Ecological requirements of the Alpine Salamander *Salamandra atra*: assessing the effects of current habitat structure and landscape dynamics on local distribution

Diplomarbeit
der Philosophisch-naturwissenschaftlichen Fakultät
der Universität Bern

vorgelegt von
Corina Geiger
2006

Leiter der Arbeit:
Dr. Benedikt Schmidt, Koordinationsstelle für Amphibien- und Reptilienschutz in der Schweiz
Prof. Raphael Arlettaz, Conservation Biology, Zoologisches Institut der Universität Bern

Table of contents

Abstract

Baseline information for the conservation of a species requires understanding how its populations are distributed and how distribution range will develop when landscape and land-use change. To improve knowledge about how such changes affect an endangered population of an endemic salamander species of the Alps, we evaluated the impact of habitat characteristics and dynamics on its distribution. A monitoring method was also tested in order to propose an efficient monitoring scheme. Four study plots (20.25 ha each) were selected along an altitudinal gradient in a side valley in the Bernese Alps. Three systematic surveys were carried out throughout the season to reveal salamander occurrence. Habitat types and features were mapped, and we checked for consistence with species occurrence using site occupancy models. Analysis of aerial pictures of the years 1960, 1975 and 1998 gave a historical perspective of the distribution pattern of habitat features and landscape evolution. Results showed that steady structures (like stabilised screes) had a positive effect on the presence of salamanders, as did pH and organic fertilisation. From a landscape dynamics viewpoint, the oldest landscape-pattern best explained the current distribution of salamanders. This suggests that *Salamandra atra* adapts its distribution pattern very slowly to habitat changes and may thus today occur in habitats which only marginally fulfill species ecological requirements. These results have implications for the development of sound habitat conservation policies. In particular it is essential to preserve rocky zones such as permanent screes, as well as boulders fields.

Keywords: Land-use-changes, site occupancy models, monitoring, *Salamandra atra*

1 Introduction

A central theme in ecology is to understand which factors govern the distribution of animals. Conservation biologists in particular are interested to know how anthropogenic land use and related habitat changes affect the distribution of rare and endangered species. In this aim they have first to design efficient monitoring programs to track changes in the distribution and abundance of species. This is an essential, basic component in any conservation programme. Second, Conservation biologists seek which factors are responsible for species distribution patterns (Bailey & Adams 2005). The challenge is often to find an appropriate set of habitat variables which best describe the distribution of the species (Pollock *et al.* 2002). Third, the historical dynamic of habitat alteration and its impact upon area of suitable habitat have to be recognised early enough given that the demography of a population reacts to environmental modifications with a given time lag. Alpine regions presently underlie dramatic landscape modifications especially regarding intensification of farming. We have to track these changes and to identify the consequences for the negatively affected species (Petranka *et al.* 1993, Findlay & Bourdages 2000). One crucial aspect in population monitoring refers to the detection of the species. One can never be certain that non detection reflects true absence rather than non detection (MacKenzie *et al.* 2003; Pellet & Schmidt 2005). Failing to account for imperfect detectability will thus result in underestimates of distribution, as well as biased estimates of local colonisation and extinction probabilities. This problem can be solved by working with an appropriate model that incorporates all factors in its calculations (MacKenzie *et al.* 2002, 2003). Several models can be created, each containing an other set of variables representing the needs and threats of the species under scope. It is useful to model species with habitat requirements applying also for other species, i. e. indicator, umbrella or flagship species. In this study we were dealing with an amphibian. Amphibians are among the most threatened animals with 32.5 % of species currently at risk (Stuart *et al.* 2004) and are declining worldwide (Heyer *et al.* 1994). Their widespread decline might have several causes, e. g. heavy extraction or significant habitat loss (Stuart *et al.* 2004). With a distribution strictly limited to the European Alps, the Alpine Salamander is a potentially vulnerable species. This is due in particular to the fact that landscape and climatic changes are especially acute in the mountainous ecosystems (Härtle *et al.* 2004). Moreover this salamander is long-lived, has a late maturity and low reproductive rate, which put it at risk. We checked how habitat features and changes thereof affect species distribution using both current and historic data on landscape structure and land-use (Meyer 2004). In addition, this allowed an assessment how slowly or rapidly the species responds to habitat changes.

For the purpose of the study we also developed a new monitoring method which accounts for imperfect detection.

The aims of this study were to investigate on the one hand, which factors explain the occurrence of salamanders best and how habitat changes can influence distribution pattern so as to draw first conservation guidelines. On the other hand, we developed a new method to monitor the species, checking how detection probability is influenced by habitat features vs environmental circumstances during field surveys.

