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On the occurrence of five pyrophilous beetle species in the Swiss Central Alps (Leuk, Canton Valais)

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Pyrophilous (literally «fire-loving» or «fire-specialist») insects are mainly found in freshly burnt habitats, where they exploit early post-fire resources. As a consequence of fire suppression management in various European countries, many pyrophilous species, mainly beetles, are threatened and included in Red Lists. In 2004, 2005, and 2006, the occurrence of pyrophilous beetles was monitored at Leuk (Canton Valais, Switzerland), where approximately 300 ha of forest were destroyed by a fire in August 2003. We sampled the beetle fauna (Coleoptera) at 18 trap sites, 12 of which were completely burnt and 6 were control plots in the intact forest.

Virtually all pyrophilous beetle species of the families Cerambycidae, Carabidae and Anthribidae known from Western and Northern Europe were sampled: *Acmaeops marginatus* and *Acmaeops septentrionis* (Cerambycidae); *Pterostichus quadrifoveolatus* and *Sericoda quadripunctata* (Carabidae); *Platyrhinus resinosus* (Anthribidae). Our results show that forest fires in the Swiss Central Alps might have an important effect on the European distribution of pyrophilous species. The conservation value of occasional local fires in the Central Alps has to be recognized in order to maintain and enhance the populations of threatened pyrophilous species in Switzerland.

Keywords: Forest fire, fire-adapted species, Coleoptera, Cerambycidae, Buprestidae, Carabidae, Anthribidae.

INTRODUCTION

Fire has a dramatic impact on organisms and its consequences remain evident for many years. Far less recognized is the positive impact of fire on biodiversity, which is the result of an evolving assemblage during the succession of fire adapted species, later successional species, and adjacent forest species. Therefore, many organisms such as plants, fungi and arthropods appear to be adapted to survive or even exploit early post-fire successions (Granström 1996; Wikars 1997; Dajoz 1998; Hermann *et al.* 1998; Moretti *et al.* 2004). In north-western Europe about 40 species of forest insects are considered pyrophilous (i.e. fire-loving or fire-specialists), and most of them are beetles (Heliövaara & Väisänen 1984; Lundenberg 1984; Wikars 1994; Ehnström *et al.* 1995). Pyrophilous forest beetles can either be «fire-favoured» species (which prefer burnt areas but can also colonize clear-cuts), «fire-adapted» species (which have fire-adapted traits such as fire-sensory organs) or «fire-dependent» species (which depend on fire for their long-term survival). This heterogeneous ecological group of pyrophilous organisms includes saproxylics, lit-

