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Population trends of *Rosalia alpina* (L.) in Switzerland: a lasting turnaround?

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Abstract Many species that depend on old trees and dead wood are suffering from habitat losses and intensive forest management. For the conspicuous cerambycid beetle *Rosalia alpina,* a relative sampling analysis combined with a distribution model showed a population decrease in Switzerland between 1900 and World War II. This negative trend can be ascribed to the abandonment of traditional management such as wooded pasture and to the expansion of high forest promoted by modern forestry. Since that period, the population of *R. alpina*, has been increasing and each single relict population of this species was maintained. These positive population trend can be explained by less intensive forest management and a shift from fuel-wood production to timber wood. Today, many more old beech trees and much more dead wood remain in Swiss forests than 50 years ago. Consequently, the habitat conditions necessary for the development of the *Rosalia* longicorn have improved, especially on steep terrain in colline and submontane regions. However, it is still uncertain whether current population sizes can guarantee the survival of this species in the long term, especially as fuel-wood production is expected to become more intensive in Switzerland in future decades. The conservation of this species requires, therefore, the establishment of natural forest reserves and dead wood islands or the restoration of wooded pastures with scattered habitat trees. The *Rosalia* longicorn could then act as an umbrella species for other species that depend on old trees and dead wood.

Keywords Saproxylic beetles · Relative sampling · Potential distribution · Forest management · Population trend

Introduction

The main factor behind the loss of biodiversity is land use change (Sala et al. 2000). Many species are becoming rarer and populations are getting more isolated due to the loss of habitat, which leads, in turn, to a higher extinction risk (Hanski and Gaggiotti 2004). Many European countries aimed to halt the loss of biodiversity by 2010, but Switzerland, like all other countries, failed to meet this goal and recommended that more effort should be put into the conservation of biodiversity. However, some positive trends can be observed as the result of specific conservation efforts and improved habitat conditions, especially at the ecosystem level.

On the one hand, as a consequence of intense forest management that has taken place over the last few centuries, almost no primeval forests are left in central Europe today (Müller et al. 2005). On the other hand, traditional management, such as wooded pastures and coppicing, has created semi-open stands with a number of old or coppiced trees that have benefited many species. Many such habitats have been replaced by managed dense forests for timber production (Brunet et al. 2012). Forest stands with no logging activity for a long period may nevertheless have features similar to primeval forests (Whitehead 1997), such

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as veteran trees, suitable habitat structures and continuously available dead wood. In such stands, many saproxylic beetle species can survive, whereas they have mostly disappeared from managed forests. Species occurring under primeval forest conditions are considered as "Urwald relict species", such as the cerambycid beetle *Rosalia alpina* (L.) (Müller et al. 2005).

Rosalia alpina is known to be an obligate saproxylic species. In Europe, this species has a plastic ecology, found on different deciduous tree species from the sea coast to about 2,000 m a.s.l. (e.g. Bense 2002; Cizek et al. 2009; Michalcewicz et al. 2011; Michalcewicz and Ciach 2012). In Switzerland, *R. alpina* has been recorded to be found at altitudes as low as 300 m a.s.l., and as high as 2,000 m a.s.l. and occurs mainly on dead beech trees or dead parts of beech. As a xerothermophilic species, it requires sun-exposed dry dead wood (Russo et al. 2011), in which larvae can develop for 3 or 4 years (Duelli and Wermelinger 2010). The resulting adults do not depend on flowers with pollen for maturation.

Rosalia alpina is protected by Annex II and IV of the EU Habitats Directive and is listed in Appendix II of the Bern Convention. Even though its populations are still declining in some countries, its protection status was reconsidered in the last Red List for saproxylic beetles in Europe. *R. alpina* was listed as critically endangered in the Red Lists of 1986, 1988, 1990 and 1994, *R. alpina* was listed as vulnerable in 1996 and as a least-concern species in the latest edition of the Red List of saproxylic beetles (Nieto and Alexander 2010). The main reason for this down-ranking is that *R. alpina* is now widely distributed across Europe with a high number of observations, especially in Western Europe (Nieto and Alexander 2010). However, this species has undergone a marked decline in the past across much of its range (Luce 1996). For example, it was known to occur in several locations during the eighteenth and nineteenth centuries in Southern Sweden, but since then it has disappeared (Lindhe et al. 2010). In Germany, there is evidence that the population decreased until 1975 and has increased in different regions in the last decade (Bense and Bussler 2003). In Switzerland, it is listed as a priority species (BAFU 2011) and is protected by law. However, quantitative information about its population trend is mostly lacking, especially when considering long-term series. Consequently, relatively little is known about quantitative changes in the population of *R. alpina* at a national level in many countries, and statements about this species rely mostly on expert knowledge or local case studies.