2 Methods

2.1 Study area

The study was conducted in the Justistal (46° 43'N, 7° 46'E, 700 – 1600 m.a.s.l.), a valley located in the Bernese Oberland (Appendix 1). From a geological point of view this valley is situated at the northern border of a tectonic unit called the Helvetic Domain (Labhart 1992). This part of the unit consists of cliffy rocks and there is still plenty of screes and debris laying about (Labhart 1992). Study plots are characterised by high habitat heterogeneity, including different forest communities, meadows with different cultivation methods, pioneer sites and a huge diversity of small-scale structures like screes, rocks, boulders, etc.

The study was carried out at four different 450 x 450 m plots (Table 1). To be selected the plots had to fulfil a set of criteria that were defined a priori and are mostly related to the accessibility of the area: 1) ≥ 1/3 of the plot is covered by forest (such that there was a mixture of different habitat types); 2) fewer than 20 houses are present within the plot; 3) no 1st class road occurring (at least 6 m wide); 4) each plot is within 300 m distance from a recent record (from the year 2005)

To optimise the sampling design each plot was divided into four subplots consisting of 20 - 21 cells of 50 x 50 m each, which were grouped together; each series of 20 – 21 cells was monitored within one morning survey. This gave 81 cells for each plot and 324 cells for all four plots together (Fig. 1).

2.2 Sampling design

2.2.1 Salamander sampling

Presence/ absence of salamanders in a cell provided the basic dataset. In search for salamanders each of the 324 (0.25 ha)- cells was visited three times from August to September 2005, following transects that crossed systematically through cells. Transects orientation (N-S, E-W, W-E) was alternated between the three seasonal surveys (Fig. 1). A transect survey was accomplished within 3 to 8 h after dawn because *Salamandra atra* is mainly active at night and dawn (Brodmann-Kron & Grossenbacher 1994). The search began as soon as there was enough light to see salamanders with the naked eye. Body temperatures recorded in salamanders range from 2°C to 27°C (Stebbins & Cohen 1995).

When ambient temperature was 8 – 20° C and soil cover was humid, salamanders were potentially active and searching by sight was applied. If weather conditions were not favourable for surface activity, cover objects were turned to search for salamanders. Exact coordinates of salamander location were registered with GPS. We randomised in which order subplots were checked and in which corner of the subplot the search started (Fig. 1). Altogether we ran 972 transects (4 study plots x 81 cells x 3 seasonal transects each).

2.2.2 Habitat variables

Variables potentially explaining the occurrence (habitat features or site covariates) or detection (sampling covariates) of salamanders were collected either in the field, or were derived from the analysis of aerial pictures. Sampling covariates were collected during the visit to each transect. Such sampling covariates were: date of the visit, time of the day, sampling method (turning-cover or by sight), temperature, atmospheric humidity one cm above the soil, precipitation (no rain; drizzle; rain shower), wind (Beaufort scale; Appendix 2), cloud cover (Appendix 3) and length of transect. Site covariates were measured in the centre of each cell: altitude, exposition, inclination and soil pH. Other site covariates were mapped area-wide by locating their borders with GPS: type of meadow [meagre vs fat; defined according to Delarze (1998)], cultivation method (pasturing, mowing, fertilisation), clearcutting, forest association [according to Steiger (1995)]. Other habitat features consisted of screes [absent, instable, stabilised (allowing growth of a vegetation cover)], boulders (craggy, homogenous) and stone cairns (Fig. 2, Appendix 4). Information for cultivation variables were gained by asking local farmers. This allows us to define some cultivation methods more finely (grazing intensity; number of cuts per year; fertilisation type).

2.3 Analysis of landscape structure

Landscape dynamics was estimated on the basis of aerial pictures taken in 1960, 1975 and 1998 (Swisstopo, Wabern). Variables were mapped and digitised with ArcView GIS 3.3 (ESRI, California). We created three GIS maps, one map for each aerial picture. Each map shows the pattern of the landscape in the four plots in one of the three years. These landscape patterns consist of the variables forest, alpine pasture (above 1000 m. a. s. l., grazing only seasonal, no mowing), agricultural area (below 1000 m. a. s. l., mowing or intensive grazing), pioneer habitat (on the aerial picture as vegetation-free recognised region) and hedge (Appendices 5 – 7). Additionally we designed two GIS maps, one with current landscape structures and one with current land-use data, based on the variables whereof the borders were registered in the field with GPS (Appendices 8 – 9). The map showing current landscape structures contained the variables scree (absent, stabilised scree, instable), boulders (craggy or homogenous), boulders and stone cairns. The map showing current land-use patterns includes the variables forest association (Calamagrostion variae piceetum, fir-beech forest, Molinio pinetum, Milio fagetum), fat meadow, meagre meadow, clearcutting, hedge and undefined area.

Each of these five maps was rastered with a 50 x 50 m grid cell system. The resulting matrix consisted of presence/ absence data for each layer cell. Therewith we obtained two data sets: a current data set containing all variables registered in the year 2005 (Appendix 10); a historical data set containing all variables gathered from the aerial pictures for the years 1960, 1975 and 1998 respectively (Appendix 11).