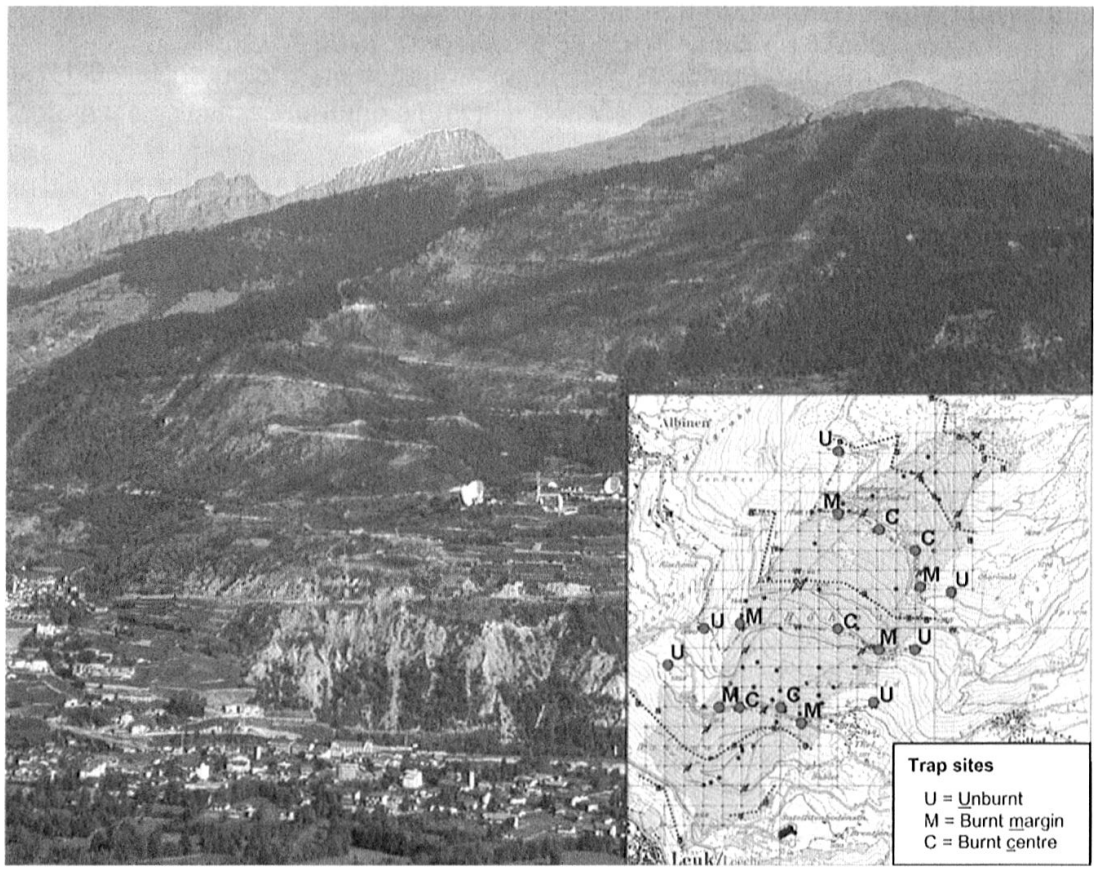

Fig. 1. Study area and trap sites (Photo M. Moretti).

ter-dwellers, and species associated with wood-decomposing fungi (Palm 1951; Muona & Rutanen 1994; Wikars 1997). Whereas an exclusive dependence on fire is the exception, wildfires appear to be extremely important for the conservation of various pyrophilous species, which are declining in numbers as a consequence of the fire suppression management in many countries (Wikars 1997; Jonsell *et al.* 1998).

Despite the considerable knowledge on pyrophilous beetles in boreal forests, little is known about the occurrence of fire-specialised beetles in the Swiss Central Alps. On August 13th, 2003 a fire (arson) destroyed more than 300 hectares of forest above Leuk, Canton Valais (Wohlgemuth *et al.* 2010). We expected to find pyrophilous beetle species during the years following this event, given the known historical occurrence of sporadic forest fires in the Swiss Central Alps (Gobet *et al.* 2003; Carcaillet & Müller 2005; Tinner *et al.* 2005). In the following three years, the arthropod fauna was collected on burnt and adjacent unburnt surfaces. This paper reports on the findings of pyrophilous beetles in Leuk and discusses their distribution in Europe, their ecological requirements, and their conservation status.

MATERIALS AND METHODS

Study area

The burnt forest area is located on a south-facing slope above Leuk (Canton Valais), in the Swiss Central Alps (Fig.1; see also Wohlgemuth *et al.* 2010).

Fig. 2. Window trap and pitfall trap of a trap site in the burnt area (Photo M. Moretti).

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 60-year old forest extended from a xerothermic mixed forest of oak (*Quercus pubescens*) and Scots pine (*Pinus sylvestris*) at 800 m a.s.l., to spruce (*Picea abies*) and open larch (*Larix decidua*) forest at timberline at approx. 2000 m a.s.l. (Moretti *et al.* 2010). Within each vegetation type the forest was homogenously structured, with the exception of small gaps of former pastures and rock outcrops. Along the altitudinal gradient, forest density and canopy coverage decreased with altitude.

During the night of the 13th August 2003, one of the largest forest fires that occurred in Switzerland in the last 30 years destroyed 300 hectares of forest from 800 m to 2200 m a.s.l., killing about 200.000 trees (Wohlgemuth *et al.* 2005). Lying and dead standing trees at different decomposition stages and a succession of various luxuriant herbaceous vegetation dominated the forest aspect during the first years after the event (Moser *et al.* 2009).

Data sampling

In the study area, 18 trap sites were placed at mutual distances of about 200 m. The 18 trapping localities were distributed according to a 3 x 3 balanced block design, in which the factors were the «fire gradient» (unburnt, burnt margin, and

burnt centre), and the «altitudinal gradient» (1200 m, 1450 m, and 1700 m a.s.l) (Fig. 1). The average distance between the burnt margin sites and the unburnt forest borderline was about 70 m.

Each trap site consisted of a window trap and a pitfall trap (Fig. 2).

Window interception traps for flying insects were made of two vertically and crosswise installed transparent sheets of plexiglass (50 cm x 40 cm), mounted above a 45 cm wide bright yellow plastic funnel filled with water, some detergent and bactericide. Traps were placed at a height of 1.5 m above ground (Duelli *et al.* 1999). Pitfall traps for surface-dwelling arthropods consisted of a 15 cm diameter plastic funnel sunk in the ground with its upper rim set flush with the soil surface. An attached bottle filled with 2 % formaldehyde solution (Obrist & Duelli 1996) collected and preserved the catch. Within each trap location, the window trap and the pitfall trap were placed at a lowest distance of 5 meters.

A preliminary sampling was performed in the first year after the wildfire, in 2004. The traps were emptied weekly from July to September. During the following two years (2005 and 2006) the traps were emptied weekly from mid April to the beginning of September.