The following two main questions will be discussed in this paper: (1) what are the population trends of the protected species *R. alpina* in Switzerland and (2) how can these trends be interpreted in view of a better understanding of the species' history and future management?

Materials and methods

In this study, we used historical and current records for the last 100 years as a proxy for population size. Since such data are based on non-standardized sampling methods, they cannot be directly used for population trend analysis. Potential bias, such as spatial and temporal variation in sampling effort and methods have to be taken into consideration (Jeppsson et al. 2010). Consequently, we related the *Rosalia* records to one reference data set as recommended by, for example, Hedenas et al. (2002) to account for varying sampling effort. Furthermore, we combined a potential distribution model of *R. alpina* with the population trend analysis.

Observation data

Three data sets were compiled: one for *R. alpina*, one for all Cerambycidae, and one for three similarly attractive species, i.e. *Aromia moschata, Cerambyx cerdo* and *Ergates faber*. The data sets on the Cerambycidae and the three attractive species were used as reference data for the relative sampling analysis. With around 180 species, the cerambycid beetle family is well distributed across Switzerland. Most species of this family are saproxylic like *R. alpina*. The records are available at the Swiss Biological Records Center (www.cscf.ch). Further data on *R. alpina* were collected by Duelli and Wermelinger (2010).

We only took records into consideration where the year and coordinates were known or where the coordinates could be reconstructed based on location data. We did not exclude any records based on sampling methods. On the one hand, the sampling method was known for only 1/3 of all records of Cerambycidae, of which 80 % were sampled manually. On the other hand, *R. alpina* was never collected by trap in Switzerland. Consequently, the focal species is not influenced by the use of traps and our results are more conservative.

Only one record per species, year and catchment area was considered in order to prevent bias arising from multiple collections, for example, from repeated observations of the same individual. We considered catchment areas at an aggregation level of 40 km^2, as this size is considered to be ecologically meaningful and is often used by the national data centres (e.g. Monnerat et al. 2007). A catchment area is defined as an area from which the surface water converges to a single point. One-thousand and eighty-one catchment areas have been identified in Switzerland by the Swiss Agency for the Environment (www.bafu.ch).

Habitat suitability model

A habitat suitability model was built using all available records of *R. alpina* with reliable coordinates prior to computing a frequency analysis. Consequently, we excluded records located outside of the natural habitat of this species in Switzerland, such as in city centres or records located below 500 m a.s.l. and above 2,000 m a.s.l. Such occurrences were most likely the result of fire wood transportation or inaccurate coordinates. Finally, 170 *Rosalia* observations were used for modelling the potential distribution. The presence data were completed with the same amount of randomly distributed pseudo-absences. We tested several model techniques [boosted regression trees (BRT), maximum entropy model and generalized linear models] and selected a logistic polynomial regression model (i.e. generalized linear model) as it performed best in terms of cross-validated area under the curve (AUC) values. This model links the observation data to environmental predictors of various kinds, which were transformed after the first-aid transformations (Mosteller and Tukey 1977) to improve the linear relationship of the regression model. To avoid multi-collinearity among predictors, we filtered predictors with correlations above 0.7. As a consequence, several climatic variables such as temperature were excluded because of their correlation with elevation.

The resulting set of predictors comprised 13 variables: four climatic variables, six topographic variables and three biological variables. The climatic variables included: a moisture index for the winter season (Zimmermann and Kienast 1999), the difference between winter and summer precipitation (Zimmermann and Kienast 1999), precipitation in autumn and the site water-balance (Guisan et al. 2006). The six topographic variables (Source: dhm25 © 2012 Swisstopo 5704 000 000) were: elevation, slope, eastness, northness, a topographic position index (TPI) calculated within a radius of 2 km and a stream power index (SPI). The latter combines the catchment area of a site with its slope steepness, and is used to describe the potential flow erosion and related landscape processes (Moore et al. 1993). The TPI describes whether a location is situated on a crest, mid-slope, in a valley or on a flat area. The biological variables comprised: the percentage of forest coverage (Source: Vector25 © 2007, Swisstopo DV033594), the percentage of beech coverage (Schmid 1961) and the modelled beech potential (Heller-Kellenberger et al. 1997).

All predictor variables except the modelled beech potential were originally available at a resolution of 25 m. To ensure a robust match with the less precise occurrence data of *R. alpina*, we aggregated the predictor layers to a resolution of 1,000 m by calculating their respective means.