2.4 Statistical analysis

Our main goal was to estimate the proportion of cells occupied by salamanders and to assess which factors affect cell occupancy. As many factors may affect the distribution and abundance of a species, we relied on modelling to assess factors explaining distribution and abundance. Models, by definition, are approximations of an unknown reality (Burnham & Anderson 2001). Even so one should try to keep models precise enough. Models with too few parameters have biases, whereas models with too many parameters may have poor precision or tend to identify effects that are in fact spurious (Burnham & Anderson 2001). A big challenge is to know whether the differences between parameters are large enough to justify inclusion in a model aimed at further inference (e.g. prediction). This is a classical model-selection problem (Burnham & Anderson 2001).

Data analysis was conducted with the computer software PRESENCE (www.proteus.co.nz/software.html#PRESENCE). This program implements the site occupancy models described by MacKenzie *et al.* (2002). The idea is that proportion of sites occupied can be estimated even if detection probability is less than one. Site occupancy models can be used to model species distribution even when detection is imperfect. In this approach, both site occupancy and the detection process are modelled.

Detectability may vary with site characteristics (like deep cracks within rocks) or survey conditions (weather), whereas occupancy relates only to site characteristics (Bailey & Adams 2005). These two kinds of variation are incorporated when estimating the proportion of sites occupied by a species. A detection history is used which contains 0s when the species was not detected and 1s when the species was observed. For example, the probability for site *i* with detection history 01010 would be

$$\psi_i(1-p_{i1})p_{i2}(1-p_{i3})p_{i4}(1-p_{i5})$$

where Ψ_i is the probability that a species is present in cell *i* and p_{it} the probability that a species will be detected in cell *i* at time *t*, given presence. Such terms are calculated for each cell, assuming independence of all cells. The product of all those terms gives the model likelihood for the observed data. When presence (Ψ_i) and detection (p_i) probabilities are constant across monitoring cells, the combined model likelihood can be written as

$$L(\psi,p)=\left[\psi^n\prod_{t=1}^{T}p_t^{n_t}(1-p_t)^{n-n_t}\right]\times\left[\psi\prod_{t=1}^{T}(1-p_t)+(1-\psi)\right]^{N-n}$$

where N is the total number of surveyed cells; T the number of distinct sampling occasions; n_t the number of sites where salamanders were detected at time *t* and n the total number of sites at which salamanders were detected at least once. Standard error of ψ is calculated using a nonparametric bootstrap method (MacKenzie *et al.* 2002).

What now remains to do is the incorporation of covariates in the model which potentially could explain a special distribution pattern. Such covariates like habitat type or weather conditions can be introduced into a model using a logistic regression model for Ψ and/ or *p*. Because by definition Ψ doesn't change over time during the sampling period, covariates with an influence on Ψ (i. e. site covariates) don't either. However, covariates for detection probability (i. e. sampling covariates) vary with time but are site-specific (e.g. humidity). Finally a model can be phrased like

Ψ(any site covariate) p(any sampling covariate).

Different models can then be compared using Akaike's information criterion (AIC, see Burnham and Anderson 2001), with

$$AIC=-2\log(L(\psi,p)+2K).$$

It is convenient to normalise these values such that they sum to 1 (Anderson *et al.* 2000):

$$\omega_i = \frac{\exp\left(-\frac{1}{2}\Delta AIC_i\right)}{\sum \exp\left(-\frac{1}{2}\Delta AIC_i\right)}$$

ΔAIC is then calculated as

$$\Delta AIC_i = AIC_i - AIC_{\min}$$

AIC_{min} is the lowest AIC-value obtained among all candidate models, i.e. it represents the best model fit. We selected models in two steps: 1) Searching covariates that describe *p* best (sampling covariates) without including any site covariate beside intercept. 2) Finding the best site covariates (that describe Ψ best) while including only the best sampling covariates in the model. Model selection was conducted with the two different data sets mentioned above (the current data set and the historical data set) (Appendices 10 and 11).

Last, the effects of the selected covariates on Ψ or p were visualised by plotting Ψ or p against the covariate. To do so, means of scores of each covariate (x_c) were multiplied with slopes of the covariate (c) . With that Ψ or p were calculated:

$$\psi, p = \frac{\exp\left(\text{int} + \sum x_c \times slope(c)\right)}{\left(1 + \exp\left(\text{int} + \sum x_c \times slope(c)\right)\right)}$$

This served as values for the y-axis while the x-axis was represented by the scores of the covariate of interest.

3 Results

The search for salamanders gave a patchily pattern of distribution (Fig. 3 and Appendix 12). *Salamandra atra* was detected in all plots but in plot A.

