-severity fire on larch forest dynamics (Fig. S2).

Relative contributions of resistance and recovery to resilience vary as a function of disturbance severity (Connell and Ghedini 2015; Hodgson et al. 2015; Nimmo et al. 2015). Where severity is high, resilience relies on recovery. Plots in the low-severity class did not experience serious changes in forest structure and composition. Therefore, we considered that these plots were resistant enough to be resilient. Likewise, more than half of the plots in the moderate- and high-severity classes had enough larch regeneration to be classified as resilient. Moreover, most of the non-resilient plots represent a partial replacement of larch by mostly pine (e.g., *Pinus sylvestris*, *Pinus uncinata*) and broadleaved species (e.g., *Betula pendula*, *Populus tremula*). Only a minor proportion of the high-severity class showed signs of succession towards other type of forests or shrub-grassland due to the lack of larch regeneration (Table 3).

Our definition of resilient space depends, at least, on four aspects. First, minimum density of larch regeneration was based on initial planting densities and management targets set for productive larch stands (Bernetti 1995). However, lower densities of larch saplings may be enough for larch stands to recover to their pre-fire state (Kashian et al. 2005; Shi et al. 2010).

Second, we acknowledge that minimum regeneration densities could be reduced as a function of time elapsed since fire due to early self-thinning dynamics (Kashian et al. 2005; Osawa and Kajimoto 2010). Nevertheless, we did not apply different minimum densities to our time classes (i.e., old, mid, and new fires) because the regression models did not show any effect of time class on larch recruitment (Table 4). Third, sapling recruitment and mortality are processes that continuously change the amount and composition of tree regeneration. Nonetheless, it is likely that most of the larch regeneration established during the first 10-20 years after the fires (Wasem et al. 2010; Harvey et al. 2016; Urza and Sibold 2017). Furthermore, we expect low levels of mortality in larch saplings in the first decades after establishment because: (1) light was still abundant in the forest floor of moderate- and high-severity areas, (2) young European larches are adapted to severe subalpine conditions (Barbeito et al. 2012), and (3) are also resistant to browsing, diseases and pests (Holtmeier 1995; Weber 1997). European larch has a low tolerance to drought (Eilman and Rigling 2012; Lévesque et al. 2013), but it is unknown if droughts cause high mortality in European larch seedlings and saplings (Dulamsuren et al. 2010; Harvey et al. 2016; Urza and Sibold 2017). Fourth, European larch is a long-lived species, with rapid initial growth, that persists for centuries before is overtaken by shade-tolerant species (Motta and Edouard 2005; Motta and Lingua 2005). Therefore, we set 51% as the minimum composition necessary for larch to dominate in the decades that follow the fire. In summary, our binary classification between resilient and non-resilient is a simplification of a more complex reality (Tautenhahn et al. 2016). We believe that our classification is conservative due to the four issues commented above, and consequently we probably underestimate larch resilience to fire.

Predictors of larch regeneration

European larch is a wind-dispersed, shade-intolerant pioneer species that requires exposed mineral soil, high light levels and enough seed source to regenerate successfully (Holtmeier 1995; Risch et al. 2003). As expected, larch regeneration showed a negative relationship with tree canopy cover. Seed dispersal distance is one of the most common limiting factors for tree regeneration in high-severity fire patches (Chambers et al. 2016; Kemp et al. 2016; Harvey et al. 2016; Tautenhahn et al. 2016). Larch regeneration diminished with increasing distance to the nearest adult larch tree. Our results generate doubts regarding the capacity of European larch to regenerate successfully in large, high-severity areas where surviving trees are scarce and seed sources are distant. We need more research on masting (Poncet et al. 2009), seed predation and dispersal to find out how dispersal distance influences larch resilience to large patches of high severity.

We hypothesized that fire severity and post-fire soil legacies were correlated (Pausas et al. 2003). We expected that areas of high severity presented longer regeneration windows with mineral soil exposed by fire (Vacchiano et al. 2014). However, bare soil cover was neither significant nor an important predictor in the models. This is probably due to the long period elapsed from burning to field sampling, which complicated the estimation of soil cover conditions when larch seedlings actually established.

As expected, there was some collinearity between fire severity and fire legacies, especially with canopy cover (r = -0.74), and to a lesser extend with snag basal area (r = 0.52). In fact, snag basal area, i.e., the abundance of dead standing trees, was the most important predictor of larch regeneration density (Fig. 5). We interpreted snag basal area as a proxy of disturbance severity rather than only a fire legacy (Harvey et al. 2014), which reinforces fire severity as a factor explaining post-fire larch regeneration. Likewise, canopy cover was essential to explain the percent of larch regeneration (Fig. 5), and could also be used as indicator of fire severity. Modelling showed maximum levels of larch regeneration when severity was between 70-90% (Fig. 6, 7). This level of fire severity, between moderate and high, seems to provide enough light, mineral soil and proximity to seed source to reach successful levels of larch regeneration.

Herbivory, especially by livestock, alters post-fire succession (Tercero-Burcado et al. 2007; Raffaele et al. 2011). Relationships between larch regeneration and grazing intensity were negative. Two issues may affect our results. First, livestock trampling exposes mineral soil and reduces competition from ground vegetation, promoting a suitable seedbed for larch seedlings (Schulze et al. 2007; Garbarino et al. 2011), but at sapling stages browsing may damage and decrease the density of young larches (Khishigjargal et al. 2013). Consequently, a positive effect of grazing may be noticeable only at the seedling stage. Second, based on our vegetation surveys and field observations, we conclude that most of the plots have not been regularly grazed after burning by domestic animals (cattle, horse, sheep and goat). Most fire sites were located in abandoned larch wood pastures (Nagler et al. 2015), and thus high grazing levels are missing from the sample. In sum, livestock probably affects negatively larch saplings, although in these specific sites it is not a limiting factor for post-fire larch regeneration given the low grazing intensity.