The final distribution model was specified by applying a forward variable selection procedure on the previous predictors, including quadratic terms. Model accuracy was tested by a tenfold cross-validation, using the AUC derived from the receiver operating characteristic (ROC) plots. To estimate the relative contribution of the variables that explain the distribution of *R. alpina*, we compared the results of three different model types: hierarchical partitioning (Chevan and Sutherland 1991; Mac Nally 2000), BRT (Leathwick et al. 2006) and Maxent (Phillips et al. 2006). Hierarchical partitioning was conducted using the logistic regression model. The method, as implemented in the "hier.part package", explores the independent contribution of a single variable. To quantify the relative contribution of a variable including its quadratic term, we extended the function to operate on those pairs.

Weighting of records

Instead of restricting the analysis to a given area where *R. alpina* had been recorded at least once, which would exclude a priori many records of Cerambycidae (reference data), we used a more sensitive continuous definition of the reference area, combining the results of the distribution model and the occurrence data set. The records of *R. alpina* and Cerambycidae were weighted prior to the relative sampling analysis using the habitat suitability model for *R. alpina* (values between 0 and 1). Records in regions with high potential for *R. alpina* received a higher value than records in regions with low potential. Consequently, records of Cerambycidae in a suitable habitat for *R. alpina* had a stronger influence on the relative sampling frequency (RSF) than records in unsuitable sites. The weighting of records is supported by the assumption that, if *R. alpina* had been present in a suitable region, it would most likely have been sampled together with the other cerambycids.

Relative sampling analysis and data selection

Relative sampling analysis is a method to compensate for the bias associated with historical records, especially the changes in sampling effort. This method has been used in several studies for different species groups (e.g. Hedenas et al. 2002; Hofmann et al. 2007; Jeppsson et al. 2010; Ponder et al. 2001). The RSF of a focal species during a given time period is calculated as the percentage of the number of occurrences of a focal species relative to the number of occurrences of a reference data set for the given time period (Hofmann et al. 2007). This method relies on the assumption that the temporal distribution of the reference records reflects the collecting activity in a region (Hedenas et al. 2002). The formula used in this study is

$$RSF = \frac{\sum_{i=1}^{n} r_i \times w_i}{\sum_{i=1}^{n} R_i \times w_i}$$

where $i = 1$–n ($n = 1{,}081$, the number of catchment areas in Switzerland), $r_i =$ the number of records for a given time period for the focal species, $w_i =$ the weighting of the records with regard to the potential distribution model and $R_i =$ the number of records during a given time period for the reference species group.

Considering the low number of records of the focal species up until the middle of the twentieth century, we pooled the decades to smooth variation due to decades with few records. In total, 6 different periods lasting from 10 to 40 years were considered. As a result, between 14 and 126 records were considered per period. To evaluate the effect of the arbitrary pooling of years, we also tested regular period lengths (5, 10 or 20 years) and random period lengths of at least 10 years for 6 periods between 1900 and 2010 (10,000 replicates).

The expected sampling frequency (ESF) of the focal species during a specific time period was calculated following the method described by Hedenas et al. (2002): $ESF = \frac{A}{B} \times C$, where A is the total number of occurrences of *R. alpina*, B is the total number of occurrences of the reference records and C is the number of occurrences for the reference record during a specific time period.

Distribution

According to Gatter (1997), the flight range of *R. alpina* is <1 km. Drag et al. (2011), however, suggested that *R. alpina* can fly up to 10 km, although they were not able to verify such distances by capture-recapture. We therefore defined a buffer of 10 km around the findings of *R. alpina* recorded after 1950 (transition from population loss to increase) in order to identify regional metapopulations (Fig. 3, hatched area). Contiguous buffers formed a distinct population. Within a distinct population, the size of the geographic distribution was determined by drawing the minimum convex polygon (convex hull) for the records prior to and after 1950.

Results

In total, 33,602 records of Cerambycidae and 236 records of *R. alpina* were considered in the relative sampling analysis for the period from 1900 to 2010. The number of observations of both *R. alpina* and the reference group (Cerambycidae) increased during the period (Fig. 1). During the first five decades of the twentieth century, *R. alpina* was observed about every third year, whereas during the last 20 years about 5–15 records were registered yearly. However, no population trends can be derived from these raw data, because the number of observations is strongly related to the increasing sampling effort of cerambycids.