3.1 Habitat features

As regards current salamander distribution the five best models are listed in Table 2. However, the first three models had to be discounted because some variables had too large variances (these models and variables are depicted with asterisk). The best resulting explanatory model included inclination, pH, fertilisation, forest, stabilised scree for Ψ; temperature, sampling method, humidity, wind and date for p.

The direction of the effect of these variables (positive or negative) on probability of occurrence Ψ is shown in Table 3. Stabilised scree, forest, inclination, pH and fertilisation all influence the occurrence probability within a cell. All other variables were not included in the best model describing site occupancy (Ψ) (meadow- and forest types, grazing, mowing, clearcutting, altitude, exposition, instable scree, absence of scree, stone cairns, homogenous boulders and craggy boulders).

3.2 Effects of landscape changes on distribution

Landscape changes between 1960 and 1998 indicate a progressive disappearance of farmland (alpine pastures and meadows disappeared in 13 grid cells, while farmland arose in only one cell (Fig. 4). In contrast, pioneer habitat (identified as vegetation-free areas) arose in 22 cells and disappeared in 8 cells. Forested areas (woodland, hedges) arose in 21 cells and disappeared in 19 cells (see also Appendices 5 – 7).

Landscape-patterns of the year 1960 turned out to fit the actual pattern of occurrence of salamanders best, whereas models with landscape-patterns of the year 1975 had less explanatory power (Table 4). Finally, 1998 had no effect on the actual occurrence of salamanders (Akaike weight close to zero). The “age” of a variable had also a strong effect on species occurrence (Table 4). Considering the slopes of the best model (top of Table 4), it turns out that the older the age of a pioneer site, the higher the probability that salamanders occur, whilst the older a forest is, the lower is the probability of occurrence (Table 5).

3.3 Impacts on detection probability

The variables temperature, sampling method, humidity, wind and date of the visit to the cell explained the detection probability (p) best (Table 6). The slopes of these 2 models (Table 7) show first that the sampling method had a positive effect on detection probability (p), which means that salamanders were more easily detected in a cell when cover items were turned. Humidity affected detectability positively. Temperature had a negative effect, with higher detection probability at low temperatures. Surprisingly wind had a positive effect and date a negative one (fewer salamanders late in the season). Cloud cover, precipitation and length of transects had no effect on detection probability, they were thus not included in the best model. Finally site characteristics (i.e. craggy boulders, which have a negative impact) influence detection probability (Tables 8 and 9.).

4 Discussion

4.1 Detection probability

Monitoring a species reliably requires standardised norms. Thus, factors influencing detection probability must be recognised. In the present study turning cover items during the search significantly altered detection probability, enhancing it under any weather circumstances. Additionally, censuses should be conducted in June – August, the main activity period (Günther 1996). Detection probability also depends on atmospheric humidity at ground level. Günther (1996) found that Alpine Salamanders retreat into places deeper in the soil during dry periods and are then difficult to detect. Checking soil cover humidity would be wise before deciding whether a census can be conducted. Craggy boulders affect detection probability negatively whilst they exert no effect on occurrence probability. The problem with this variable is that cracks are very deep and complex, offering lots of hidden refuges. The fact that craggy boulders don't affect probability of occurrence could thus be a consequence of lack of detectability and not of an actual absence.

4.2 Monitoring abundance based on a small-scale monitoring

A very large part of the global distribution range of the Alpine Salamander is within Switzerland. Therefore, Switzerland has a responsibility for the conservation of this species. Population monitoring is a first step in the development of any conservation policy. Our study provides first guidelines for a monitoring scheme: small-scale distribution censuses could be used as a surrogate for monitoring abundance (MacKenzie & Nichols 2004). However, given the patchy distribution of the species at the landscape level (3 of 4 plots revealed salamanders in this study), areas with proven occurrence should be selected for establishing a suitable monitoring network. Regular censuses within such a network would provide the necessary basic information with regards to population demographic trends.

4.3 Habitat features and salamander occurrence

Our systematic censuses revealed that *Salamandra atra* is patchily distributed in the study area, both at a larger scale (we detected no salamanders in one of four plots) and at a smaller scale (i.e. within plots). Multiple factors affect the distribution in different ways. This study establishes first that the availability of stabilised screes affect the occurrence of the Alpine Salamander positively. This agrees with statements by Günther (1996) who found large populations in stabilised screes whilst instable screes were avoided because unsafe refuges with moving stones may cause mortality. Second, Alpine Salamanders are more likely to occur at places with high soil pH values. This may be explained by the fact that acidic environments are problematic for salamanders (Sugalski & Claussen 1997; Wyman & Hawksleylescault 1987). It could also explain a preference for deciduous forests (high soil pH) noted by Steiger (1995) against coniferous forests (low soil pH); (Brodman-Kron & Grossenbacher 1994). Interestingly the distribution of *Salamandra atra* in the Alps coincides with that of alkaline limestone substrates (Günther 1996). Third, grazing and mowing don't affect the probability of occurrence. Natural organic fertilisation influences the occurrence, which might reflect the fact that fat meadows are generally more humid than meagre meadows, thus providing better conditions for salamanders. The contribution of forest is unexpected given that the distribution of *Salamandra atra* is often found above the timber line in the Alps. Actually, this is a bias since among the 104 cells including stabilised screes, 94 (90%) were in woody habitats.

