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Fire-induced taxonomic and functional changes in saproxylic beetle communities in fire sensitive regions

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It is often suggested that fire acts as an environmental filter that selects species and functional traits, and reduces trait variability within communities, affecting ecosystem function and underlying services. This may be particularly important in fire-sensitive ecosystems, such as the central European Alps, where fires are scarce. According to climate and land use change scenarios in Europe, fire risk will increase during the next decades, raising important questions about the maintenance of ecological and functional resilience in these regions. We used two families of saproxylic beetles (i.e. Cerambycidae and Buprestidae) as model group to test the combined effect of fire and altitude on species and trait composition in the central Alps of Switzerland. Trait response was based on weighted means and variation of 15 traits over the communities. Our results showed an overall positive effect of fire on taxonomic and functional diversity, while indicator species and community analyses revealed that the response to fire was also modulated by altitude. The positive effect of fire and the presence of large populations of pyrophilous species suggest co-evolution with fire and adaptation to disturbance in the Alps. Biodiversity in the central Alps might thus be more resilient to fire than expected. In the light of climatic and land use changes, forest management and species conservation in the central Alps have to consider fire one of the major disruptive factors that have shaped and will shape species composition and ecosystem services.

In many European countries the fire regime has changed during the last decades as a consequence of the combined effects of land use and climate changes. The latter implies an increase in mean temperature and longer periods of drought (Folke et al. 2004, Schumacher and Bugmann 2006). Correspondingly, there has been an increase in biomass and a shift in vegetation assemblages with a higher proportion of stress-tolerant species (Thuiller et al. 2008), particularly in the Alps (Bolliger et al. 2000). According to climate and land use change scenarios in Europe, the fire regime will further change and the risk of ignition of ecosystems that are less prone and adapted to fire, such as the Alps (Stähli et al. 2006) and old-growth forests of the Carpathians, could increase in the next decades (Conedera et al. 2006, Schumacher and Bugmann 2006). The subalpine forests are mainly dominated by coniferous species (obligator seeders) and therefore particularly vulnerable to fire (Tinner et al. 2000). The combination of these factors with the physical and chemical changes in the soil induced by fire and the steep slopes in the Alps will have consequences on the ecosystem function (Moretti and Legg 2009) and may be detrimental to the human infrastructures and settlements in the valley bottoms in the Alps (Conedera et al. 2003).

This raises a serious conservation concern as well as questions about the ecological resilience of fire-sensitive ecosystems in Europe (sensu Pausas et al. 2008), considering biodiversity at both the taxonomic and functional levels. Only a few studies, particularly on plants, have focused on the community response to fire from a functional perspective, and even fewer have considered the post-fire interaction between plants and animals in a multi-trophic context (Kay et al. 2008, Moretti and Legg 2009), linking changes in community composition to ecosystem function and underlying services (Diaz and Cabido 2001).

While most of the current knowledge on community and functional responses to fire has been carried out on plants, most studies on arthropods have focussed on species composition or single functional attributes. Furthermore, they have been mainly conducted in fire-prone ecosystems such as boreal forests (Saint-Germain et al. 2005, Buddle et al. 2006), tropical savanna (Andersen et al. 2005), and dry temperate ecosystems, where organisms are adapted to post-fire conditions (Moretti et al. 2009). Far less is known about the effect of fire in potentially fire vulnerable European regions, such as the central Alps (Tinner et al. 2005), where fires are relatively rare compared to the southern regions of Europe.

In the past, the Alps have been heavily impacted through grazing and forestry (Tasser and Tappeiner 2002), whereas historical fires had dramatically affected the vegetation (Tinner et al. 2005). The Alps are nonetheless considered one of the species-richest regions of Europe, where rare and endemic species live. Fire sensitivity of the Alps is mainly related to high risk of post-fire natural hazards following changes in environmental conditions and soil stability (Wohlgemuth et al. 2006). In this regard, invertebrates may play an important role in the regeneration processes such as soil formation, decomposition, pollination and pest control. Studies on the effects of natural disturbances in the Alps, such as windthrows or avalanches, have shown that occasional extreme events enhance overall invertebrate biodiversity (Wermelinger et al. 2002, Bouget and Duelli 2004). Nevertheless, we can expect that the environmental changes induced by severe fire and post-fire conditions may elicit different taxonomic and functional responses of the communities (Moretti and Legg 2009, Moretti et al. 2009).

The overall bias in our knowledge about the effect of fire in prone regions of Europe raises important questions about the consequences of fire in fire-sensitive ecosystems in Europe. This is particularly interesting in the Alps, where the disruptive effect of fire interacts with altitude as an important factor that shapes and structures vegetation (Wohlgemuth et al. 2008). The major aim of this study is to assess the taxonomic and functional response of communities to fire along an altitudinal gradient in a low fire-prone region of the Alps.

Saproxylic invertebrates were selected as a multi-functional model group composed of forest-dwelling and wood-feeding species. In the context of this study, saproxylics play an essential ecological role in decomposition and nutrient cycling and are thus an important functional component of forest ecosystems (see Dajoz and de Rougemont 2000 for a synthesis).

Since forest fires are rare in the central European Alps, and experimental or controlled burning is forbidden by law, in this paper we assess the effect of fire by analysing the response of saproxylic communities to a single large forest fire that occurred in the region of Leuk (Canton Vallis) in 2003. The specific aims of this paper are to: 1) assess the response of saproxylic communities to fire at both taxonomic and functional levels; 2) study the interaction between fire and altitude on post-fire responses of species and functional traits; and 3) provide recommendations for forest managers to enhance biodiversity and ecological resilience of alpine forests.

Material and methods

Saproxylics as a model functional group

Among the saproxylic invertebrates, we selected the longhorn beetles (Cerambycidae) and the jewel beetles (Buprestidae), two species-rich and abundant saproxylic groups in the Alps, which are considered good indicators of rapid and marked reactions to environmental changes in forest ecosystems (Wermelinger et al. 2002, Saint-Germain et al. 2008). Systematic and functional attributes of these two groups are well known and the nomenclature is relatively stable at least in central Europe (Moretti and Barbalat 2004). Cerambycids and buprestids exhibit a broad range of trait states, which allows them to exploit different habitats and environmental conditions (Supplementary material Table S1), while six pyrophilous species (highly fire-adapted species) are known in the northern and central Europe (Wikars 1997). Overall, considering the multiple ecological attributes of the Cerambycidae and Buprestidae, the results of this study allow some generalization with respect to other saproxylic groups with similar life history and life form.