Relative sampling analysis

The results of the relative sampling analysis are given in Fig. 2. A decrease in the RSF could be observed between the first period (1900–1939) and the second period (1940–1959). This period represents the lowest frequency for *R. alpina*. From the 1960s on (even from the 1950s on if single decades are considered), the frequency of *R. alpina* steadily increased until 2010. Choosing different period lengths (regular, random) did not change this trend. The same population trends of *R. alpina* were also found using the reference data set composed of *A. moschata, C. cerdo* and *E. faber*, i.e. a decrease between 1900 and 1950 and an increase from 1950 to the present.

The ratio between the observed (RSF) and expected sampling frequencies (ESF) showed that until the 1990s, the observed values were lower than expected (Fig. 3). From 1990 to 2010, this ratio was higher than one, because *R. alpina* was collected disproportionately frequently.

Distinct population and geographic distribution

Most of the records could be attributed to 6 distinct populations (see Fig. 4, hatched zones). In 5 of the 6 identified populations, *R. alpina* had already been observed prior to 1950. Only for the population in the western Jura (see number 2, Fig. 4) are there no records prior to 1950, even though 74 cerambycid records were made between 1900 and 1950 in this zone.

The distribution range for all Swiss records expanded from 21,000 km^2 (<1,950) to 30,000 km^2 ($\geq$1,950). This trend was also true for the six distinct populations identified in Switzerland (Fig. 4). In each of these populations, the distribution polygon increased markedly, comparing the period prior to and after 1950 (Table 1).

Potential distribution

The habitat suitability model (Fig. 5) shows the occurrence potential of *R. alpina* in Switzerland. The lowlands of the Swiss plateau appear to be rather unsuitable for this species, whereas the Jura, the Pre-Alps and the Alps offer more suitable habitats. A cross-validated AUC value of 0.94 demonstrates the high accuracy of this model.

The different approaches used to quantify the relative contribution of the individual predictors yielded comparable results. Most of the variation was explained by three biological variables (forest coverage, beech coverage and modelled beech potential) and three topographic variables