4.4 Landscape dynamics and distribution

Alpine Salamanders show a strong fidelity to a limited area of a few square metres not only during one season but also from year to year (Bonato & Fracasso 2003). Hence, adaptation to spatial changes of the landscape is likely to be a lengthy process in this species (Knapp *et al.* 2003). Our results confirm this since the older a favourite habitat type, the better it matches the current distribution. A logical consequence thereof is that long-term changes in the landscape (1960 – 1998) have a limited effect on the probability of occurrence. We speculate that a population of *Salamandra atra* would need several decades if not more to adapt its distribution area to a new landscape mosaic (see Herbeck 1999; Knapp *et al.* 2003). This is also partly due to the fact that Alpine Salamanders have an extremely slow generation turnover (Günther 1996). Ageing of forest had a negative impact in general. This might be due to the fact that forests in the study area consisted mostly of coniferous trees whose litter decomposes very slowly and accumulates as acidic layer on the ground (Härtle *et al.* 2004). Litter accumulation within screes and among boulders could also contribute to rendering the habitat unsuitable to salamanders because of a reduced amount of refuges.

4.5 Relevance for conservation

With its very slow generation turnover the Alpine Salamander needs several decades for adaptation to new landscape patterns. The permanency of a habitat has thus to be considered evaluating the quality of a salamander habitat. We showed that old pioneer habitats fulfil the requirements of salamanders better than new ones while coniferous forests are less occupied the older they are. Additionally the availability of permanent structures which offer safe refuges is apparently an important factor for the occurrence of *Salamandra atra*. Pooled together, the Alpine Salamander might thus be threatened by strong landscape dynamics as it is done by clearcutting, ground levelling for ski slopes or by removal of stones and other structures on alpine pastures. We suggest to preserve rocky zones and permanent boulder fields with a scanty vegetation cover for the conservation of this species.

Acknowledgements

Special thanks go to my co-supervisor Dr. Benedikt Schmidt who supported me with lots of experience, motivation, humour and a huge amount of patience. I am also grateful to Prof. Dr. Raphaël Arlettaz for giving me the opportunity to do this diploma work in the division of Conservation Biology, for his comments on my thesis and for assessing it. Many thanks go to Mungga and Sabine of the alp “Chlins Mittelbärgli” who invited me spontaneously to live with them on the alp, who shared everything with me and who introduced me to the real life in the Justistal. I also thank all cultivators of the Justistal who so nice informed me about their cultivation methods. KARCH for the financial support of my diploma work. Further thanks go to Andi Meyer for providing me with orthofotos and digital maps and for offering help in any case. To Severin Erni for introducing me to the analysis of the aerial pictures and for intending to provide me with his data. I also thank Veronique Helfer for introducing me to the practical work with salamanders. Gerold Knauer and the team of the ‘Amt für Wald des Kantons Bern’ for helping me to define the forest communities. The community of Sigriswil which gave the permission for doing fieldwork in the Justistal. Melanie, Chris and Susanne is thanked for the pleasured time in the office. I am very grateful to my parents having so much interest in my work and for their believe in me. I especially thank my sister Anina finding always time for a cup of coffee during my tired field-free days, for her open ears and encouragement. Not to forget my closest friends Carmen, Tinu and Irene for the motivation and their interest in my wellgoing and Tinu also for offering me help if sites were not really accessible. Last but not least I thank Martin for making a hard job easy.

References

Anderson, D. R., K. P. Burnham, W. L. Thompson. 2000. Null Hypothesis testing: problems, prevalence, and an alternative. Wildlife Management. 64(4):2000.

Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research. 28:111-119.

Bailey, L., M. Adams. 2005. Occupancy models to Study Wildlife. Fact Sheet 2005-3096.

Beebee, T. J. C. 1996. Ecology and Conservation of Amphibians. Chapman & Hall.

Bonato, L., G. Fracasso. 2003. Movements, distribution pattern and density in a population of Salamandra atra aurorae (Caudata : Salamandridae). Amphibia-Reptilia. 24(3):251-260.

Brodmann-Kron, P., and K. Grossenbacher.1994. Unsere Amphibien. Naturhistorisches Museum Basel. p 28.

Burnham, K. P., and D. R. Anderson. 2001. Kullback-Leibler information as a basis for strong inference in ecological studies. Wildlife Research. 28:111-119.