Study site

The study site was located in the Swiss central Alps near Leuk (Canton Valais; 46°20′N, 7°39′E) along a south-facing slope ranging from 800 up to 2200 m a.s.l. close to the upper timber line. The climate is continental with cold winters and dry summers (Zumbrunnen et al. 2009). Mean annual temperature decreases from 8.6°C at 640 m a.s.l. to 5.2°C at 1500 m a.s.l., while annual precipitation ranges from 600 mm at 640 m a.s.l. to 1000 mm at 1500 m a.s.l. (1961–1990) (Aschwanden et al. 1996).

The wildfire (arson) occurred on 13 August, 2003 and burnt 300 ha. The burnt area encompassed a gradient in vegetation ranging from xerothermic mixed forest of oak *Quercus pubescens* and Scots pine *Pinus sylvestris* at 800–1200 m a.s.l., to larch *Larix decidua* woodland pasture at ca 2000 m a.s.l. The forest was homogeneous within each vegetation type, but along the altitudinal gradient forest density and canopy coverage decreased with altitude. Small gaps of former pasture activity and rock outcrops shaped the forest structure at high altitudes (Wohlgemuth et al. 2008).

Vegetation structure

Burnt and unburnt sites (defined as sites without fires at least during the last 60 yr according the Swiss Wildfire Database, Zumbrunnen et al. 2009) contrast strongly with respect to tree and grass cover, as well as forest structure (Supplementary material Table S1). Forest canopies were more open and the grass more luxuriant at burnt sites. Because fire consumed the dead biomass, burnt sites had less litter and dead wood on the ground but more dead standing trees, most of them injured or freshly killed by fire. The Shannon diversity for vegetation cover types was lower in the burnt area (Supplementary material Table S1).

Design and data sampling

We set up a two-way crossed balanced sampling design with 3 levels coding for fire (i.e. unburnt, burnt margin, and central burnt area), and 3 levels representing the altitudinal gradient, at 1200, 1450, and 1700 m a.s.l. Within each of the nine distinct experimental conditions, we set two trap sites (replicates). The mean distance between trap sites was 285 ± 83 m (min. 200 m). The average distance between trap sites in the burnt margin and the remaining forest was 71.4±32.9 m. Each sampling site included one combination trap (i.e. window trap and yellow pan) (Duelli et al. 1999) to catch flying species and one pitfall trap (13 cm diameter) for the epigaeic species. The window and pitfall traps were separated by ca 5 m. Trap types and sampling methods follow a standard procedure (see Duelli et al. 1999 for details). The combination of window traps and pitfall traps has been shown to be efficient for the capture of a wide range of cerambycid and buprestid species with different ecological requirements (Duelli et al. 1999, Moretti and Barbalat 2004, Wermelinger et al. 2007). The traps were emptied weekly from mid-April to early September 2005 and 2006, resulting in a total of 36 weekly sampling periods over two years. All adult individuals were identified to species using the nomenclature of the Fauna Europaea <www.faunaeur.org> (see literature in Moretti and Barbalat 2004). Voucher specimens of each species are stored at the Swiss Federal Research Inst. WSL in Bellinzona, Switzerland.

Functional traits

We assessed the ecological and functional response of the selected saproxylic community to the fire event by selecting 23 species traits (Table 1) that we considered important with regard to the fire and altitudinal gradient factors. For each trait and site, we computed two complementary indices that are increasingly used in studies assessing functional composition of biotic communities (Mason et al. 2005, Lavorel et al. 2008, Villeger et al. 2008, Moretti et al. 2009): 1) community weighted mean traits (CWM) and 2) functional diversity (FD) as a measure for the variation of traits within the community, thus assessing how evenly the species share the available niche space (Mason et al. 2005). Community weighted trait means (CWM) were calculated for each single trait listed in Table 1 as the mean of values present in the community weighted by the relative abundance p_i of the i-th species carrying each value x_i as described by Garnier et al. (2004) and Lavorel et al. (2008):

$$CWM = \sum_{i=1}^{S} p_i x_i \tag{1}$$

Functional diversity (FD) values were calculated for each trait in Table 1 (bounded between 0 and 1 to standardize trait dimensions) using the Rao diversity index, which is the sum of the dissimilarities d_{ij} for all pairs of species i and j, weighted by the product of the species' relative abundances p_i and p_j (Rao 1982, Leps et al. 2006):

$$FD = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} p_i p_j \tag{2}$$

Species dissimilarities (d_{ij}) range from 0 (two species have exactly the same traits) to 1 (the two species have completely different traits) in the case of continuous traits, while they are equal to 0 or 1 in the case of nominal traits. The variation (FD) of a continuous trait x_i is higher in communities where species trait values have a broad range.

Table 1. Description of saproxylic beetle functional traits used in this study to calculate trait means (CWM) and functional diversity (FD) per trait and per site. Traits were described for each species according to published sources. Threat degree of red listed species and pest degree of economically problematic species are not considered as functional traits, but treated qualitatively (Supplementary material Table S2).

	Trait category	Trait	Description	Type
	Body size	BodySize	Length of the body in mm	continuous
Micro-habitat	Habitat specificity	HabitatSp	Narrow habitat[1]; Wide habitat	nominal
	Altitude preference	Mountain	Mountain[1]; Lowland	nominal[2]
	Macrohabitat	Forest	Forest[1]; Open habitat	nominal[2]
Micro-climatic conditions	Microclimate	Thermo	Preferred climatic conditions: warm [Thermo]; dray [Xero]; sunny [Helio]	nominal
		Xero		nominal
		Helio		nominal
	Daily activity time	Diurnal	Diurnal[1]; Nocturnal	nominal
	Phenology	ActStart	Activity season start [ActStart]; end [ActEnd]; duration [ActDuration] in months	continuous
		ActEnd		
		ActDuration		
Feeding and reproduction sources and substrate types	Host tree	Conifers	Conifers[1]; Broadleaves	nominal[2]
		LargeTree	Large trees[1]; Small trees and shrubs	nominal
	Wood feeding substrate [FeedSubst]	Arboricol	Larvae feeding substrate at the host tree: on the surface [Arboricol]; under the bark [Corticol]; in the wood [Lignicol]; on decomposed wood [Xylodetriticol]	nominal[2]
		Corticol		
		Lignicol		
		Xylodetriticol		
	Decay stage of the host tree [DecayStage]	Living	Decay stage of the larvae host tree: living tree [Living]; weakly dying [Dying]; recently dead [RecentDead]; weakly decayed [WeaklyDecayed]; decayed and decomposed [Decayed]	nominal[2]
		Dying		
		RecentDead		
		WeaklyDecayed		
		Decayed		
	Feeding on flowers	Floricol	Adults feeding on nectar and pollen of flowers	nominal

[1] Variable used in the analyses to avoid collinearity.

[2] Nominal value range from 0 to 1 to better describe the attribute to the species.