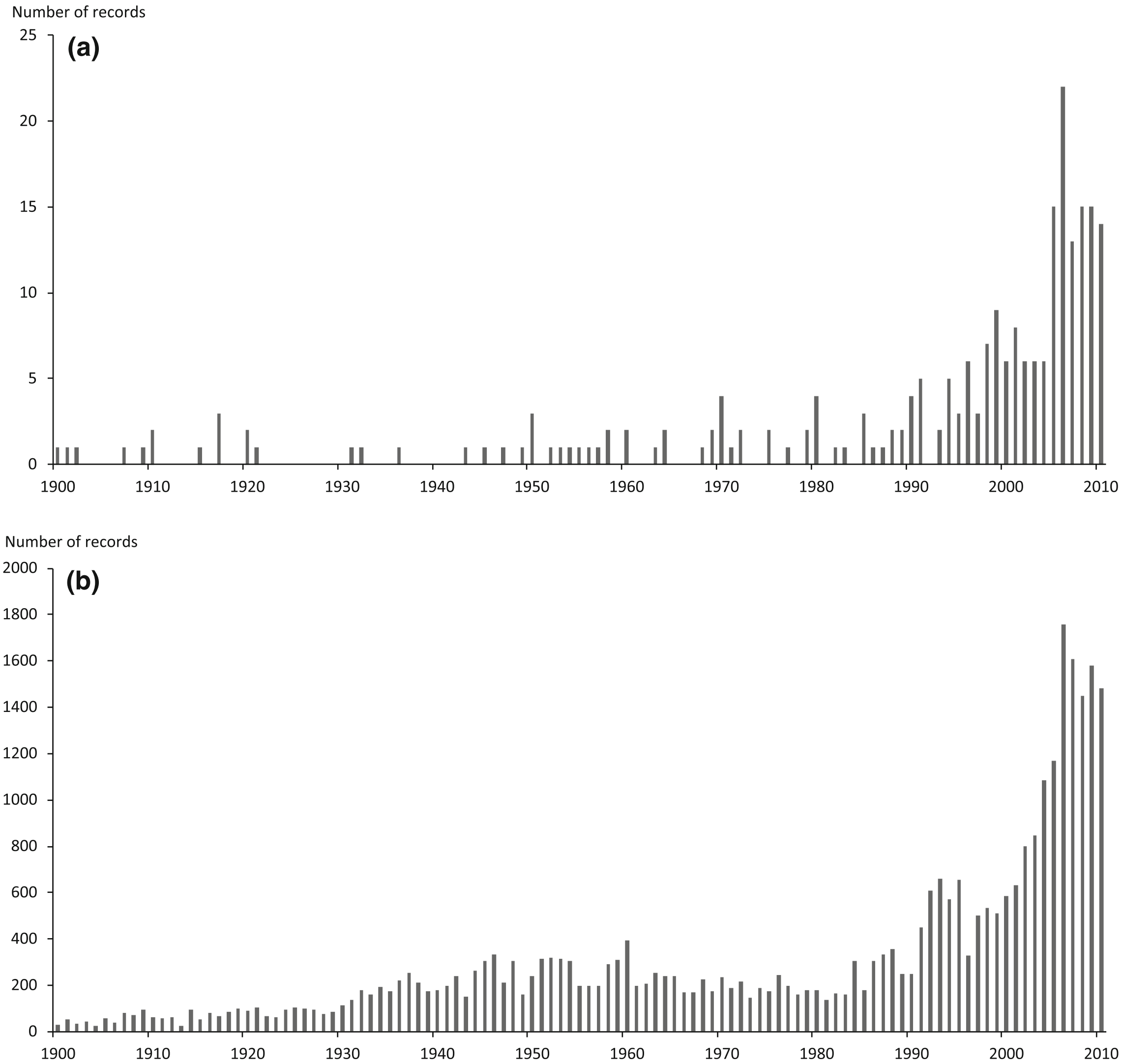

Fig. 1 Number of records per year and catchment area **a** for *R. alpina* and **b** for all species of the family Cerambycidae

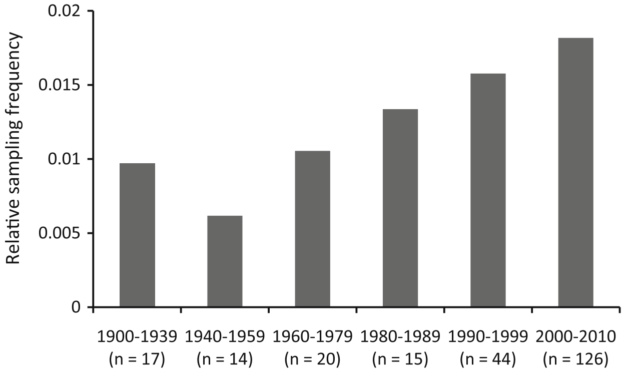

Fig. 2 Relative sampling frequency (RSF) for *R. alpina* in Switzerland. Note the unequal period lengths (*n* number of individuals per time period)

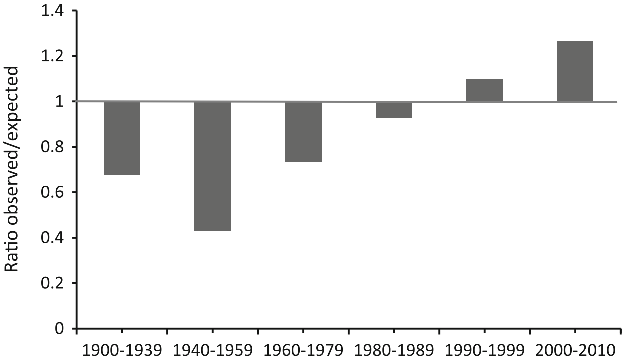

Fig. 3 Ratio between relative and expected sampling frequency (RSF). *Value >1* the observed value is higher than the expected value, *value <1* the observed value is lower than the expected value

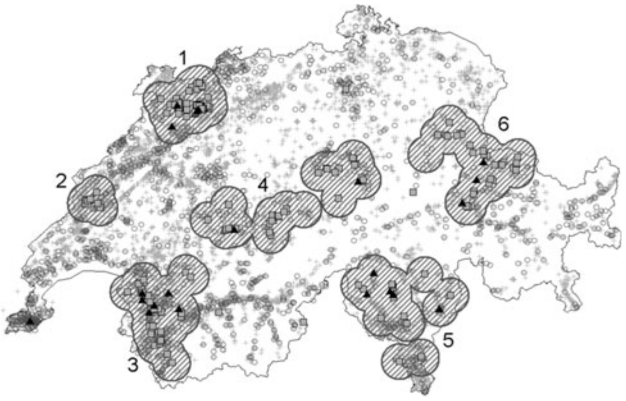

Fig. 4 Distribution of records of *R. alpina* before 1950 (*black triangles*) and after 1950 (*grey squares*). *Grey circles* indicate the records of Cerambycidae prior to 1950 and *grey crosses* indicate records after 1950. *Hatched areas* (1–6) highlight distinct populations