Beetle identification and data processing

Sampled invertebrates were sorted to different taxonomical groups. All adults of Cerambycidae (longhorn beetles), Buprestidae (jewel beetles) and Carabidae (ground beetles) collected in 2004, 2005 and 2006 were identified to species level using standard keys (Freude *et al.* 1966, 1979; Trautner & Geigenmüller 1987; Pesarini & Sabbadini 1994; Bense 1995; Forsythe 2000; Freude *et al.* 2006). The identification of further beetle families, including Anthribidae (fungus weevils), is in progress. Nomenclature is held in accordance to the current version of the Fauna Europaea (2007).

Pyrophilous species were classified according to Wikars (1994, 1997). Information on the ecology of the species is based on the following literature: Cerambycidae (Picard 1929; Palm 1951; Palm 1959; Freude *et al.* 1966; Sama 1988; Koch 1992; Pesarini & Sabbadini 1994; Bense 1995; Wikars 1997), Carabidae (Jeannel 1941, 1942; Magistretti 1965; Lindroth 1974; Freude *et al.* 1976; Barndt 1982; Casale *et al.* 1982; Trautner & Geigenmüller 1987; Koch 1989; Marggi 1992; Wikars 1997; Du Chatenet 2000; Forsythe 2000; Dajoz 2002; Luka 2004; Du Chatenet 2005; Freude *et al.* 2006), Anthribidae (Koch 1992; Wikars 1997). Swiss redlist categories for carabids were taken from Marggi (1994), while the status of cerambycids and buprestids is based on the Swiss Center of Fauna Cartography (CSCF, http://www.cscf.ch; the Swiss Red List for cerambycids and buprestids is still in preparation). Species distributions in Europe were taken from the Fauna Europaea (2007).

RESULTS AND DISCUSSION

Pyrophilous beetle species

Five pyrophilous species were trapped in Leuk: the cerambycid *Acmaeops marginatus* (37 individuals; Fig. 3a), the cerambycid *Acmaeops septentrionis* (88