FD of nominal trait *x* (0 or 1) is highest in communities with equal probabilities finding species with trait values 0 and 1, and lowest when all species have the same value. Compared to other indices of functional diversity, the Rao index includes information on species abundances, which is a relevant variable modulating the effects of species and trait composition on several ecosystem processes (Ricotta (2005), Petchey and Gaston (2006) and Laliberté and Legendre (2009) for a review on FD indices, and Moretti et al. (2009) for an application).

Cerambycid and buprestid species were finally characterized according to their conservation concern (i.e. threatened species) mainly based on Red lists of Switzerland and Germany (Moretti and Barbalat 2004) and economic impact (pest species, or not) (Schwenke 1974, Lieutier et al. 2004).

Statistical analyses

We analyzed the response of the selected saproxylic species to fire, altitude, and time since the fire, as well as their interactions on six different community aspects: three univariate data sets (i.e. species richness, number of individuals, Simpson's diversity index) and three multivariate data tables (i.e. species composition, and functional trait composition measured by both CWM and FD); Fig. 1, Step 1. For the univariate data sets, we used three-way ANOVAs with Tukey's post-hoc tests. P-values were adjusted using Holm's correction to avoid increases of type error I due to multiple testing (Legendre and Legendre 1998). The number of individuals was $\log_{10}$-transformed to fulfil the assumption of normality of the data (tested using the Shapiro-Wilk test).

For the multivariate data, we used Canonical Redundancy Analyses (RDA) as a form of multivariate analysis of variance to test the relationship between a response matrix (e.g. species abundance data) and the three crossed factors, i.e. fire, altitude, and time (Legendre and Anderson 1999, Laliberté et al. 2009). Orthogonal dummy variables, also called Helmert contrasts (Venables and Ripley 2002), were used to process three crossed factors in the regression context. The number of individuals was Hellinger-transformed to reduce the influence of extreme values and the effect of the double-absences in the data matrix (Legendre and Gallagher 2001).

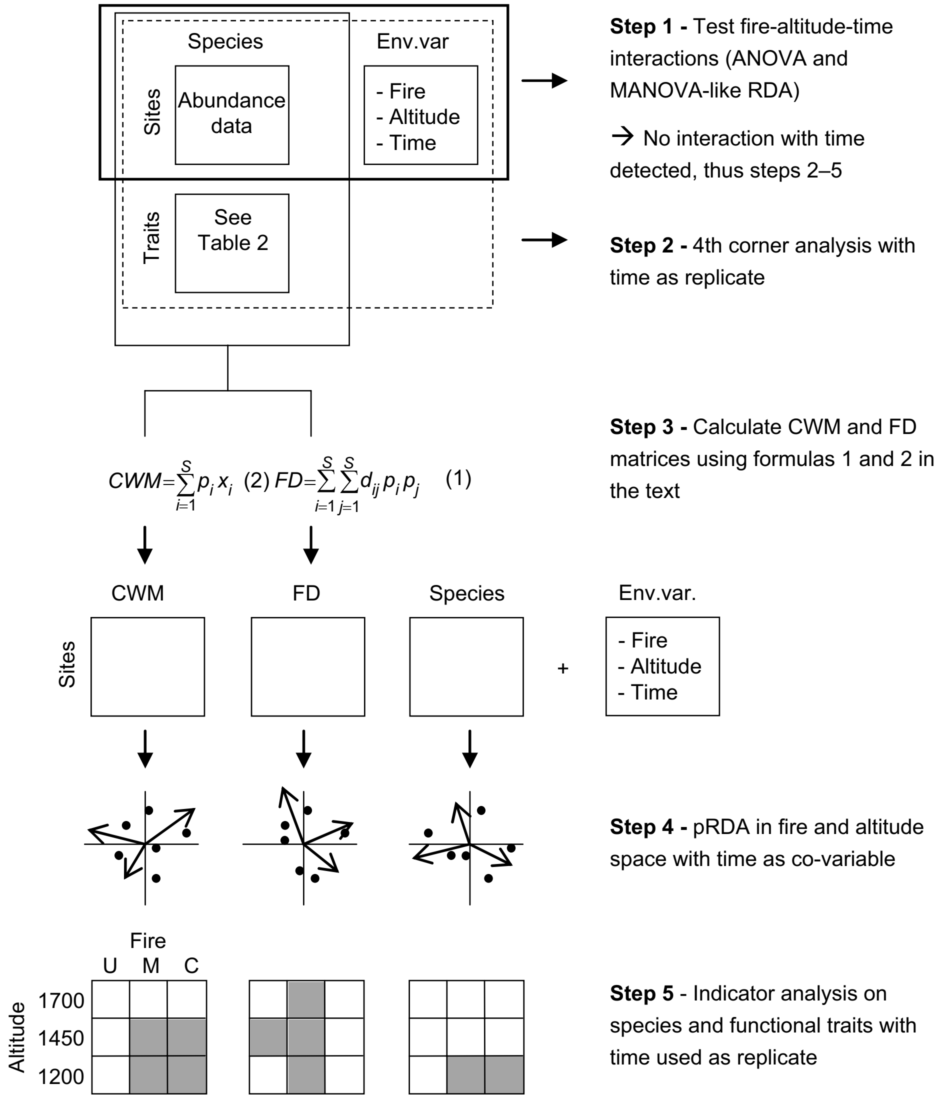


Figure 1. Diagram showing step-by-step statistical methodology (see Methods).

Since the interactions fire by time and altitude by time, as well as fire by altitude by time were not significant, fire, altitude, and time were modelled using 3-way ANOVA and partial Redundance Analyses.

In the next steps of the analyses (Fig. 1, Steps 2–4), the relationship between species functional traits and environmental conditions induced by fire and altitude was tested in one single step using the fourth-corner analysis (Legendre et al. 1997, Dray and Legendre 2008) with permutation model 1. This model is based on the null hypothesis (H_0) that individuals of a species are randomly distributed with respect to site characteristics and on the alternative hypothesis (H_1) that individuals of a species are distributed according to their preferences for site conditions (Dray and Legendre 2008). Partial RDA (pRDA) was then used to summarize the multivariate responses of species and functional trait composition (CWM and FD) to fire and altitude while controlling for time since fire. Species occurring only in one trap site were removed from the multivariate analyses, in order to avoid possible distortions in the analyses, while the species abundance data were Hellinger-transformed (see above).