Climate also controls larch regeneration. Density of larch recruitment decreased with Icc (thermal continentality), whereas the percent of larch increased. Like other subalpine tree species, post-fire larch regeneration declines with increasing elevation due to climatic constraints (Coop et al. 2010). Nonetheless, European larch tolerates harsh conditions and exhibits higher survival than other tree species at high elevation (Barbeito et al. 2012). Relationships of larch regeneration with the Gams index (hygric continentality) were less clear and non-significant. Topographic conditions, for example slope steepness, may also influence larch regeneration, and we found a significant positive association between larch establishment and slope.

Implications for European larch resilience to wildfires

A forest is resilient to fire if it recovers to the same type of forest after burning (Stephens et al. 2013). Thus, the concept of forest resilience to fire is often associated to recovery, i.e., enough natural regeneration and of the same tree species following fire. If this is not the case, a fire causes a shift to a different state (Larson et al. 2013; Gärtner et al. 2014; Tautenhahn et al. 2016). Larch resilience to fire depends on both initial resistance to burning and post-fire regeneration. As a long-lived pioneer species, abundance and dominance of larch relies on initial patters of post-disturbance regeneration (Johnstone et al. 2010). However, land use and climate changes are altering disturbance regimes and imposing new environmental conditions in the Alps (Valese et al. 2014; Bebi et al. 2017). Several factors can affect future larch resilience to wildfires (Johnstone et al. 2016): (1) changes in the fire regime, (2) interactions with land use, and (3) climate warming.

European larch is a fire resister species due, among other reasons, to its thick bark (Frejaville et al. 2013). Thick bark may be an adaptive trait evolved under fire regimes characterized by frequent low- and moderate-intensity fires (Pausas 2015). In fact, *Larix* species are associated with low-severity fires in boreal Asian forests (Rogers et al. 2015), and mixed-severity fire regimes in western North America (Marcoux et al. 2015). Ecological memory may enhance resilience of larch forests to mixed-severity fires, because information legacies (fire adaptations such as thick bark) reduce mortality from burning (Belote et al. 2015), and material legacies (e.g., surviving trees) facilitate a rapid recovery (Johnstone et al. 2016). However, larch forests may not be so resilient to a combination of increased fire severity and size caused by extreme fire weather and fuel build-up that follows land abandonment (Valese et al. 2014). In large patches of high severity, lack of seed delivery from surviving trees is a limiting factor of tree regeneration (Johnstone et al. 2016; Tautenhahn et al. 2016). In fact, negative relationships between post-fire larch regeneration and distance to seed source have been found for *Larix sibirica* (Otada et al. 2013) and *Larix occidentalis* (Urza and Sibold 2017). In brief, resilience of European larch to large, high-severity fires might be low, although further research must address this matter.

In the absence of wildfires, land use has been the main historical driver of larch forests expansion in the Alps (Schulze et al. 2007; Garbarino 2011). Traditional silvo-pastoral activities interrupted natural succession for centuries by maintaining open woodlands and soil erosion, condition under which European larch regenerated and dominated. In contrast, the current land use regime is substantially different from the past cultural landscapes that originated the present larch forests (Bourcet 1984). Ongoing land abandonment may control forest resilience by changing forest structure and composition, e.g., densification and increase of shade-tolerant species (Motta et al. 2006), which in turn affects information and material fire legacies (Johnstone et al. 2016; Torres et al. 2016). We did not explore how pre-fire structure and composition, driven by land use, impacted post-fire larch regeneration. Nevertheless, we think that such understanding could help to predict resilience to future forest fires more accurately.

Finally, impacts of climate on resilience become more apparent when a disturbance like fire occurs (Johnstone et al. 2010). In the Alps, temperatures are projected to increase at high elevation, while precipitation is projected to decrease in summer and increase in winter during the 21st century (Gobiet et al. 2014). Less severe continental conditions could favor not only post-fire recruitment of larch but also other tree species, and droughts could also change the composition of post-fire regeneration (Moser et al. 2010). As a result, burned larch stands may be more likely to shift towards mixed forests under climate change.

Conclusions

To our knowledge, this is the first study of post-fire dynamics of European larch in multiple fire sites of the Alps. European larch exhibited similar resilience to fire as other species of *Larix* around the world. Fire had a positive effect on European larch recruitment. Post-fire larch regeneration was successful and highly variable, which caused diverse recovery paths towards pure and mixed larch forest stands. Mixed-severity fires generated legacies, such as open canopies and short distances to seed trees, that provided suitable conditions for larch establishment. However, we suspect that large patches of high severity may limit larch regeneration. In conclusion, our findings suggest that larch forests in the western Alps own a high level of resilience to mixed-severity fires, although resilience to future fire regimes driven by global changes remains to be tested.

Conflict of interest

The authors declare that they have no conflict of interest.

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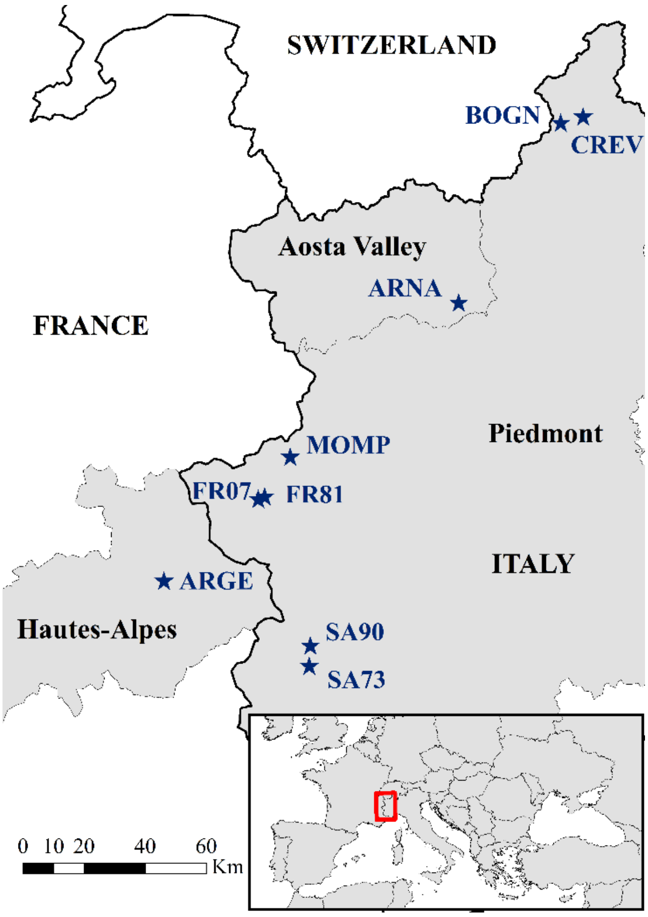