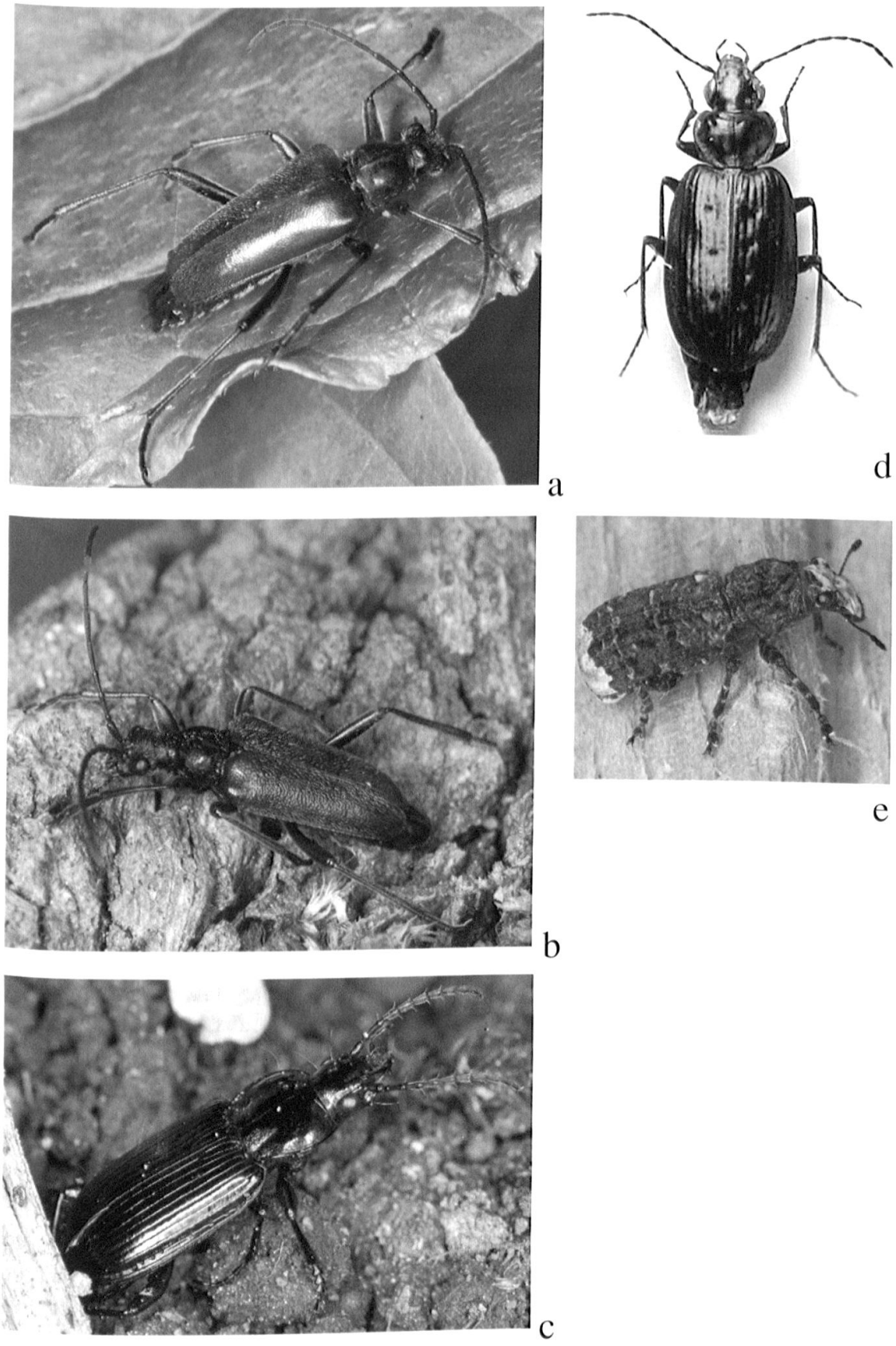

Fig. 3. Pictures of the five pyrophilous beetles: a) *Acmaeops marginatus*; b) *Acmaeops septentrionis*; c) *Pterostichus quadrifoveolatus*; d) *Sericoda quadripunctata*; e) *Platyrhinus resinosus* (Photos: a–c, e: B. Wermelinger; d: Y. Chittaro).

Tab. 1. Overall numbers of individuals of pyrophilous species sampled per: a) sampling year, b) fire gradient, and c) altitudinal level. * = Identification of anthribids is still in progress.

		Acmaeops marginatus	*Acmaeops septentrionis*	*Pterostichus quadrifoveolatus*	*Sericoda quadripunctata*	*Platyrhinus resinosus* *
Overall N. of individuals		37	88	473	716	2
a) sampling year	2004	-	3	1	10	-
	2005	14	27	86	201	2
	2006	23	58	386	505	-
b) fire gradient	unburnt	5	17	1	1	-
	burnt margin	17	55	279	368	2
	burnt centre	15	16	193	347	-
c) altitude level	1200m a.s.l.	28	19	52	35	1
	1450m a.s.l.	7	45	238	195	1
	1700m a.s.l.	2	24	183	486	-

individuals; Fig. 3b), the carabid *Pterostichus quadrifoveolatus* (473 individuals; Fig. 3c), the carabid *Sericoda quadripunctata* (716 individuals; Fig. 3d), and the anthribid *Platyrhinus resinosus* (2 individuals identified till now; Fig. 3e) (Tab. 1).

According to the European pyrophilous species list (Wikars 1994, 1997), the pyrophilous beetle species collected in Leuk represent almost all pyrophilous cerambycid, carabid, and anthribid species known to occur in Europe. There is only one notable exception: we did not find the carabid Sericoda bogemannii, which has never been reported from Switzerland, and also no longer been found in Europe since 1943 (Freude *et al.* 2006). Thus, burnt forests such as the one in Leuk represent important resources for pyrophilous species. The wide ecological range of the pyrophilous species observed in Leuk (i.e. two saproxylics, two soil-dwellers, and one species associated with fungi) suggests that fire and early post-fire succession provide a mosaic of environmental conditions suitable for highly specialized species.

Despite these interesting findings, we did not sample any pyrophilous buprestid species, and this may be the most alarming result of our investigation. In particular the absence of the fire-adapted buprestid *Melanophila acuminata*, which has a particular ability to perceive long-distance infrared radiation emitted from forest fires, might be a warning signal for the conservation status of this very rare beetle, strictly associated with burnt conifer forests and observed three times in Switzerland, i.e. in 1892 in the Canton Bern, in 1946 in the Canton Geneva, and the last time in the Canton Valais in 1951 (CSCF, http://www.cscf.ch).

Pyrophilous beetles found in Leuk

Acmaeops marginatus (Fabricius, 1781) – In the study area, clearly the highest abundance of this pyrophilous beetle was observed in the burnt margin and the burnt centre sites, whereas considerably fewer individuals were collected in the unburnt forest (Tab. 1). The presence of *A. marginatus* in Leuk is noteworthy as, despite its wide distribution, it is restricted in Europe to few localities in burnt forests. The burnt area above Leuk is the only place in Switzerland where the species has ever been observed (Tab. 2).

Tab. 2. Description of the five pyrophilous species sampled in Leuk. * = Information based on Swiss distribution maps and experts' considerations (http://lepus.unine.ch/carto/, CSCF Neuchâtel).