We used indicator species analysis (Dufrêne and Legendre 1997) to investigate the habitat preferences of species taken individually, by finding their preferred combination of fire and/or altitude levels. We computed the association of the species to all possible combinations of the nine experimental conditions, i.e. 3 fire × 3 altitudes, which is $(2^9 - 1) = 511$ combinations including the set of all 9 conditions (Fig. 1, Step 5). As the association measure, we used the indicator value (IndVal) statistic (Dufrêne and Legendre 1997) on log-transformed data. We then selected the combination of fire and altitude that was mostly strongly associated with the species and assessed its statistical significance. For the functional components of the communities, we used a similar approach to detect the habitat combination causing higher means (CWM) or variability (FD) of individual traits. In that case, we used the point-biserial correlation coefficient (De Cáceres and Legendre in press) as the statistic, which corresponds to the Pearson correlation for binary (site groups) vs quantitative data (CWM and FD in our case). We will refer to "indicator species" and "indicator traits" for those species and traits with significant indicator or correlation values. All statistical analyses were performed using R 2.7.2 (R Development Core Team 2007).

Results

Interactions between fire, altitude, and time

A total of 29 308 individuals were collected, representing 62 species (45 Cerambycidae, 17 Buprestidae) with a mean of 1628 individuals and 23 species per site. Thirty-seven species had five or more individuals, whereas 15 species were observed in a single study site.

The six community data sets considered in the analyses (i.e. species richness, number of individuals, Simpson's diversity index, species composition, CWM-community weighted mean traits, and FD-functional diversity; Table 2) were significantly affected by fire and altitude. The number of individuals, species composition and FD were also affected by time (Table 2). The 3-way interaction between fire, altitude and time was never significant. The interaction between fire and altitude was significant in four of the six data sets. In contrast, the 2-way interactions time by fire

Table 2. a) Three way Analysis of Variance of the number of species (N species), number of individuals (Log × N ind.), and Simpson index (Simpson); b) Three way Redundance Analyses (with 9999 permutation Monte Carlo test) on species composition (Spp. composition), trait composition (CWM), and functional diversity (FD) for the factors time, T (2005, 2006), fire, F (unburnt, burnt margin, burnt center), altitude, A (1200, 1450, 1750 m a.s.l.), and their interactions. P-values *<0.05, **<0.01, ***<0.001.

a)

Factors	DF	N species		Log × N ind.		Simpson	
		F	p-value	F	p-value	F	p-value
Time	1	2.934	0.104	22.707	<0.001***	2.549	0.128
Fire	2	52.185	<0.001***	52.925	<0.001***	19.938	<0.001***
Altitude	2	21.018	<0.001***	15.409	<0.001***	7.248	<0.005**
T × F	3	0.155	0.858	0.684	0.518	1.514	0.247
T × A	3	0.231	0.796	0.440	0.651	0.144	0.867
F × A	4	5.161	0.006**	0.835	0.521	3.527	0.027*
F × A × T	4	0.067	0.991	0.541	0.708	0.247	0.908

b)

Factors	DF	Spp. composition		CWM		FD	
		F	p-value	F	p-value	F	p-value
Time	1	3.022	0.003**	1.754	0.168	2.925	0.022*
Fire	2	40.129	<0.001***	15.039	<0.001***	9.810	<0.001***
Altitude	2	4.396	<0.001***	4.058	0.003**	3.432	0.001**
T × F	3	1.348	0.151	0.707	0.586	1.434	0.154
T × A	3	0.924	0.569	1.818	0.148	1.415	0.168
F × A	4	1.680	0.009**	1.233	0.297	2.470	0.003**
F × A × T	4	0.555	0.990	0.721	0.668	0.949	0.536

and time by altitude were never significant. As a consequence, we used time since fire as a covariable in the pRDA.

Species richness and species diversity

We found higher values in burnt compared with unburnt areas for the mean number of individuals per site ($t = -5.037$, $p < 0.001$), species richness ($t = -6.285$, $p < 0.001$), and Simpson species diversity ($t = -3.627$, $p = 0.0034$), particularly at the low and mid altitudes (see details in Supplementary material Table S2). At the same time, the burnt margin area always accounted for higher values of number of individuals ($F_{2,36} = 6.55$, $p = 0.004$), species richness ($F_{2,36} = 21.12$, $p < 0.001$), and diversity ($F_{2,36} = 12.31$, $p < 0.001$) than unburnt and centre burnt areas.

Regarding the species of conservation concern, the traps captured 22 threatened species (Supplementary material Table S4a); 12 of them were exclusively found in the burnt area (margin or centre). Among the remaining species, 7 were exclusively found at the margin and 4 at both the unburnt and margin sites. Only one endangered species (*Cortodera femorata*, Cerambycid) was collected exclusively in the unburnt forest. 13 pest species were also captured in the study area (Supplementary material Table S4b); 8 species were found exclusively in the burnt area and none only in the unburnt area. While the number of individuals of both threatened and pest species was significantly higher in the burnt than in the unburnt areas (threatened species: $F_{2,36} = 36.04$, $p < 0.001$; pest species: $F_{2,36} = 8.11$, $p < 0.01$), the overall abundance of threatened species in the burnt area (7337 individuals) was 53 times higher than those of pest species (138 individuals) captured in the same area.

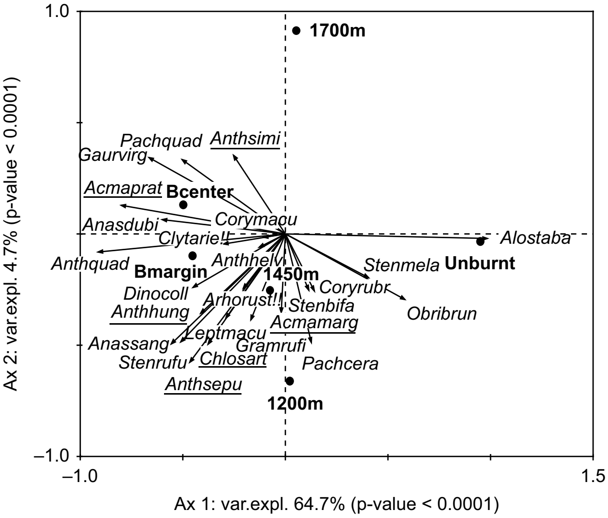


Figure 2. Partial Redundancy Analyses (pRDA) of cerambycid and buprestid species composition to fire (unburnt, burnt margin [Bmargin], burnt center [Bcenter]) and altitude (1200, 1450, 1700 m). P-values from a Monte Carlo test of significance of the first axis (9999 iterations). Time since the fire was used as covariable. Only the species most correlated to the first two canonical axes and those selected as indicator species (Fig. 3) are shown. Underlined species are red list species; Species followed by !! are pest species (see Methods). Short species names (i.e. 4 letters of the genus and 4 letters of the species) listed alphabetically: *Acmaeops pratensis*, *Acmaeops marginatus*, *Alosterna tabacicolor*, *Anastrangalia dubia*, *Anastrangalia sanguinolenta*, *Anthaxia helvetica*, *Anthaxia hungarica*, *Anthaxia quadripunctata*, *Anthaxia sepulchralis*, *Anthaxia similis*, *Arhopalus rusticus*!!, *Chlorophorus sartor*, *Corymbia maculicornis*, *Corymbia rubra*, *Clytus arietis*!!, *Dinoptera collaris*, *Gaurotes virginea*, *Grammoptera ruficornis*, *Leptura maculata*, *Obrium brunneum*, *Pachyta quadrimaculata*, *Stenurella bifasciata*, *Stenurella melanura*, *Stenopterus rufus*.