Fig. 1 Location of the nine forest fires studied

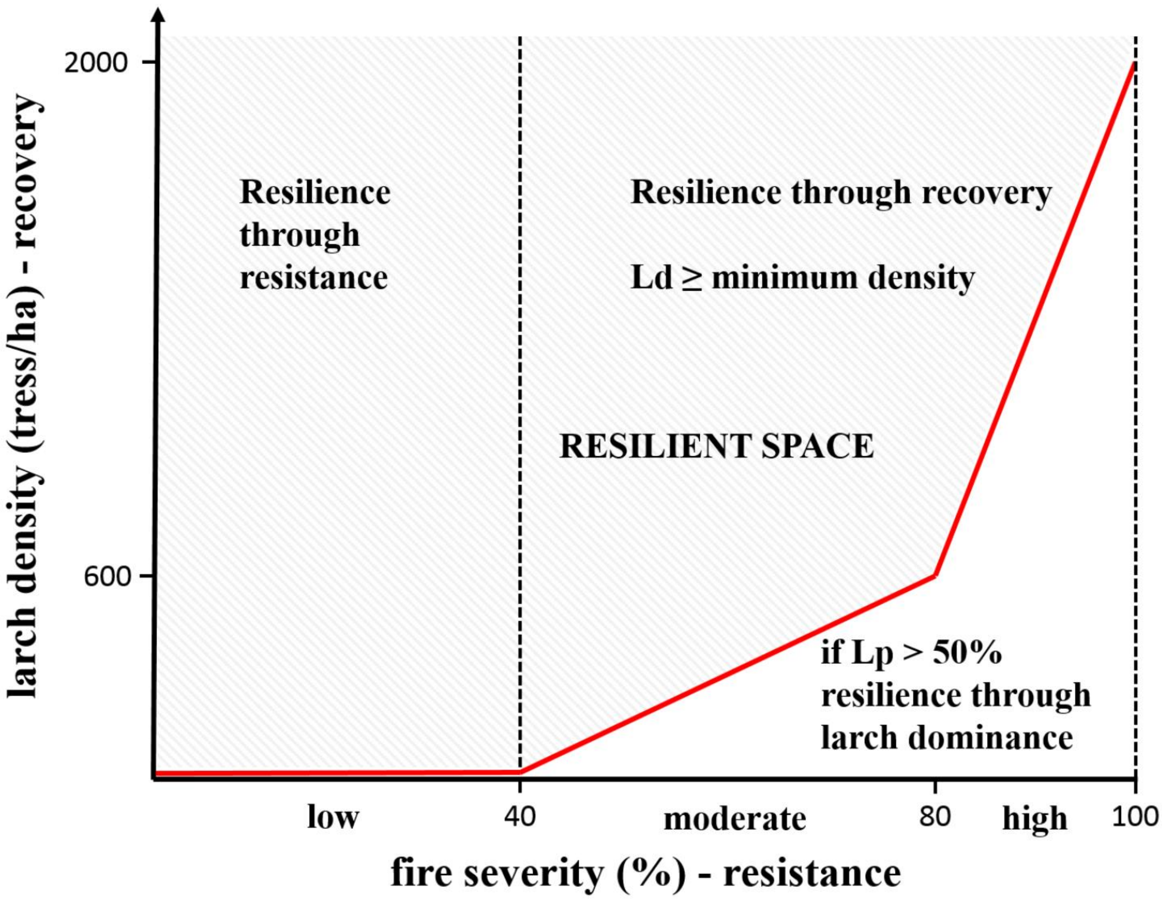

Fig. 2 Resilient space of European larch stands to forest fires. The resilient space is defined by fire severity (inversely related to fire resistance), and post-fire recovery (density and percent of larch regeneration). When severity is low, resistance is high enough to maintain a similar structure and composition. When severity is moderate or high, only abundant and/or dominant larch regeneration is able to recover a larch forest (i.e., succession with no replacement). Moderate and high severity with scarce and minor larch regeneration gives as result succession paths with partial or total species replacement (i.e., lack of resilience to fire). Ld: larch_density; Lp: larch_percent