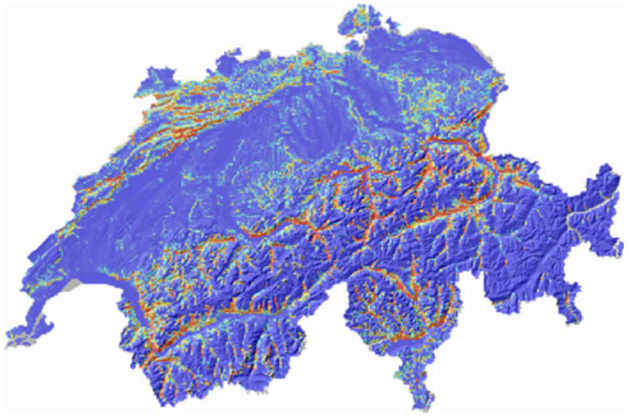

Fig. 5 Habitat suitability model for *R. alpina* in Switzerland (*grey* no data, *blue* low potential, *yellow* medium potential, *red* high potential). (Color figure online)

(SPI, slope and elevation). Among these predictors, beech coverage and the SPI was most important (see Table 2). The relative contribution of climatic variables was remarkably low with all model types.

Discussion

Forest beetles are known to be strongly influenced by forest changes, especially if they depend on resources that tend to diminish in managed forests, such as dead wood for saproxylic species. This makes saproxylic species sensitive to forest management practices (Grove 2002). Therefore, the history of human impact on forests helps us to understand the reaction of forest species and might improve the planning of conservation measures.

During the first half of the twentieth century, the population trend for *R. alpina* in Switzerland was negative and reached the lowest level during World War II. Since then, the population of this species have been increasing. The most likely explanations for this trend are discussed below.

Table 2 Contribution in % of the six main environmental variables (after hierarchical partitioning) to the distribution model of *R. alpina* using 3 different methods

Environmental variable	Hierarchical partitioning	Boosted regression trees	Maxent
Beech coverage	9	17	17
Stream power index (SPI)	8	23	16
Modelled beech potential	8	7	11
Elevation	8	5	5
Forest coverage	8	12	12
Slope	7	12	12

Public awareness

More findings of *R. alpina* in Switzerland have been recorded since the 1990s than expected (see Fig. 3). This is probably the result of the increasing popularity of this flagship species. In 2002, a Swiss stamp was devoted to it and the beetle was assigned the status of an emerald species

Table 1 Distribution range (minimal convex polygon) in km^2 for populations of *R. alpina* in Switzerland grouped into two time periods (1900–1949 and 1950–2010)

	Northern Jura (1)	Western Jura (2)	Valais (3)	Pre-Alps (4)	Tessin (5)	East (6)	Switzerland
1900–1949	78	0[a]	173	0.2[b]	258	14	21,399
1950–2010	338	36	1,523	2,387	1,531	1111	29,624

Populations (1–6) are numbered according to the different population areas shown in Fig. 4

[a] No record prior to 1949

[b] Only 2 records

in the framework of the European emerald network of conservation areas. Thus, more people may have actively searched for this conspicuous and easily recognizable species. This might partially explain the positive trends in the last two decades. However, the population of *R. alpina* already increased in Switzerland from the 1950s on. A reference data set composed of three other conspicuous longhorned beetle species (*A. moschata, C. cerdo* and *E. faber*) showed very similar trends compared to the reference data set composed of all Cerambycidae species. If attractive species had been systematically oversampled, the relative frequency of *R. alpina* would have been more or less constant. We conclude therefore, that the positive trend observed for *R. alpina* after 1950 is not only due to its increasing popularity or attractiveness, but that other factors also influence this species.

Changes in forest management practices

According to Noble and Dirzo (1997), forests can be considered as ecosystems shaped by humans. After the last glaciations, the forested area declined as forests were cleared for agriculture, and forest structure and composition also drastically changed through management (Thirgood 1989). Several studies across Europe highlight the importance of traditional forest management (e.g. coppices with standards and wooded pastures) for saproxylic species dependent on sun-exposed substrates (see e.g. Russo et al. 2011; Buse et al. 2007). The abandonment of these traditional management types with the establishment of modern forestry and agriculture is considered to be the major cause of the decline of *R. alpina* (Drag et al. 2011). In Switzerland, coppices with standards were mainly managed at lower altitude in stands dominated by oaks where *R. alpina* does not occur (Swiss Forest Statistics 1912). Therefore, their conversion to high forests should not have influenced *R. alpina*. Wooded pastures, on the other hand, may have played a major role as long as scattered old beech trees with moribund parts were maintained. Grossmann (1927) reported that even though beech trees were not numerous in wooden pastures because of their sensitivity to browsing, wooded pastures with beech trees were found in the Jura, Southern Alps and Eastern Pre-Alps. The author even mentioned wooded pastures purely stocked by beech trees in Southern Jura and Alps. Between the eighteenth and nineteenth centuries, most wooded pastures were abandoned (Grossmann 1927). At the same time, high forests became the prevailing forest type (Bürgi 1999). The growing stock has since doubled, and amounts today to more than 360 m^3/ha on average (LFI3). As a result, Swiss forests are generally getting darker (Brändli and Abegg 2009). The abandonment of wooded pastures and the expansion of dark high forests might be the main cause of the negative population trends we observed for *R. alpina* between 1900 and 1950 (Fig. 4).