Response of species composition

Partial Redundance Analysis of species composition revealed a strong gradient along the first axis that was related to fire (64.7% variance explained; $p < 0.0001$) (Fig. 2). The effect of the altitude gradient was far less important (4.7%; $p < 0.0001$). The left-hand side of the biplot (Fig. 2) shows that most of the species were associated with the margin and centre burnt sites, including three red-listed species (*Acmaeops pratensis*, Cerambycids; *Anthaxia similis*, *A. hungarica*, Buprestids), while only two species (*Alosterna tabacicolor*, *Obrium brunneum*, Cerambycids) were associated with the unburnt area at the right-hand side of the biplot.

Indicator species analysis (Fig. 5) resulted in 24 (38.7%) species being significantly associated with 14 different patterns of fire-altitude combinations. Among these species, fifteen were indicators of burnt conditions (Fig. 5, patterns B), predominantly at low to medium altitudes, while seven were indicators of combinations including burnt and unburnt sites (patterns C). Six red-listed species were indicators of burnt conditions, i.e. three species (*Chlorophorus sartor*, *Acmaeops marginatus*, Cerambycids; *Anthaxia hungarica*, Buprestids) were restricted to burnt sites at very low altitudes, while the other three (*Acmaeops pratensis*, Cerambycids; *Anthaxia sepulchralis*, *A. similes*, Buprestids) showed no altitudinal preference within the burnt area. In contrast, only two pest species were indicators of burnt conditions: *Arhopalus rusticus* (Cerambycids) was restricted to the central burnt area at low altitude, while *Clytus arietis* (Cerambycids) did not show particular preferences.

Response of the mean functional traits

Partial RDA on the community weighted traits mean (CWM) (Fig. 3) resulted in fire explaining a large and significant amount of variance (42.8%; $p < 0.0001$) in trait composition, while only 10.2% ($p = 0.0195$) was explained by altitude. The burnt area at both the margin and centre at the left hand side of the biplot were characterised by communities dominated by species that possessed traits that exhibited the following preferences: warm (+Thermo) and dry conditions (+Xero), narrow (+HabitatSp) and forest (+Forest) habitats. These species also preferred feeding underneath the bark (+Corticol) of recent dead (+RecentDead) and weakly decayed (+WeaklyDecayed) trees. At the other side of the biplot, unburnt areas positively affected species feeding on wood (+Lignicol) and decomposing woody parts (+Xylodetriticol) of decayed (+Decayed) trees.

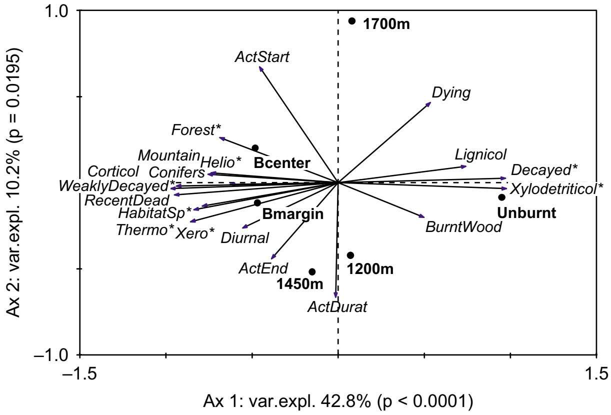


Figure 3. Partial Redundancy Analyses (pRDA) of the community weighted mean traits (CWM) of cerambycids and buprestids to fire (unburnt, burnt margin [Bmargin], burnt center [Bcenter]) and altitude (1200, 1450, 1700 m). P-values from a Monte Carlo test of significance of the first axis (9999 iterations). Time since the fire was used as covariable. For trait codes, see Table 1. Traits marked with * were significantly related to one of the 6 factors (fire and altitude) based on the fourth-corner analysis (see detail in Table 6).

The fourth-corner analysis (Supplementary material Table S3) showed that most of these traits were significantly associated with fire ($p < 0.05$) regardless of location (margin and centre) in the burnt area. Altitude tends to affect communities according to their phenology, by favouring communities dominated by species with a late start of seasonal activity (+ActStart) and short duration (−ActDuration) at high altitudes (see also Fig. 3).

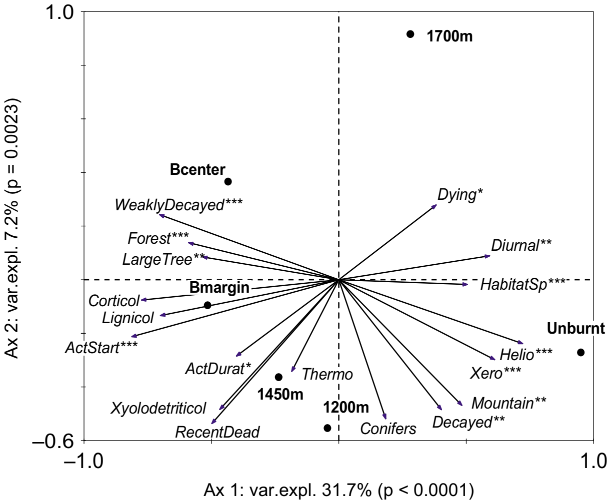


Figure 4. Partial Redundancy Analyses (pRDA) of the response of functional diversity (FD) of the cerambycid and buprestid communities to fire (unburnt, burnt margin [Bmargin], burnt center [Bcenter]) and altitude (1200, 1450, 1700 m). P-values from a Monte Carlo test of significance of the first axis (9999 iterations). Time since the fire was used as covariable. Only traits with FD most correlated to the first two canonical axes and those selected as indicator traits (Fig. 3) are shown. For trait codes, see Table 1. Traits marked with * are significantly related to fire (ANOVA; p values *<0.5, **<0.01, ***0.001).

The analysis of indicator traits (Fig. 6) provided additional details on the distribution of the functional traits along the gradients of fire and altitude. Overall, 18 (78.3%) traits were significantly correlated with 8 different patterns of fire-altitude site combinations. Among them, 4 traits were exclusively associated with the unburnt sites (Fig. 6, pattern A), 6 traits to the burnt sites (pattern B), and 12 traits to combinations of burnt and unburnt sites (pattern C). In the burnt area, the response of 15 traits over 18 (i.e. all but ActStart, Dying, and ActDuration) was positive at all altitude levels. This homogenous effect of fire mainly affected traits related to feeding and reproduction (e.g. Xylodetriticol, Decayed, Lignicol), as well as traits that respond to climatic conditions (e.g. Helio, Xero, Diurnal); Fig. 6 and Supplementary material Table S3.