Delarze, R. 1998. Guide des milieux naturels de suisse. CSCF, BUWAL, pro natura, delachaux et niestlé.

Erni, S. 2004. Landschaftswandel in Lebensräumen der Aspisviper *Vipera aspis* (LINNAEUS 1758), im östlichen Berner Oberland seit dem ausgehenden 19. Jahrhundert. pp. 93-114. Diplomarbeit Universität Bern.

Findlay, C. S., J. Bourdages. 2000. Response time of wetland biodiversity to road construction on adjacent lands. Conservation Biology. 14:86-94.

Grossenbacher, K. 1988. Verbreitungsatlas der Amphibien der Schweiz. Documenta faunistica helvetiae 7: 1-207.

Günther, R., and K. Grossenbacher. 1996. Alpensalamander – *Salamandra atra* LAURENTI 1768. Jena: Gustav Fischer Verlag. pp 70-81.

Härtle, W., J. Ewald and N. Hölzel: 2004. Wälder des Tieflandes und der Mittelgebirge. Eugen Ulmer GmbH & Co. p 79.

Herbeck, L.A., D. R. Larsen. 1999. Plethodontid salamander response to silvicultural practices in Missouri Ozark forests. Conservation Biology. 13(3):623-632

Heyer, W. R., M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, and M. S. Foster. 1994. Measuring and monitoring biological diversity: standard methods for amphibians. Smithonian Institution Press, Washington D. C., USA.

Jeanneret, F. 1998. Jahreszeitliche Temperatur/ Jahreszeitliche Niederschläge. C. Pfister, H.- R.: Historisch- Statistischer Atlas des Kantons Bern, pp. 22-25. Bern: Historischer Verein des Kantons Bern.

Knapp, S. M, C. A. Haas, D. N. Harpole et al. 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conservation Biology. 17(3):752-762

Labhart, T. 1992. Geologie der Schweiz. Thun: Ott Verlag. p211.

Lauber, A. 2004. Methodenevaluation zum Monitoring der Alpensalamanderpopulation. Diplomarbeit, ETH Zürich, Schweiz.

MacKenzie, D. I. and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461-467.

Mac Kenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248-2255.

Mac Kenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonisation, and local extinction when a species is detected imperfectly. Ecology. 84(8):2200-2207

Meyer, A. 2004. Landschaftswandel in Lebensräumen der Aspisviper, *Vipera aspis* (LINNAEUS 1758), des östlichen Berner Oberlandes seit dem ausgehenden 19. Jahrhundert. Pages 153-164. Diplomarbeit Universität Bern.

Pellet, J., and B. R. Schmidt. 2005. Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. Biological Conservation. 123:27-35

Petranka, J. W., M. E. Eldrige, K. E. Haley. 1993. Effects of timber harvesting on southern appalachian salamanders. Conservation Biology. 7(2):363-377

Pollock, K. H., J. D. Nichols, T. R. Simons, G. L. Farnsworth, L. L. Bailey, and J. R. Sauer. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. Environmetrics. 13:105-119

Stebbins, R. C., and N. W. Cohen. 1995. A natural history of amphibians. Princeton University Press.

Steiger, P. 1995. Wälder der Schweiz. Ott Verlag.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, R. W. Waller. 2004. Status and Trends of Amphibian Declines and Extinctions Worldwide. Science. 306:1783-1786.

Sugalski, M. T. and D. L. Claussen. 1997. Preference for soil moisture, soil pH, and light intensity by the salamander, Plethodon cinereus. Journal of Herpetology. 31(2):245-250.

Wyman, R. L. and D. S. Hawksleylescault. 1987. Soil acidity affects distribution, behaviour, and physiology of the salamander *Plethodon-cinereus*. Ecology. 68(6):1819-1827.

Tables

Table 1. Frequency of occurrence of variables (numbers of 50 x 50 m cells) in the four study plots (A – D).