***Acmaeops marginatus* (Fabricius, 1781), Cerambycidae**	
Ecology	Stenotopic species of open and sunny forests. Mountain and subalpine species. The xylophagous larvae develop for 2 years in the thick bark of conifers (especially *Pinus*) injured by fire. The pupation takes place in spring, after the larval overwintering, under the soil at the base of trunks. Adults emerge from May to June. Found on host plants, flowers or flying during day-time.
Distribution in Europe	Norway, Sweden, Finland, Germany, Netherlands, Belgium, Luxembourg, France, Spain, Italy, Switzerland, Austria, Poland, Czech Republic, Slovakia, Bosnia, Serbia, Greece, Northern Russia, Northwestern Russia, Central Russia, Southern Russia, Estonia, Latvia, Lithuania, Belarus, Ukraine.
Distribution in CH	Only one previous report in 1964 in Leuk
Status in CH*	Very uncommon
***Acmaeops septentrionis* (Thomson, 1866), Cerambycidae**	
Ecology	Stenotopic species of open and sunny forests, also in clear-cuts. Mountain and subalpine species. The xylophagous larvae develop for 2 years in or under the bark of conifers (especially *Picea*) injured by fire. The pupation takes place in spring, after the larval overwintering, under the soil or under the bark at the base of trunks. Adults emerge from May to August. Found on host plants, flowers or flying during day-time.
Distribution in Europe	Norway, Sweden, Finland, Germany, France, Italy, Switzerland, Austria, Poland, Czech Republic, Slovakia, Slovenia?, Northern Russia, Northwestern Russia, Eastern Russia, Southern Russia, Estonia, Latvia, Lithuania, Belarus, Ukraine, Romania, Bulgaria.
Distribution in CH	Distributed along the alpine regions.
Status in CH*	Uncommon
***Pterostichus quadrifoveolatus* (Letzner, 1852), Carabidae**	
Ecology	Eurytopic and xerophilous species, observed especially in open, dry, warm and sunny forests affected by fire. Mountain and subalpine species. Adults, omnivorous, are active from April to June. They overwinter and breed during the following spring. Macropterous (able to fly). The Genus *Pterostichus* is typically nocturnal.
Distribution in Europe	Norway, Sweden, Finland, Great Britain, Denmark, Germany, Netherlands, Belgium, Luxembourg, France, Spain, Italy, Switzerland, Austria, Poland, Czech Republic, Slovakia, Slovenia, Bosnia, Serbia, North-Russia, Northwestern Russia, Eastern Russia, Central Russia, Estonia, Latvia, Lithuania, Belarus, Ukraine, Moldavia, Bulgaria
Distribution in CH	Few records on northern slope of Alps: central Jura and northwestern lowlands.
Status in CH*	Endangered
***Sericoda quadripunctata* (De Geer, 1774), Carabidae**	
Ecology	Eurytopic species, it prefers burnt, uncut forests where it's probably a breeding pioneer. Mountain species. It lives as a predator under the bark of trees damaged or killed by fire, feeding on other species attracted to the same trees. Adults emerge from May to September. They overwinter and breed during the following spring. Day-active and macropterous.
Distribution in Europe	Norway, Sweden, Finland, Great Britain, Denmark, Germany, France, Italy, Switzerland, Austria, Poland, Czech Republic, Slovakia, Slovenia, Bosnia, Northern Russia, Northwestern Russia, Eastern Russia, Central Russia, Estonia, Latvia, Lithuania, Belarus, Ukraine, Hungary.
Distribution in CH	Few records in Canton Valais and southern slope of Alps.
Status in CH*	Endangered
***Platyrhinus resinosus* (Scopoli, 1763), Anthribidae**	
Ecology	Stenotopic species of sun exposed deciduous forests, especially in clearings and along the margins of forest. Not an alpine species. The larvae feed specifically within the ascomycetes *Daldinia concentrica*, during the spore producing stage of the fungus. The pupation occurs in the fungus. Adults are found on dead trees and stumps from May to September. Adults overwinter in the dead ascomycetes.
Distribution in Europe	Norway, Sweden, Finland, Great Britain, Denmark, Germany, Netherlands, Belgium, Luxembourg, France, Spain, Italy, Switzerland, Austria, Poland, Czech Republic, Slovakia, Slovenia, Croatia, Bosnia, Serbia, Albania, Macedonia, Greece, European Turkey, Northern Russia, Estonia, Latvia, Lithuania, Ukraine, Hungary, Romania, Bulgaria.
Distribution in CH	Records from all biogeographical regions of Switzerland.
Status in CH*	Common

The saproxylophagous larvae of *A. marginatus* are strictly dependent on trees freshly killed by fire. This requirement, in addition to a preference for coniferous mountain forests, indicates that wildfires in the Swiss Central Alps are extremely favourable for the development and conservation of this rare species.