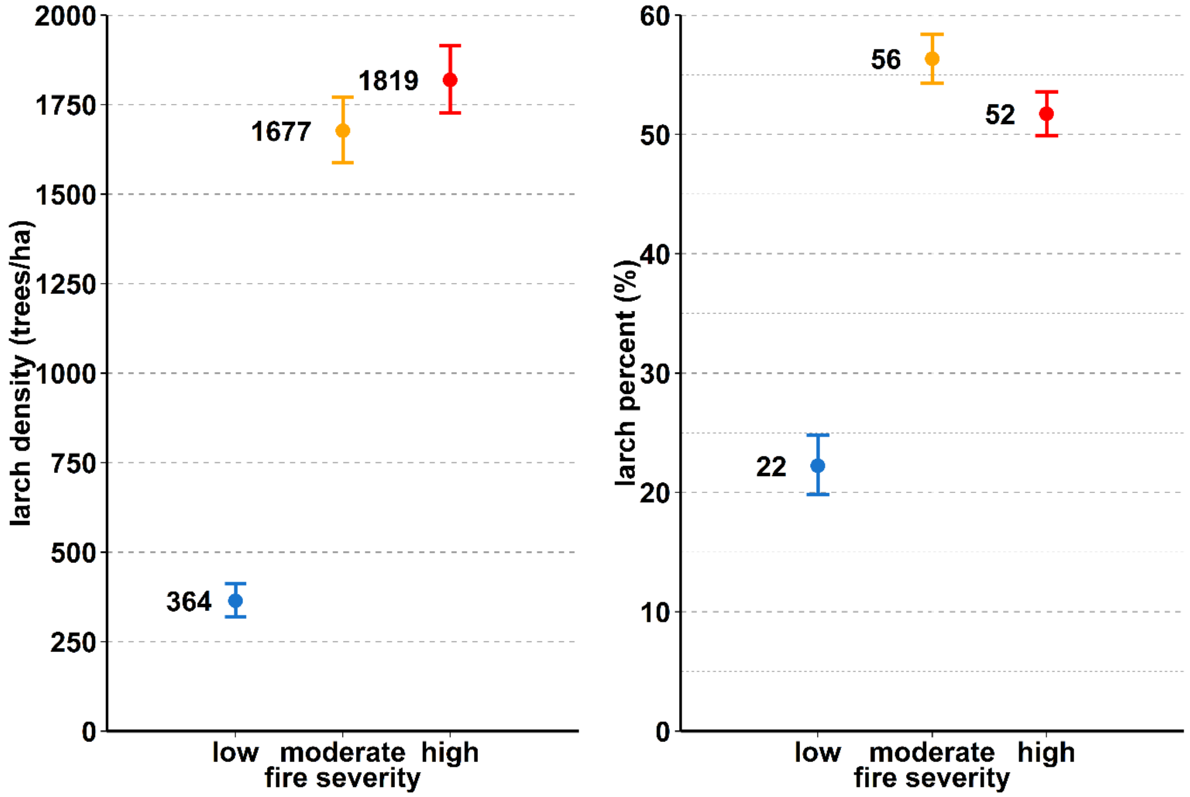

Fig. 3 Mean values of post-fire European larch natural regeneration in three fire severity classes: larch_density (left) and larch_percent (right). Fire severity: % of trees killed by fire; low: 0-40%, moderate: 41-80%, high: 81-100%. Error bars represent 95% CIs. Number of plots per severity class: low 60, moderate 69, high 71

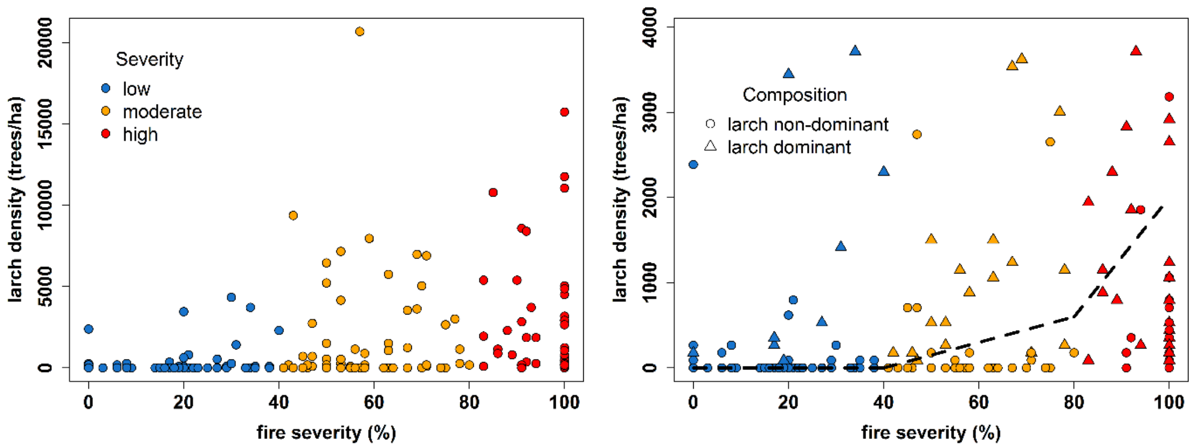

Fig. 4 Post-fire European larch natural regeneration along a gradient of fire severity. Left: density of larch regeneration in 200 plots. Right: closer view into the resilient space. Dots above the dashed line and triangles in any position represent plots resilient to fire, whereas dots under the dashed line were classified as non-resilient. Larch non-dominant: larch_percent ≤ 50%; larch dominant: larch_percent > 50%