Response of the variability of functional traits (FD)

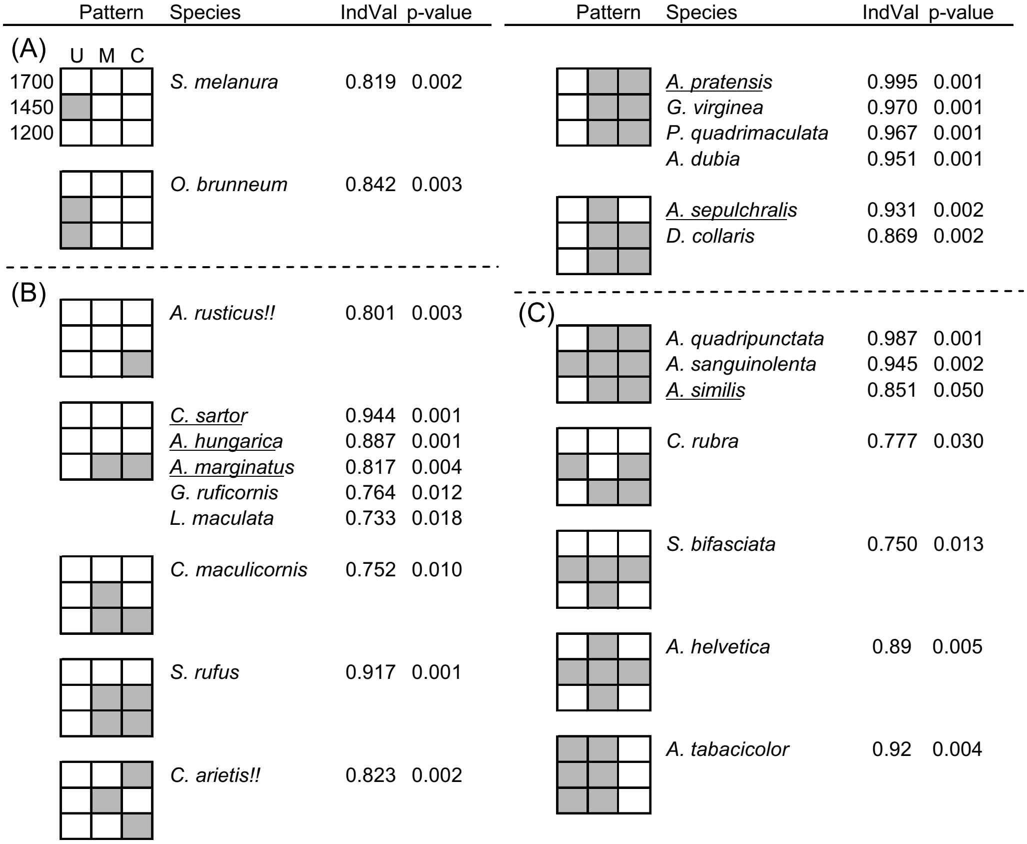
When considering functional diversity (FD) as the variation of single traits, the pRDA (Fig. 4) showed that fire explained a significant amount of variance (31.7%, $p < 0.0001$) while only 7.2% ($p = 0.0023$) was explained by altitude. The selected beetle communities living in the burnt areas (margin or centre) were more functionally diverse for traits associated with habitat (Forest), feeding/reproduction substrates (e.g. WeaklyDecayed, LargeTree, Corticol, Lignicol), and phenology (ActStart, ActDurat), but they were less diverse for traits associated with climatic conditions (e.g. Helio, Xero, Diurnal), habitat specificity (HabitatSp), and woody decay (Decayed).

The analysis of indicator traits showed that the variation (FD) of 18 (75%) traits was positively correlated with 12 patterns of fire-altitude site combinations (Fig. 7). Four traits, mainly related to climatic conditions (i.e. Xero, Diurnal, Helio), were more variable at unburnt sites (Fig. 7, pattern A), three traits (i.e. ActStart, WeaklyDecayed, Forest) at burnt sites (margin or centre) (pattern B), while 11 traits increased variation at both the burnt and unburnt sites (pattern C). Regarding the altitude distribution of the change in trait variation (FD), eight traits (out of 18) mainly related to feeding and reproduction were positively affected by fire (higher FD) along the entire altitude. In contrast, the 4 traits that lost variation after fire (low FD) were mainly associated with climatic conditions.

Discussion

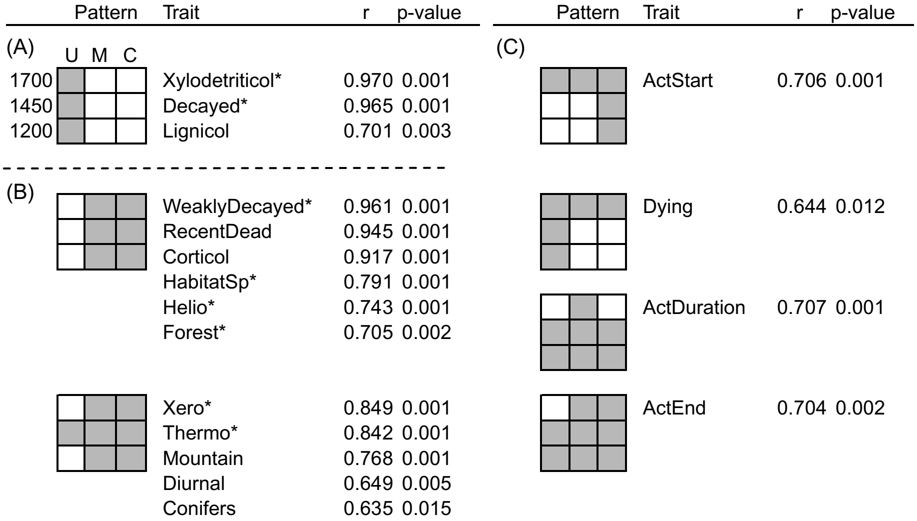
Response of saproxylic communities to fire

Our results show that species richness and diversity of the saproxylic taxa under study were higher in burnt areas relative to the unburnt areas and that the dominance distribution among the most abundant species changed, affecting community and functional composition. This is consistent with the general pattern of invertebrate community response (especially of mobile species) to disruptive events, including fire, in disturbance-prone regions (Bouget and Duelli 2004, Saint-Germain et al. 2008). Thus, Cerambycidae and Buprestidae in the central European Alps may respond to fire following the same principles that drive biodiversity under intermediate disruption regimes,