We assume that a habitat shift from wooded pastures to abandoned beech forest stands explains the positive trend of *R. alpina* after World War II. Since 1900, management intensity, calculated as the ratio between the amount of wood harvested and the total growing stock, has decreased by a factor of two. According to the national forest inventory, 18 % of Swiss forests have not been managed in the last 50 years and this value is even above 50 % in regions where the topography hampers management (e.g. Southern Alps). Due to the growing proportion of forests without management, we expect an increase in potential habitats for *R. alpina* in Switzerland since after already 30 years without harvesting, large amounts of dead wood can have accumulated (Bütler and Lachat 2009). The simultaneous death of 1–3 canopy trees can create gaps (Kenderes et al. 2009) and therefore increases sun exposure, which might already be attractive for *R. alpina*.

Increase in dead wood and decrease in fuel-wood demand

In Switzerland, data on dead wood have only been available since the second National Forest Inventory (NFI2) started in 1993. During the last decade, the average volume of dead wood has increased from 11.9 m^3/ha (NFI2, 1993–1995) to 18.5 m^3/ha (NFI3, 2004–2006) (Brändli 2010). The increase in dead wood during the last decade is due first to the unfavourable economic situation in the wood industry, second, to extensive wind throws occurring in 1990 and 1999, and third, to the growing awareness of the importance of this substrate for forest biodiversity. Even though data are lacking before this period, it is widely accepted that hardly any dead wood could be found in the forests around 1900 (Bürgi 1998) and that after World War II, the amount of dead wood increased as a consequence of less intense forest management and less demand for fuel-wood (Speight 1989). Fuel-wood was the most important source of primary energy (Pfister and Messerli 1990) until coal became the main source around 1910 (Marek 1994). As a result, the production of fuel-wood from broadleaved trees decreased continuously until around 1980, except during the two world wars. Consequently, trees of lower economic value such as over-mature or veteran trees, crippled or damaged individuals, windthrown or fallen trees on rugged slopes, became more likely to remain in the forest. This increase in over-mature beech trees is very beneficial to *R. alpina* especially if these trees are allowed to decay in the forest in a sunny location.

The lowest RSF for *R. alpina* was reached during the intensive exploitation of fuel-wood around World War II. Other saproxylic species may have experienced similar decreases during this period. However, when reference records for the Cerambycidae are taken into consideration, *R. alpina* appears to have decreased most. This might be explained by populations already being weakened due to the over-exploitation of fuel-wood and to the abandonment of wooded pastures during and prior to this period. The planting of conifers in broadleaved forests or the conversion of broadleaved forests to conifer forests may also have had direct negative effects on *R. alpina*. This might have strengthened the negative trend until World War 2. After this period, the higher amount of beeches completing much or all of their natural cycle in the forest appeared to compensate for the loss through the planting of conifers.

Threats and conservation measures for *Rosalia alpina* in Switzerland

New management plans for the next decades aim to harvest about 2.7–3.2 million m^3 of energy wood/year from Swiss forests, compared with 1.5 million m^3/year today (www.bafu.ch). This intensification will have a strong influence on saproxylic species, as most trees as well as branches and twigs can be used for fuel-wood, including even those of poor quality formerly left to decay in situ. This will lead to a decrease in dead wood and to an impoverishment of suitable habitats for saproxylic species. Furthermore, more intense forest management may mean a shorter rotation period, which in turn might negatively affect many saproxylic beetle species (Ohsawa and Shimokawa 2011) because the continued availability of dead trees and adequate habitat structures will be reduced (Ranius et al. 2003).

Besides the direct impact of wood removal, logs and fuel wood stockpiled at forest edges are likely to act as ecological traps for saproxylic beetles because many species are strongly attracted to these piles. The problem is that these piles are then removed after some months and chipped. Hedin et al. (2008) noticed how the outer layer of forest fuel piles was especially attractive to saproxylic species. A first conservation measure could be to leave this layer in the forest. As a conservation measure for *R. alpina*, Duelli and Wermelinger (2010) recommend installing standing dead logs of beech in the vicinity of log piles and to leave these artificial snags with the larvae along the forest edge. These measures would allow at least some of the larvae to complete their development.