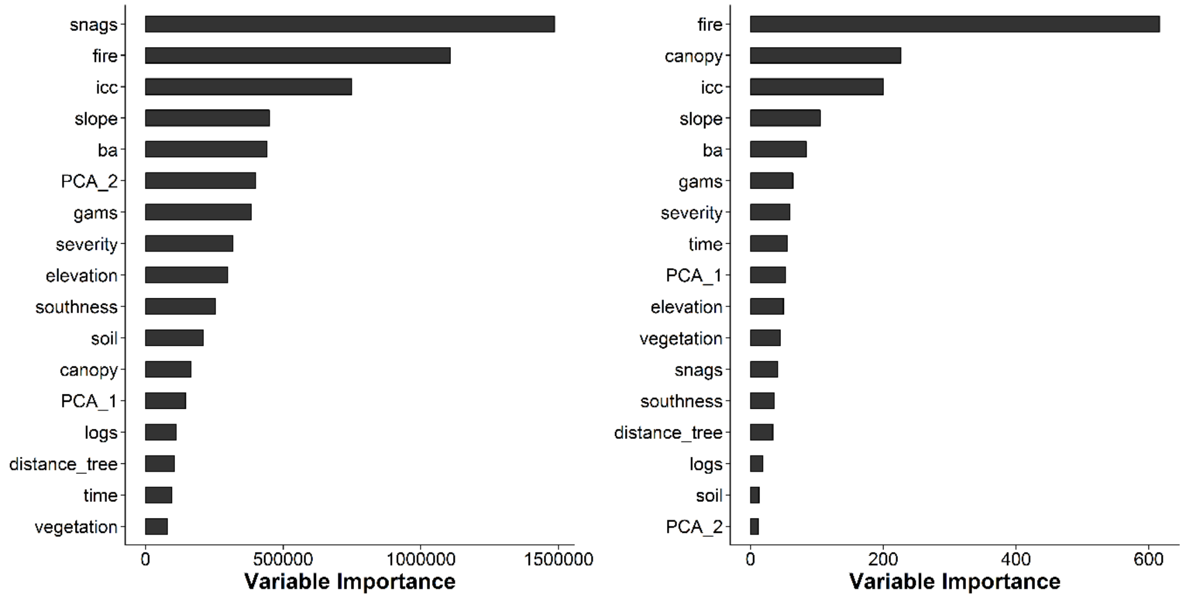

Fig. 5 Variable importance (VIMP) rankings from RF of predictor variables that explain post-fire European larch natural regeneration: larch_density (left) and larch_percent (right)

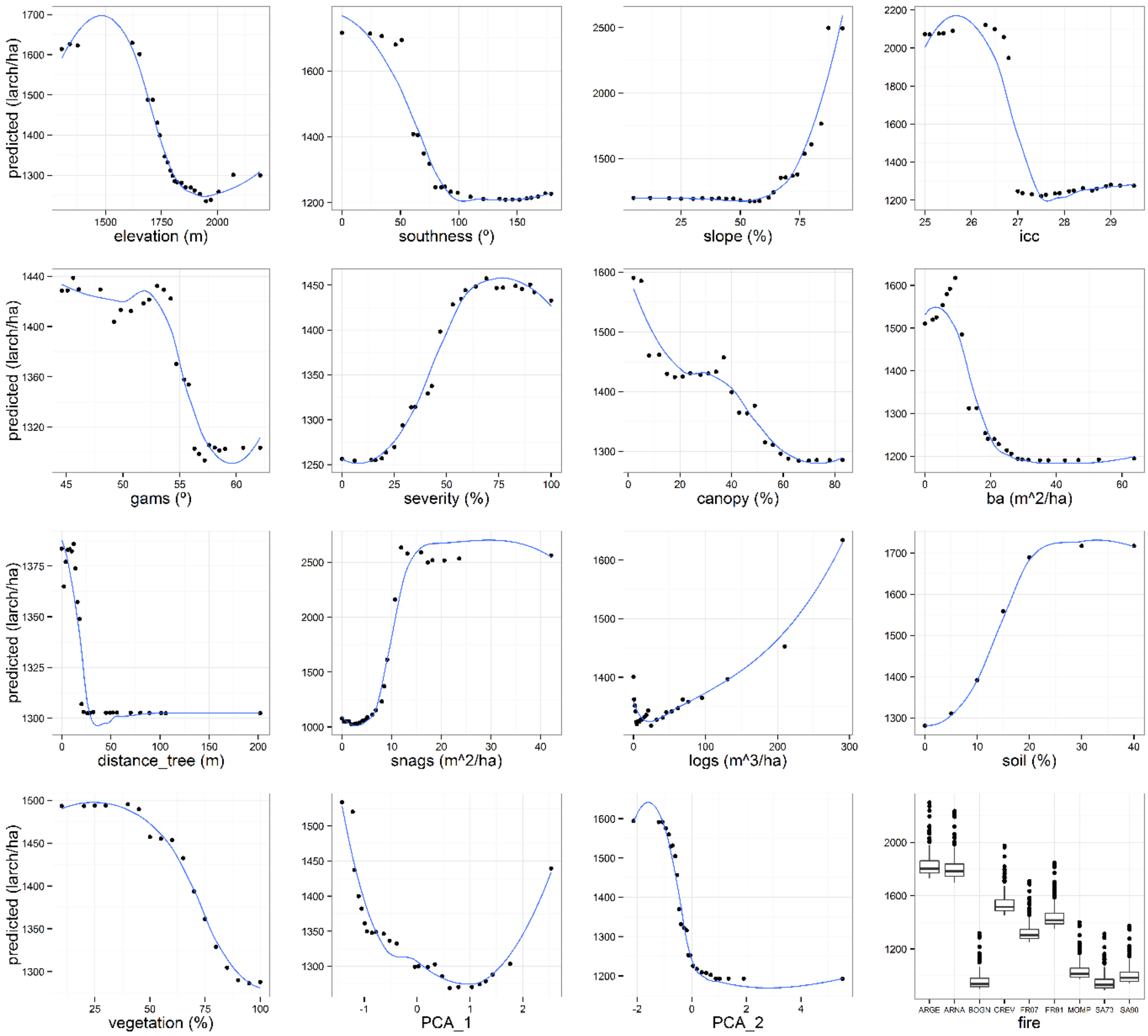

Fig. 6 Partial dependence plots from RF of post-fire density of European larch natural regeneration. A partial dependence plot shows the effect of a particular predictor on the response variable after integrating the effect of the rest of predictors. Dot: average prediction for a particular value of the predictor of interest; blue line: smooth curve