Variable	**A**	**B**	**C**	**D**	**total area**
Altitude (average of m. a. s. l.)	813	1216	1401	1392	1206
Inclination (average of %)	37	25	33	28	31
pH (average)	6.6	6.3	7.1	6.3	6.6
Exposition (average of deflection from N)	220	150	146	140	164
Fat meadow	9	25	10	63	107
Meagre meadow	3	0	0	0	3
Pasturing	19	28	10	63	120
Mowing	3	0	0	0	3
Fertilisation	0	29	10	63	102
Fir- beech- forest	0	65	58	38	161
Calamagrostio variae piceetum	0	0	21	16	37
Milio fagetum	78	0	0	0	78
Molinio pinetum	4	0	0	0	4
No forest	30	30	38	72	170
Clearcutting	6	0	28	0	34
Instable scree	6	5	15	9	35
Stabilised scree	3	4	66	37	110
Scree absent	80	34	63	44	221
Stone cairns	0	0	0	44	44
Homogenous boulders	0	27	0	0	27
Craggy boulders	0	58	10	0	68
Forest in 1998	78	63	77	42	260
Alpine pasture in 1998	0	29	9	59	97
Agricultural area in 1998	12	0	0	0	12
Pioneer habitat in 1998	0	0	20	21	41
Hedge in 1998	7	3	0	0	10
Forest in 1975	75	66	75	37	253
Alpine pasture in 1975	0	29	13	63	105
Agricultural area in 1975	14	0	0	0	14
Pioneer habitat in 1975	0	0	21	22	43
Hedge in 1975	14	0	0	0	14
Forest in 1960	78	67	77	36	258
Alpine pasture in 1960	0	28	12	64	104
Agricultural area in 1960	16	0	0	0	16
Pioneer habitat in 1960	0	0	20	7	27
Hedge in 1960	11	0	0	0	11
Changes of landscape (1960 – 1998)	26	7	25	29	87
Change of forest between 1960 and 1975	-3	-1	-2	1	-5
Change of alpine pasture between 1960 and 1975	0	1	1	-1	1
Change of pioneer habitat between 1960 and 1975	0	0	1	15	16
Change of forest between 1975 and 1998	3	-3	2	5	7
Change of alpine pasture between 1975 and 1998	0	0	-4	-4	-8
Change of pioneer habitat between 1975 and 1998	0	0	-1	-1	-2

Table 2. Model ranking for site covariates considering the current data set. Best models always include the variables temperature, sampling method, humidity, wind, date [as regards p detectability (p(sc))]. Models with * incorporate one or repeated variables with a high standard error of the slopes and were estimated unreliable. AIC: Akaike's information criterion; ΔAIC: difference between AIC of the best model and the AIC of the respective model; w: Akaike weight; ψ: proportion of sites occupied; SE(ψ): standard error of ψ; K: total number of variables in the model sampling covariates (sc) included.

model	**AIC**	**ΔAIC**	**w**	**ψ**	**SE(ψ)**	**K**
*ψ(Inclination, pH, fertilisation, *calamagrostio variae piceetum, forest, instable scree, stabilised scree, *homogenous boulders) p(sc)	340.93	0.00	0.5314	0.2310	0.0242	13
*ψ(Inclination, pH, fertilisation, *calamagrostio variae piceetum, forest, stabilised scree, *homogenous boulders) p(sc)	341.28	4.25	0.4461	0.2482	0.0291	12
*ψ(Inclination, pH, fertilisation, forest, instable scree, stabilised scree, *homogenous boulders) p(sc)	348.21	8.96	0.0139	0.2432	0.0259	12
Ψ(Inclination, pH, fertilisation, forest, stabilised scree) p(sc)	349.20	14.75	0.0085	0.2657	0.0317	10
Ψ(inclination, pH, forest, instable scree, stabilised scree) p(sc)	357.93	12.17	0.0001	0.2589	0.0308	10

Table 3. The contribution of site covariates to ψ are given by the slopes of variables fitted to the best retained model (see Table 2). SE (slope): standard error of the slope.

Site covariate (ψ)	Slope	SE (slope)
stabilised scree	3.0425	0.5562
forest	1.5011	0.6575
inclination	8.7593	4.3037
pH	15.1166	4.8434
fertilisation	2.0893	0.7006

Table 4. Ranking of models with variables expressing landscape features at different time periods (1960, 1975, 1998) as well as landscape changes. Sampling covariates (temperature, sampling method, wind and date) were fixed in all models [p(sc)] as they best explain the detection probability. Models with * indicate problematic variables, e.g. a very high standard error of the slope (see Table 5: pioneer habitat in 1960). Note the drop between the first ranked (w) and the subsequent models.

model	**AIC**	**ΔAIC**	**w**	**ψ**	**SE(ψ)**	**K**
Ψ(age-for, age-pion) p(sc)	377.71	0.00	0.9679	0.3269	0.0286	6
*ψ(for60, *pion60) p(sc)	386.73	9.02	0.0106	0.3648	0.0332	6
ψ(for75, pion75) p(sc)	387.03	9.32	0.0092	0.3371	0.0306	6
*ψ(for60, alp60, *pion60) p(sc)	388.03	10.32	0.0056	0.3800	0.0376	7
ψ(for75, alp75, pion75) p(sc)	388.95	11.24	0.0035	0.3312	0.0364	7
*ψ(for60, alp60, *agri60, *pion60) p(sc)	389.18	11.47	0.0031	0.3661	0.6531	8
*ψ(for75, alp75, *agri75, pion75) p(sc)	396.94	19.23	0.0001	0.3272	0.0364	8
ψ(for98, pion98) p(sc)	407.85	30.14	0.0000	0.3692	0.0380	6
ψ(for98,alp98, pion98) p(sc)	409.85	32.14	0.0000	0.3692	0.0380	7
*ψ(for98, alp98, *agri98, pion98) p(sc)	411.05	33.34	0.0000	0.5112	0.0054	8
ψ (ch-for75-98, ch-pion75-98) p(sc)	423.94	46.23	0.0000	0.3591	0.0420	6
ψ(ch-for75-98, ch-alp75-98, ch-pion75-98) p(sc)	427.55	49.84	0.0000	0.5169	0.0091	7
*ψ(*ch-for60-75,ch-pion60-75) p(sc)	428.12	50.41	0.0000	0.5098	0.0052	6
ψ(ch-for60-75, ch-alp60-75, ch-pion60-75) p(sc)	428.44	50.73	0.0000	0.5127	0.0082	7