Acmaeops septentrionis (Thomson, 1866) – The largest numbers of individuals of this species were trapped at the margin of the burnt forest. Equal numbers of individuals were collected in both unburnt and central burnt locations. The ecological requirements of *A. septentrionis*, which is more common than *A. marginatus* in the Alpine regions of Switzerland, suggest that this beetle is not exclusively associated with fire. Thus the predilection for the burnt margin may rather be related to the ecotone structure, which also favours *A. septentrionis* in clear-cuts and open forests.

Pterostichus quadrifoveolatus (Letzner, 1852) – In the Leuk study area this carabid species showed an extremely strong attraction to burnt sites, with 472 individuals collected in the burnt sites versus only 1 individual in the unburnt forest. Although *P. quadrifoveolatus* may develop also in open and dry habitats, our results indicate that this species is strongly associated with burnt sites. Since this is the first record of *P. quadrifoveolatus* in the Swiss Central Alps and the most southern Swiss observation, the abundant occurrence of this rare carabid in Leuk was obviously due to the effect of fire. Our results highlight the role of fire to extend the range of this endangered species.

Sericoda quadripunctata (De Geer, 1774) – Like *P. quadrifoveolatus*, also *S. quadripunctata* was most strongly attracted to the burnt sites, with 715 individuals in the burnt sites versus 1 individual in the unburnt forest, and not showing any significant difference in abundance between the margin and the centre of the burnt area. Its ecology is strongly associated with fire and the known distribution in Switzerland emphasizes its presence in fire-prone regions such as the southern slope of the Alps. Here also, occasional or sporadic fires are very important for the conservation of *S. quadripunctata* in Switzerland.

Platyrhinus resinosus (Scopoli, 1763) – Only two individuals of *P. resinosus* were identified till now (we may expect to find further individuals when identification will be concluded), however they are worthy of mention, given their documented pyrophilous status. Although *P. resinosus* appears commonly in broadleaf forests in Switzerland, in Leuk it was trapped in burnt margin sites in a coniferous stand at high altitudes (1450 m a.s.l.). This may be the result of a post-fire spread of its specific feeding substrate, the ascomycete *Daldinia concentrica*. The presence in burnt areas of this fungus, which can survive in exceptionally dry conditions (Ingold 1965), and its role as food source for pyrophilous beetles have already been reported in the literature (Hingley 1971; Wikars 1997).

CONCLUSIONS

Our results show that the Swiss Central Alps represent an important habitat for rare and threatened beetles favoured by fire. The five pyrophilous beetle species sampled in Leuk have a wide distribution from northern boreal forests to southern temperate forests, suggesting a great capacity of adaptation to different geographical and climatic conditions, which is a quite exceptional trait among insects. Nonetheless, their scattered populations in Switzerland, and throughout Europe, may re-

present a relict heritage from the past, when forest fires were more frequent and widespread. In central Europe today, freshly fire-killed trees are quite an ephemeral substrate. Saproxylic species disperse during their lifespan to find freshly dead trees for oviposition, while litter-dwelling predators risk competition by late successional species. According to Saint-Germain *et al.* (2008), not only the fire suppression but also the degradation of the surrounding unburnt forests might be limiting factors for pyrophilous beetles. This is particularly true for saproxylics that have multiple ecological and habitat requirements during their developing stages, which partially also involve unburnt areas. Further efforts should be taken to investigate the long-term effect of fire on pyrophilous species, especially the required frequency and intensity of wildfires, as well as the quality of unburnt natural and managed habitats.

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REFERENCES

Aschwanden, A., Beck, M., Haeberli, C., Haller, G., Kiene, M., Roesch, A., Sie, R. & Stutz, M. 1996. Bereinigte Zeitreihen. Die Ergebnisse des Projekts KLIMA90. Band 1: Auswertungen. Reihe Klimatologie der Schweiz, Klimatologie 1961-1990. Schweizerische Meteorologische Anstalt.

Barndt, D. 1982. Die Laufkäferfauna von Berlin (West); mit Kennzeichnung und Auswertung der verschollenen und gefährdeten Arten (Rote Liste) - 2. Fassung. — Landschaftsentwicklung und Umweltforschung, 11: 233–265.

Bense, U. 1995. Longhorn beetles. — Illustrated Key to the Cerambycidae and Vesperidae of Europe. Margraf Verlag, 512 pp.

Carcaillet, C. & Müller, S.D. 2005. Holocene tree-limit and distribution of *Abies alba* in the inner French Alps: anthropogenic or climatic changes? — The Boreas, 34: 468–476.

Casale, A., Sturani, M. & Vigna-Taglianti, A. 1982. Fauna d'Italia Coleoptera XVIII. Carabidae. I. Edizione Calderoni Bologna, 499 pp.