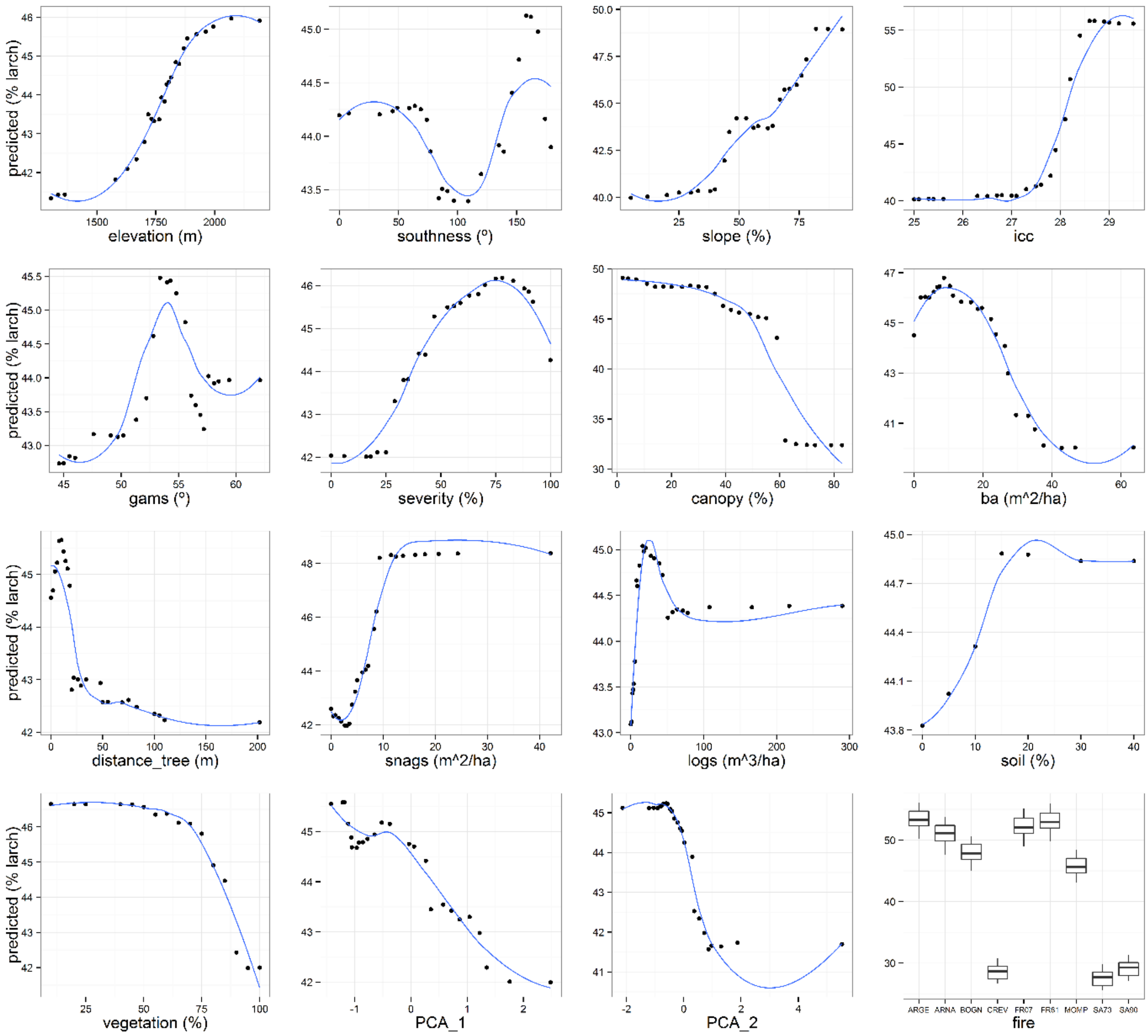

Fig. 7 Partial dependence plots from RF of post-fire percent of European larch natural regeneration. A partial dependence plot shows the effect of a particular predictor on the response variable after integrating the effect of the rest of predictors. Dot: average prediction for a particular value of the predictor of interest; blue line: smooth curve

Table 1 Characteristics of the selected fires

Code	Site	Area	Date	Years	Plots	Temp	Precip	Elevation
FR07	Pragelato	207	11.11.2007	8	22	4.2	1244	1890-2191
ARGE	L'Argentière	245	07.07.2003	12	25	4.0	1230	1575-1823
BOGN	Bognanco	60	18.01.2002	13	25	2.2	1570	1720-2034
SA90	Sampeyre	720	05.03.1990	25	20	4.5	1159	1731-2025
ARNA	Arnad	371	11.03.1990	25	24	4.4	1285	1598-1787
CREV	Crevoladossola	582	25.03.1990	25	20	5.8	1325	1305-1649
FR81	Usseaux	125	05.02.1981	34	21	4.5	1210	1737-2005
MOMP	Mompantero	220	11.12.1980	35	21	3.4	1329	1711-1937
SA73	Sampeyre	108	16.11.1973	42	22	4.5	1155	1688-1905

Site: municipality; Area: estimated burned area (ha); Date: start date of fire; Years: number of years from the fire to the field survey in 2015; Plots: number of plots placed within the fire perimeter; Temp: annual mean temperature (°C); Precip: annual precipitation (mm); Elevation: range of elevation of the plots (m)

Table 2 Variables included in the statistical analyses

Category	Variable	Description	Unit	Sampling
Larch regeneration	larch_density	Density of larch regeneration	trees ha^{-1}	6 m
	larch_percent	Percent of larch in the total tree regeneration	%	6m
Topography	elevation	Altitude above sea level	m	DEM
	southness	180º - |aspect - 180º|	º	DEM
	slope	Steepness	%	Hypsometer
Climate	gams	Annual precipitation / elevation	º	GCD
	icc	Temp July - temp January + (elevation * 0.6/100)		GCD
Fire severity	severity	Percent of trees killed by fire	%	12 m
Fire legacies	canopy	Percent of canopy cover	%	Photo
	distance_tree	Horizontal distance from plot center to the nearest adult living larch tree	m	Hypsometer
	ba	Basal area of living trees	m^2 ha^{-1}	12 m
	snags	Basal area of snags	m^2 ha^{-1}	12 m
	logs	Total volume of logs	m^3 ha^{-1}	12 m
Ground cover	soil	Percent of mineral soil	%	6 m
	vegetation	Percent of vegetation	%	6 m
Grazing intensity	PCA_1	First principal component (Fig. S1)		6 m
	PCA_2	Second principal component (Fig. S1)		6 m
Site variables	fire	Fire site: CREV, BOGN, ARNA, MOMP, FR81, FR07, ARGE, SA90, SA73	factor	
	time	Time since fire; old: fires before 1990, mid: 1990-1999, new: 2000 and later	factor	