	Pattern (U M C)	Species	IndVal	p-value
(A)	1700 ☐☐☐ 1450 ▨☐☐ 1200 ☐☐☐	*S. melanura*	0.819	0.002
	☐☐☐ ▨☐☐ ▨☐☐	*O. brunneum*	0.842	0.003
(B)	☐☐☐ ☐☐☐ ☐☐▨	*A. rusticus!!*	0.801	0.003
	☐☐☐ ☐☐☐ ☐▨▨	*C. sartor*	0.944	0.001
		A. hungarica	0.887	0.001
		A. marginatus	0.817	0.004
		G. ruficornis	0.764	0.012
		L. maculata	0.733	0.018
	☐☐☐ ☐▨☐ ☐▨▨	*C. maculicornis*	0.752	0.010
	☐☐☐ ☐▨▨ ☐▨▨	*S. rufus*	0.917	0.001
	☐☐▨ ☐▨☐ ☐☐▨	*C. arietis!!*	0.823	0.002
	☐▨▨ ☐▨▨ ☐▨▨	*A. pratensis*	0.995	0.001
		G. virginea	0.970	0.001
		P. quadrimaculata	0.967	0.001
		A. dubia	0.951	0.001
	☐▨☐ ☐▨▨ ☐▨▨	*A. sepulchralis*	0.931	0.002
		D. collaris	0.869	0.002
(C)	☐▨▨ ▨▨▨ ☐▨▨	*A. quadripunctata*	0.987	0.001
		A. sanguinolenta	0.945	0.002
		A. similis	0.851	0.050
	☐☐☐ ▨☐▨ ☐▨▨	*C. rubra*	0.777	0.030
	☐☐☐ ▨▨▨ ☐▨☐	*S. bifasciata*	0.750	0.013
	☐▨☐ ▨▨▨ ☐▨☐	*A. helvetica*	0.89	0.005
	▨▨☐ ▨▨☐ ▨▨☐	*A. tabacicolor*	0.92	0.004

Figure 5. Site-group combination analyses of the indicator values (IndVal by Dufrêne and Legendre 1997) for indicator species and correlation values (IndVal) of cerambycid and buprestid communities along fire (unburnt [U], burnt margin [M], burnt center [C]) and altitudinal (1200, 1450, 1700 m a.s.l.) gradients. The grey squares indicate positive correlations. The order follows positive association patterns with (A) unburnt sites; (B) burnt sites; (C) burnt and unburnt sites. Only significant results are shown (p-value). For species names, see Fig. 2.



	Pattern (U M C)	Trait	r	p-value
(A)	1700 ▨☐☐ 1450 ▨☐☐ 1200 ▨☐☐	Xylodetriticol*	0.970	0.001
		Decayed*	0.965	0.001
		Lignicol	0.701	0.003
(B)	☐▨▨ ☐▨▨ ☐▨▨	WeaklyDecayed*	0.961	0.001
		RecentDead	0.945	0.001
		Corticol	0.917	0.001
		HabitatSp*	0.791	0.001
		Helio*	0.743	0.001
		Forest*	0.705	0.002
	☐▨▨ ▨▨▨ ☐▨▨	Xero*	0.849	0.001
		Thermo*	0.842	0.001
		Mountain	0.768	0.001
		Diurnal	0.649	0.005
		Conifers	0.635	0.015
(C)	▨▨▨ ☐☐▨ ☐☐▨	ActStart	0.706	0.001
	▨▨▨ ▨☐☐ ▨☐☐	Dying	0.644	0.012
	☐▨☐ ▨▨▨ ▨▨▨	ActDuration	0.707	0.001
	☐▨▨ ▨▨▨ ▨▨▨	ActEnd	0.704	0.002

Figure 6. Site-group combination analyses of the correlation coefficients for the community weighted mean traits (CWM) of cerambycid and buprestid communities along fire (unburnt [U], burnt margin [M], burnt center [C]) and altitudinal (1200, 1450, 1700 m a.s.l.) gradients. The grey squares indicate positive correlations. The order follows positive association patterns with (A) unburnt sites; (B) burnt sites; (C) both burnt and unburnt sites. Only significant results are shown (p-value). See Table 1 for definition of trait names. Traits marked with * are significantly related to fire and/or altitude, based on the fourth-corner analysis (Table 4).

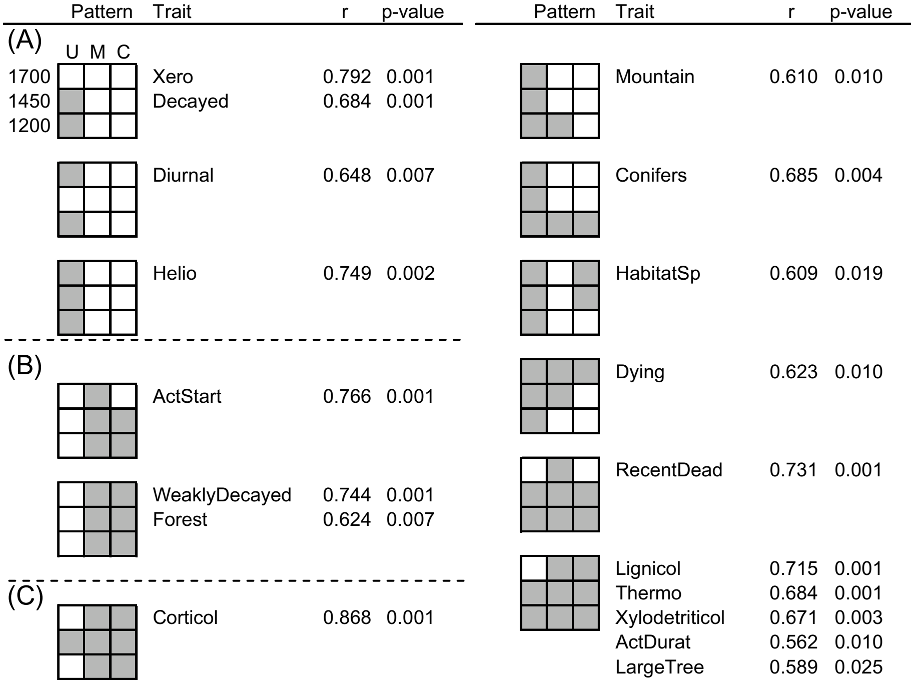


Figure 7. Site-group combination analyses of the correlation coefficients for the functional diversity (FD) of cerambycid and buprestid communities along fire (unburnt [U], burnt margin [M], burnt center [C]) and altitudinal (1200, 1450, 1700 m a.s.l.) gradients. The grey squares indicate positive correlations. The order follows positive association patterns with (A) unburnt sites; (B) burnt sites; (C) both burnt and unburnt sites. Only significant results are shown (p-value). See Table 1 for definition of trait names.

such as the dominance reduction principle and intermediate disturbance hypothesis (Connell 1978). This might be true also for other saproxylic organisms with similar ecological and functional characteristics.