Further measures such as the artificial creation of dead wood in closed beech forests or the restoration of traditional management practices such as wooded pastures with beech trees would also benefit *R. alpina*, as well as many other saproxylic species.

Distribution of *R. alpina*

Understanding the habitat preferences of a saproxylic species primarily requires analysing tree- and stand-level conditions. Buse et al. (2007) and Russo et al. (2011) found that variables such bark depth or distance from the next colonized tree had higher predictive power on species suitability than landscape-level predictors (Buse et al. 2007). However, in the present study we demonstrated the benefit of landscape-level variables to predict the habitat suitability of *R. alpina* across a broad geographic range. Even though such variables do not have any direct physical relationship with species occurrence, they were able to provide valuable indirect information about species distribution. The variables contributing most to the predictive power of the distribution models of *R. alpina* were beech coverage (real and potential), forest coverage, SPI, slope and elevation.

It seems obvious that variables regarding total tree cover and host tree coverage are among the most important variables that explain the potential distribution *of R. alpina*. However, slope and SPI offer additional important predictive power. The latter is highest along rivers and on the lower slopes of steep mountains, especially when slopes are strongly grooved by streams. *R. alpina* is known to be a xerothermophilic saproxylic species and prefers elevations between 700 and 900 m a.s.l. Snags of beech on steep slopes therefore offer suitable habitats, as the canopy of the surrounding living trees does not completely shade the snags. Moreover, the reduced accessibility of steep slopes and the rough terrain hampers the harvesting of wood in general. Consequently, steep slopes have always been under less harvesting pressure even during intensive forest management in the past. In the second part of the nineteen century, Swiss foresters were reluctant to conduct large-scale clear cutting in steep terrain, partly because they feared it could cause devastating erosion (Bürgi and Schuler 2003). Wood-piles in mountainous regions are often installed along forest roads in the vicinity of rivers at the bottom of the valley. The high contribution of the SPI might have something to do with the attractiveness of wood-piles for *R. alpina.* This observation may highlight the detrimental effect of such piles as ecological traps for saproxylic species. However, observations might also be biased towards such locations as they are more accessible, which could lead to more intense sampling on valley floors. If this were the case, however, the TPI would have been expected to have relatively greater significance, whereas it was, in fact, rather low.

The *Rosalia* populations identified before and after 1950 at a national level (Fig. 4) showed that this species occurred in most suitable parts of the country prior to 1950, and it still does inhabit them today. This can be considered a positive fact as many *Rosalia*-populations are known to have disappeared regionally across Europe. A new population even appeared in the western Jura (see Fig. 4, region 2), where no records of *R. alpina* were previously known. However, considering the isolation of this population, a new colonisation from the nearest populations is unlikely. Rather, this small population had probably been overlooked. One record of *R. alpina* prior to 1950 from the city centre of Geneva (West-Switzerland) remained the single observation site that was not repeated in its vicinity after 1950. However, this single observation might be due to fuel-wood import rather than to the extinction of a population. The increase in the area of the distribution polygons observed at the regional and national scale (Table 1) cannot be directly interpreted as an increase in the distribution area of *R. alpina* because of the large influence of single records in such analyses. However, *R. alpina* was observed in many forest stands after 1950 where it had not been known before, even though other Cerambycidae specimens were recorded prior to this date.

Conclusions

Due to its appearance, *R. alpina* has always appealed not only to entomologists, but also the wider public. This is why it has been featured on postal stamps in 12 countries (Duelli and Wermelinger 2010) and was declared "insect of the year 2001" in Austria (Gepp 2002). Furthermore, it has benefited from specific conservation programs on local and regional scales. Despite its popularity, historical records of its occurrence are very scarce. We found that combining species distribution modelling with relative sampling analysis was a good strategy to assess the species' long-term population development. The population increase observed in the past 50 years is a very positive sign for species conservation and nature protection in general. It shows that saproxylic species can recover from very low population levels under poor habitat conditions even if a habitat change is needed. However, the future intensification of fuel-wood production could again negatively impact the population of *R. alpina* unless adequate conservation measures are taken. These could involve setting-aside natural forest reserves, installing dead wood islands or restoring wooded pastures with scattered habitat trees. The *Rosalia* longicorn could then act as an umbrella species for other species that depend on old trees and dead wood.

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