DEM: 10-m digital elevation model; GCD: 1-Km global climate data (http://www.worldclim.org); 12 m: 12-m radius circular plot (452 m^2); 6 m: 6-m radius circular subplot (113 m^2); Photo: hemispherical photograph analyzed with CanopyDigi

Table 3 Resilience matrix of European larch stands to forest fires

Fire severity class	Resilient (larch forest)	Not resilient (mixed forest)	Not resilient (other forest)	Not resilient (non-forest)
Low	60 (100%)	–	–	–
Moderate	35 (51%)	34 (49%)	–	–
High	37 (52%)	20 (28%)	9 (13%)	5 (7%)

Numbers indicate the amount of plots in each successional class (relative abundance per severity class between brackets). We considered four major successional trajectories in the high-severity fire class: (1) larch forest (no species replacement) where larch regeneration is abundant and/or dominant; (2) mixed-larch forest (partial species replacement) where larch regeneration is scarce and non-dominant; (3) other forest types (total species replacement) where larch regeneration is absent; (4) non-forest (replacement towards shrub-grassland) where tree regeneration is not present

Table 4 Results from GLMM of post-fire European larch natural regeneration

	larch_density			larch_percent		
Variable	beta	se	OR	beta	se	OR
southness	0.23	0.25	–	0.20	0.29	–
slope	0.35 *	0.17	1.41	0.56 **	0.21	1.74
icc	-0.78 **	0.30	0.46	0.41	0.37	–
canopy	-1.12 ***	0.20	0.33	-1.20 ***	0.23	0.30
distance_tree	-0.77 ***	0.15	0.46	-0.86 ***	0.23	0.42
snags	0.50 **	0.15	1.64	0.35 •	0.19	1.42
logs	0.20	0.15	–	0.13	0.19	–
soil	0.02	0.19	–	0.02	0.22	–
PCA_1	-0.56 *	0.25	0.57	-0.89 **	0.30	0.41
PCA_2	-0.53 **	0.18	0.59	-0.35 •	0.21	0.70
timenew[1]	0.71	1.19	–	2.22	1.21	–
timeold[1]	-0.30	1.19	–	0.25	1.21	–
Marginal R^2_{GLMM}	0.43			0.29		
Conditional R^2_{GLMM}	0.78			0.64		

[1]timemid is the reference category; se: standard error; OR (odds ratio): exponentiated regression coefficients (beta); dashes are given for non-significant variables; significance codes: • $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Appendix 1. Supplementary material

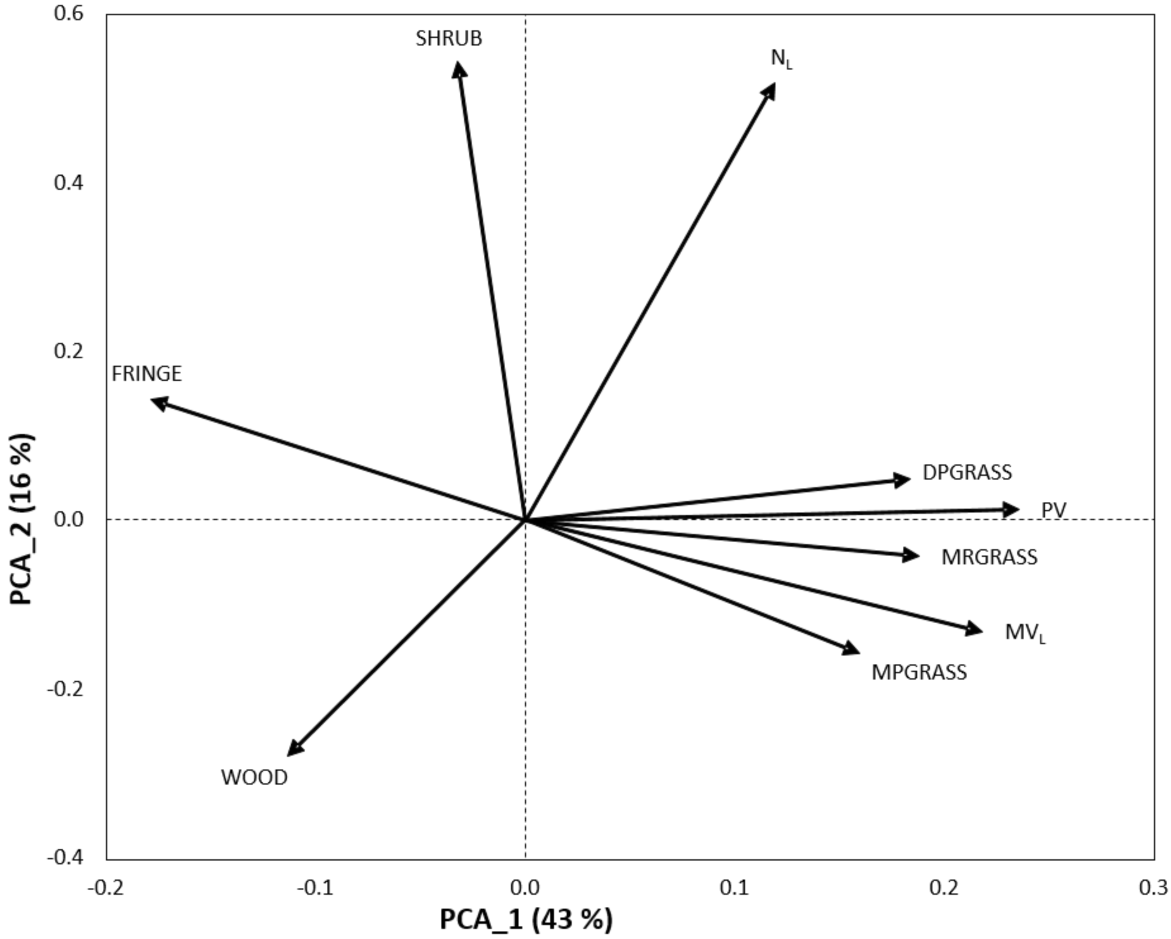

Figure A1. Principal Component Analysis (PCA) performed on three grazing indicators (N_L, MV_L, PV) and relative abundances of six vegetation units (WOOD, SCHRUB, FRINGE, DPGRASS, MPGRASS, MRGRASS) derived from the plant communities in 200 subplots. PCA_1 explained 43% of the total variation and PCA_2 16%.