The higher number of threatened species and individuals (some of them pyrophilous, thus highly adapted to fire) compared to the more generalist and ubiquist pest species sampled in the burnt areas (margin and centre) provides insights into the ecological value of burnt areas as an ecologically valuable habitat and source of resources.

Considering species and functional composition, the large number of indicator species associated with burnt areas (margin and centre) (i.e. 15 species, 41.7% of the species sampled with at least 5 individuals) (Fig. 3) and the threatened species associated to the same areas (Supplementary material Table S4a) suggest that a large proportion of saproxylics with specific habitat requirements profit from the new habitats created by fire. Three main mechanisms may explain the change in community and functional composition along the fire gradient: a) fire and post-fire conditions release new resources (e.g. injured and newly dead wood, open habitats) which attract communities dominated by pioneer forest-dwellers with larvae feeding on sapwood under the bark (e.g. *Anthaxia quadripunctata*; *Acmaeops pratensis*; *Gaurotes virginea*). This leads to the observed shift of the weighted mean values (CWM) of most of the functional traits; b) the altered post-fire climatic conditions reduce niche space and select species with narrow climatic requirements, i.e. xerothermic, heliophilous, diurnal species. This leads to the observed decrease in variation of traits related to climatic conditions (low FD; thus functional convergence); c) at the same time, fire and post-fire conditions increase the range of food sources and reproduction substrates on plants of different types, sizes, and decay stages, expanding the trophic and reproductive niche space of the investigated saproxylic beetles in the burnt area (high FD; thus functional divergence).

While trait shift and functional convergence as a reaction to fire (see points a and b above) are consistent with studies on functional traits of plant and surface-dwellers after severe disturbances (Pausas 2006, Moretti and Legg 2009), functional divergence (point c) provides new insight into post-fire resource assemblage and distribution related to dead wood and wood decomposition as primary resource for saproxylic invertebrates (Dajoz and de Rougemont 2000). Evidence of contrasting functional feedbacks to fire were provided by Moretti et al. (2009) and indirectly by Potts et al. (2003) in pollinator trait response to fire in the Mediterranean vs temperate forests of southern Switzerland.

Interaction between fire and altitude on species and functional traits

While fire acts as an environmental filter (Garnier et al. 2004) selecting species and traits adapted to the adverse and narrow post-fire environmental conditions (Pausas and Verdu 2008), altitude is one of the most important factors that structure species assemblages and beta diversity. In our study there were several combinations of fire and altitude effects which may evolve in different ways. Different vegetation types and fuel load along altitudinal gradients influence fire behaviour and fire intensity creating the initial spatial heterogeneity for post-fire succession. Moser and Wohlgemuth (2006) showed that the ash layers (as an indicator of fire intensity) were thicker in the central part of the burnt area at our study site than at the margins. This affected cover and regeneration rate of the vegetation along the altitudinal and climatic gradient.

In our study, indicator species and trait analyses clearly highlighted the importance of both "fire-altitude" interactions and the "burnt-unburnt" mosaic in explaining community composition; the latter can easily be overlooked in pure gradient analyses, as in Fig. 2–4. This indicates that for many species and functional attributes, such as feeding and reproduction traits (e.g. WeaklyDecayed, LargeTree, Corticol) as well as phenology (ActStart, ActDurat), fire alone cannot explain the functional divergence (high FD) observed in the burnt area. We can thus assume that in the Alps the mosaic of burnt and unburnt areas changes along altitude as an additional source of spatial variation enhances niche space and thus coexistence of species. However, fire by no means favours only the ubiquists and generalists. Our results show that stenotopic (narrow habitat) species (HabitatSp) prevailed after the fire and that a larger number of species (many of them of conservation concern; Supplementary material Table S4a) occurred in the margin and centre of the burnt area. Mobile species with a high degree of specialisation often depend on a mosaic of habitats to satisfy the species-specific requirement of distinct life stages (larvae vs adults; ontogenic habitat shift) or distinct functions (e.g. feeding, mating, reproduction).

Role of fire for saproxylics in the Alps

Despite our study was based on two well known saproxylic beetles families, our results suggests that at our study site fire had a positive effect on species richness and functional diversity of saproxylic invertebrates in general. We see three reasons: first, the spatial heterogeneity and variation in resources created by the interaction between fire and altitude, and the mosaic of burnt and unburnt sites allows the coexistence of species that would exclude each other under more stable conditions in time and space (competitive exclusion principle, Hardin 1960). Such spatio-temporal patch dynamics might also explain the mechanism allowing early successional communities (mainly dominated by highly mobile species) to survive long periods without fire. Second, the presence of large populations of pyrophilous species suggests adaptation to fire in the study region. This is corroborated by the finding of four additional pyrophilous beetle species in the study area (3 carabids and 1 fungi weevil). Third, the long history of traditional land use in the Alps, based on agro-silvo-pastoral subsistence farming (Tasser and Tappeiner 2002), combined with occasional extreme natural disturbances such as avalanches, pest outbreaks, windthrows), and fire (accidental, e.g. by lightning, or intentional, e.g. pastoral fire) has contributed to maintain a large-scale dynamic mosaic of open and closed habitats of remnant forests, as well as a range of intermediate successional stages.

The importance of maintaining a mosaic of forest landscape with open habitats, successional stages, and remnants of old-growth stands has been postulated by several authors (Harris 1984, Gandhi et al. 2001) in order to maintain late successional species as well as specialists that require both early and late successional stages. Saint-Germain et al. (2008) observed that the forest matrix surrounding the burnt patches in the boreal forests was as important as the burnt area itself to enhance a wide range of community types of saproxylics, including pyrophilous species.

Conclusions, recommendations and perspectives

Our study provides a novel multiple analysis approach to assess taxonomic and functional response to fire and a new perspective about the distribution of species and functional traits. Our results suggest that, under the present fire regime in the study area (Zumbrunnen et al. 2009), fire plays an important role for both the species and functional turnover of the selected saproxylic groups. This is probably also true for other saproxylic groups with life history and life form similar to those of the Cerambycidae and Buprestidae. In order to maintain or promote biodiversity in forests, Wohlgemuth et al. (2008) suggest that, in central Europe, managed forests should be directed towards a controlled reduction of dominance with traditional and alternative timber harvesting methods based on small-scale controlled forest management practices that mimic the effects of natural disturbances. Our results support that recommendation.

Our results further suggest that fire should be more clearly recognised as a factor that shapes species and communities in the Alps. Its importance should be incorporated in forest management and species conservation plans, in order to increase species richness and maintain resilience to drought and fire under scenarios of climatic and fire regime changes (Folke et al. 2004).

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