Dajoz, R. 1998. Le feu et son influence sur les insectes forestiers. Mise au point bibliographique et présentation de trois cas observés dans l'ouest des États-Unis. — Bulletin de la Société entomologique de France, 103: 299–312.

Dajoz, R. 2002. Les Coléoptères Carabidés et Ténébrionidés, Écologie et Biologie. Editions TEC&DOC, Paris, 522 pp.

Du Chatenet, G. 2000. Coléoptères phytophages d'Europe, Tome 1. N.A.P. Editions, 359 pp.

Du Chatenet, G. 2005. Coléoptères d'Europe, Carabes, Carabiques et Dytiques. Volume 1, Adephaga. N.A.P. Editions, 625 pp.

Duelli, P., Obrist, M. K. & Schmatz, D.R. 1999. Biodiversity evaluation in agricultural landscapes: above-ground insects. — Agriculture Ecosystems & Environment, 74: 33–64.

Ehnström, B., Langström, B. & Hellqvist, C. 1995. Insects in burned forests – forest protection and faunal conservation (preliminary results). — Entomologica Fennica 6: 109–117.

Fauna Europaea, 2007. Version 1.3 (19. April 2007). URL: http://www.faunaeur.org/.

Forsythe, T.A. 2000. Ground Beetles. — Naturalists' Handbooks 8. The Richmond Publishing Co. Ltd., 96 pp.

Freude, H., Harde, K.W. & Lohse, G.A. 1966. Die Käfer Mitteleuropas. Cerambycidae, Chrysomelidae. Band 9. Goecke & Evers Verlag, Krefeld, 299 pp.

Freude, H., Harde, K.W. & Lohse, G.A. 1976. Die Käfer Mitteleuropas. Adephaga 1. Band 2. Goecke & Evers Verlag, Krefeld, 302 pp.

Freude, H., Harde, K.W. & Lohse, G.A. 1979. Die Käfer Mitteleuropas. Diversicornia. Band 6. Goecke & Evers Verlag, Krefeld, 367 pp.