Short description of the vegetation-based indicators of grazing intensity:

- Nutrient indicator value (N_L): a proxy of soil fertility, mostly nitrogen, ranging from 1 (low requirement) to 5 (high requirement) in an ordinal classification. Expected to be positively related with grazing intensity due to the effect of dung deposition.
- Mowing tolerance value (MV_L): a proxy of defoliation tolerance, ranging from 1 (low tolerance) to 5 (high tolerance) in an ordinal classification. Expected to be positively related with grazing intensity.
- Pastoral Value (PV): a synthetic value that summarizes forage yield and nutritive value, ranging from 0 to 100. Expected to be positively related with grazing intensity because overgrazing is absent in the study sites given their marginal location and pastoral management.

Short description of the vegetation units according to a gradient from ungrazed to regularly grazed land:

- Woodlands (WOOD): include species belonging to *Querco-Fagetea*, *Erico-Pinetea*, *Pyrolo-Pinetea* and *Vaccinio-Piceetea excelsae* classes.
- Shrubs and thickets communities (SHRUB): include species belonging to *Betulo carpaticae-Alnetea viridis*, *Cratego-Prunetea*, *Roso pendulinae-Pinetea mugo*, *Salicetea purpureae*, *Cytisetea scopario-striati*, *Calluno-Ulicetea* and *Loiseleurio-Vaccinietea* classes.
- Fringes and tall herbs communities (FRINGE): include species belonging to *Trifolio-Geranietea sanguinei*, *Epilobietea angustifolii* and *Mulgedio-Aconitetea* classes.
- Dry nutrient-poor grasslands (DPGRASS): include species belonging to *Festuco-Brometea* class.
- Mesophilous nutrient-poor grasslands (MPGRASS): include species belonging to *Nardetea strictae*, *Juncetea trifidi* and *Elyno-Seslerietea variae* classes.
- Mesophilous nutrient-rich grasslands (MRGRASS): include species belonging to *Molinio-Arrhenatheretea* class.

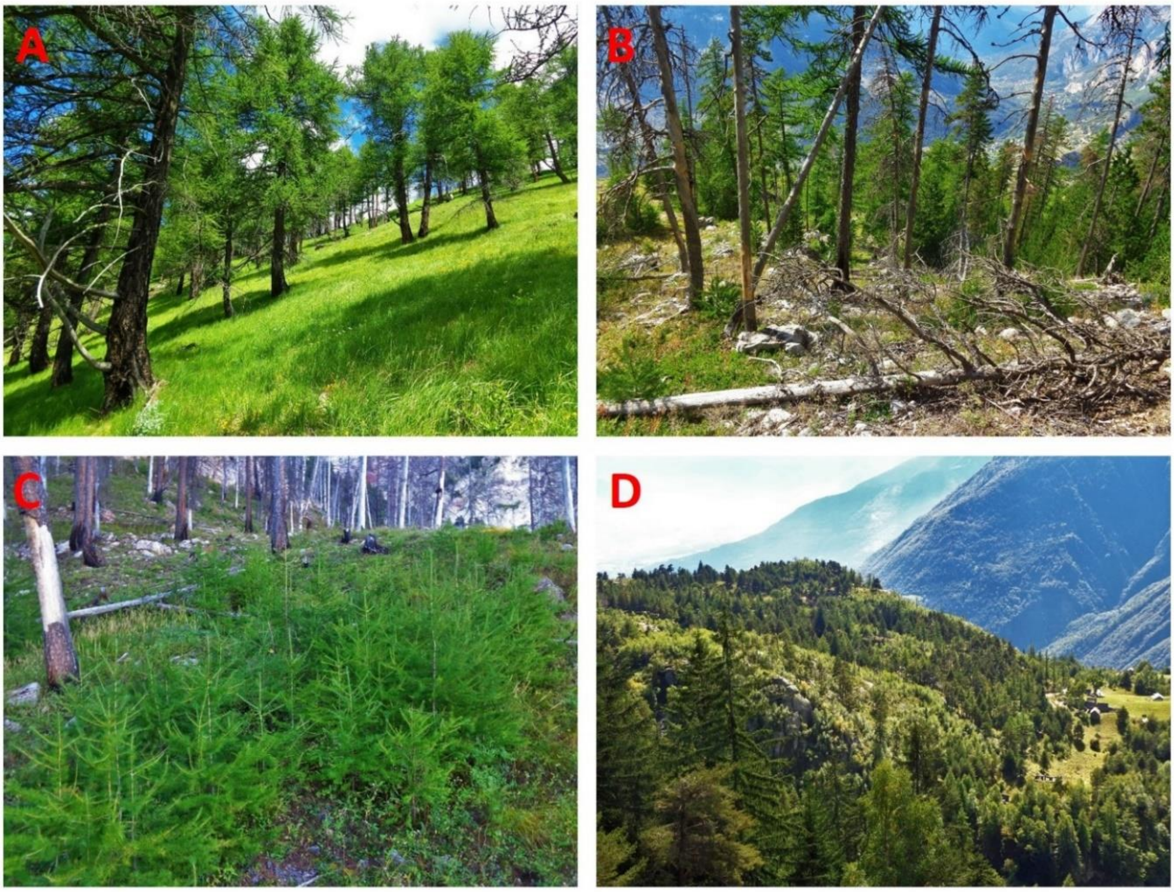

Figure A2. Photos of wildfires and post-fire natural regeneration in European larch forests. A: low-severity fire with no tree regeneration. B: moderate-severity fire with larch regeneration. C: high-severity fire with dense larch regeneration. D: mosaic of different successional patches created by a mixed-severity fire.