Freude, H., Harde, K.W. & Lohse, G.A. 2006. Die Käfer Mitteleuropas. Adephaga 1. Band 2. Elsevier, 521 pp.
Gobet, E., Tinner, W., Hochuli, P.A., van Leeuwen, J.F.N. & Ammann, B. 2003. Middle to Late Holocene vegetation history of the Upper Engadine (Swiss Alps): the role of man and fire. — Vegetation History and Archaeobotany 12: 143–163.
Granström, A. 1996. Fire ecology in Sweden and future use of fire for maintaining biodiversity. *In*: Goldammer J.G. & Furyaev V.V. (eds), Fire in Ecosystems of Boreal Eurasia. Kluwer Academic Publishers, Dordrect, pp. 445–452.
Heliövaara, K. & Väisänen, R. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. — Acta Forestalia Fennica 189: 1–32.
Hermann, S.M., Van Hook, T., Flowers, R.W., Brennan, L.A., Glitzenstein, J.S., Streng, D.R., Walker, J.L. & Myers, R.L. 1998. Fire and biodiversity: studies of vegetation and arthropods. Transactions of the 63rd North American Wildlife and Natural Resources conference; 1998 March 20–25; Orlando, FL. Washington, DC: Wildlife Management Institute, pp. 384–401.
Hingley, M. R. 1971. The Ascomycete Fungus, *Daldinia concentrica* as a Habitat for Animals. — The Journal of Animal Ecology 40: 17–32.
Ingold, C. T. 1965. Spore liberation. Clarendon Press. Oxford, 210 pp.
Jeannel, R. 1941. Faune de France. Coléoptères Carabiques, première partie, 39. Paris, 571 pp.
Jeannel, R. 1942. Faune de France. Coléoptères Carabiques, deuxième partie, 40. Paris, 602 pp.
Jonsell, M., Weslien, J. & Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. — Biodiversity and Conservation 7: 749–764.
Koch, K. 1989. Die Käfer Mitteleuropas Ökologie. Band 2. Goecke & Evers Verlag, Krefeld, 382 pp.
Koch, K. 1992. Die Käfer Mitteleuropas Ökologie. Band 3. Goecke & Evers Verlag, Krefeld, 389 pp.
Lindroth, C.H. 1974. Handbooks for the Identification of British Insects Coleoptera, Carabidae. — Royal Entomological Society of London 4: 1–148.
Luka, H. 2004. Ecological evaluation of landscape elements with arthropods. Opuscula Biogeographica Basileensia 4. — Wepf & Co. Basel, Schweiz, 243 pp.
Lundenberg, S. 1984. The beetle fauna of burnt forest in Sweden. — Entomologisk Tidskrift 105: 129–141.
Magistretti, M. 1965. Fauna d'Italia Coleoptera VIII. Cicindelidae, Carabidae. Catalogo topografico. Edizione Calderoni Bologna, 512 pp.
Marggi, W. 1992. Faunistik der Sandlaufkäfer und Laufkäfer der Schweiz (Cicindelidae & Carabidae) Coleoptera unter besonderer Berücksichtigung der «Roten Liste». Documenta Faunistica Helvetiae 13, Teil 1/ Text, Teil 2/Verbreitungskarten. Neuchâtel, 477 pp.
Marggi, W. 1994: Rote Liste der gefährdeten Laufkäfer und Sandlaufkäfer der Schweiz. *In*: Duelli P.: Rote Liste der gefährdeten Tierarten der Schweiz. BUWAL, Bundesamt für Umwelt, Wald und Landschaft, 97 pp.
Moretti, M., Obrist, K.M. & Duelli, P. 2004. Arthropod biodiversity after forest fires: Winners and losers in the winter fire regime of the Southern Alps. — Ecography 27: 173–186.
Moretti, M., De Cáceres, M., Pradella, C., Obrist, M.K., Wermelinger, B., Legendre, P. & Duelli, P. 2010. Fire-induced taxonomic and functional changes in saproxylic beetle communities in fire sensitive regions. — Ecography 33: 760–771.
Moser, B. Temperli, C., Schneiter, G. & Wohlgemuth, T. 2010. Potential shift in tree species composition after interaction of fire and drought in the Central Alps. — European Journal of Forest Research 129: 625–633.
Muona, J. & Rutanen, I. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. — Annales Zoologici Fennici 31: 109–121.
Obrist, M.K. & Duelli, P. 1996. Trapping efficiency of funnel- and cup-traps for epigeal arthropods. — Mitteilungen der Schweizerischen Entomologischen Gesellschaft 69: 361–369.
Palm, T. 1951. Die Holz- und Rindenkäfer der Nordschwedischen Laubbäume. Meddelanden, Statens Skogsforskningsinstitut Stockholm 40: 1–242.
Palm, T. 1959. Die Holz- und Rinden-Käfer der Süd- und Mittelschwedischen Laubbäume. Opuscula Entomologica, Supplement 16. Lund, Sweden, 374 pp.
Pesarini, C. & Sabbadini, A. 1994. Insetti della Fauna Europea Coleotteri Cerambicidi. — Natura, Rivista di Scienze Naturali, 85 (1/2), 132 pp.
Picard, F. 1929. Faune de France. Coléoptères Cerambycidae, 20. Paris, 167 pp.
Saint-Germain, M., Drapeau, P. & Buddle, C.M. 2008. Persistence of pyrophilous insects in fire-driven boreal forests: population dynamics in burned and unburned habitats. — Diversity and Distributions 14: 713–720.
Sama, G. 1988. Fauna d'Italia Coleoptera XXV. Cerambycidae. Catalogo topografico e sinonimico. Edizione Calderoni Bologna, 216 pp.

Tinner, W., Conedera, M., Ammann, B. & Lotter, A.F. 2005. Fire ecology north and south of the Alps since the last ice age. — The Holocene 15: 1214–1226.

Trautner, J. & Geigenmüller, K. 1987. Sandlaufkäfer Laufkäfer. Illustrierter Schlüssel zu den Cicindeliden und Carabiden Europas. Joseph Margraf Verlag, 488 pp.

Wikars, L.O. 1994. Effects of forest fire and the ecology of fire-adapted insects. Introductory Research essay No.12. Department of Zoology, Section of Entomology University of Uppsala, Sweden, 22 pp.

Wikars, L.O. 1997. Effects of forest fire and the ecology of fire-adapted insects. Acta Univ. Ups. Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology, 272. Uppsala, 35 pp.

Wohlgemuth, T., Duelli, P., Ginzler, C., Gödickemeier, I., Hadirn, S., Hagedorn, F., Küttel, P., Lüscher, P., Moretti, M., Schneiter, G., Sciacca, S. & Wermelinger, B. 2005. Ökologische Resilienz nach Feuer: die Waldbrandfläche Leuk als Modellfall. — Schweizerische Zeitschrift für Forstwesen 156: 345–352.

Wohlgemuth, T., Brigger, A., Gerold, P., Laranjeiro, L., Moretti, M., Moser, B., Rebetez, M., Schmatz, D., Schneiter, G., Sciacca, S., Sierro, A., Weibel, P., Zumbrunnen, T. & Conedera, M. 2010: Leben mit Waldbrand. — Merkblatt für die Praxis 46: 16 pp.

Zumbrunnen, T., Bugmann, H., Conedera, M. & Bürgi, M. 2009. Linking forest fire regimes and climate - a historical analysis in a dry inner Alpine valley. — Ecosystems 12: 73–86.

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