Abbreviations work after the following pattern: age (age of the following variable); for (forest); pion (pioneer habitat); 60, 75, 98 indicate for which year applies the pattern of the variable; alp (alpine pasture); agri (agricultural area); ch (change of the following variable); 60-75 (time span for which the change of a variable applies).

Table 5. Slopes of variables contained in the first three models selected (Table 4). Note the direction of the slopes (+ vs -). The magnitude of the contribution cannot be deduced from the steepness of the slope. * indicates a high standard error of the slope.

Site covariate (ψ)	Slope	SE(slope)	Variable of the model
age of forest	-5.6746	0.9786	Ψ(agefor, agepion) p(sc)
age of pioneer habitat	16.6062	3.8206	Ψ(agefor, agepion) p(sc)
forest in 1960	-1.0825	0.2452	*ψ(for60, *pion60) p(sc)
*pioneer habitat in 1960	27.068	140835	*ψ(for60, *pion60) p(sc)
forest in 1975	-1.4774	0.5830	ψ(for75, pion75) p(sc)
pioneer habitat in 1975	2.9331	4.5469	ψ(for75, pion75) p(sc)

Table 6. Ranking of models with sampling covariates of the current data set. Ψ was held constant. Note the big difference in model fit between the two models (w).

model	**AIC**	**ΔAIC**	**w**	**ψ**	**SE(ψ)**	**K**
ψ(.) p(temp, method, humidity, wind, date)	411.31	0.00	0.9998	0.3944	0.0551	6
ψ(.) p(temp, method, humidity, wind, cloud)	428.33	17.02	0.0002	0.3696	0.0534	6

Table 7. The contribution of sampling covariates to p are given by the slopes of variables fitted to the best retained model (see Table 5).

Sampling covariate (ψ)	**Slope**	**SE(slope)**
method	3.0664	0.5911
humid	1.1247	0.7716
temp	-33.7177	4.6454
wind	4.3897	2.1769
date	-36.7558	8.4169

Table 8. Models showing that complex structures like deep cracks reduce detection probability p. In these models ψ was held constant (.). Note the increase of the AIC between the first two models (not including complex landscape structures) and the last one which includes cracks. * indicates variables with a high standard error of the slope (see Table 9).

model	**AIC**	**ΔAIC**	**w**	**ψ**	**SE(ψ)**	**K**
ψ(.) p(temp, method, humidity, wind, date)	411.31	0.00	0.9998	0.3944	0.0551	6
ψ(.) (temp, method, humidity, wind, cloud)	428.33	17.02	0.0002	0.3696	0.0534	6
*ψ(.) (*temp, method, humidity, wind, *date, cracks)	485.61	74.30	0.0000	0.2981	0.0419	7

Table 9. The contribution of sampling covariates to p are given by the slopes of variables fitted to the best retained model (see Table 7). The variable of interest is cracks which has a negative effect on detection probability and degrades the model (AIC gets higher when 'cracks' is included). * indicates variables with a high standard error of the slope.

Sampling covariate (ψ)	**Slope**	**SE(slope)**
method	1.9199	0.4507
humid	-1.0577	0.5899
*temp	-18.2488	1293.2306
wind	-3.4514	1.8397
*date	-18.2488	1293.2306
cracks	-1.4512	0.5756

Figure captions

Fig. 1. Schematic view of the sampling design applied in a study plot. Dashed lines indicate the 50 x 50 m grid. Arrows represent daily survey transects in the four subplots. The direction of transects was alternated between seasonal visits. The transect started in a randomly selected corner. See methods for more details.

Fig. 2. Habitat types recognised: (A) stabilised scree; (B) instable scree; (C) scree absent; (D) craggy boulders; (E) homogenous boulders; (F) stone cairn.

Fig. 3. The distribution of detected salamanders within the 4 study plots. Each white dot represents one record. Dashed lines figure the 50 x 50 m raster grid (81 cells per plot). Note the patchy distribution of the species along the gorges filled with screes.

Fig. 4. Landscape changes between 1960 and 1998 within the four study plots.

Figures

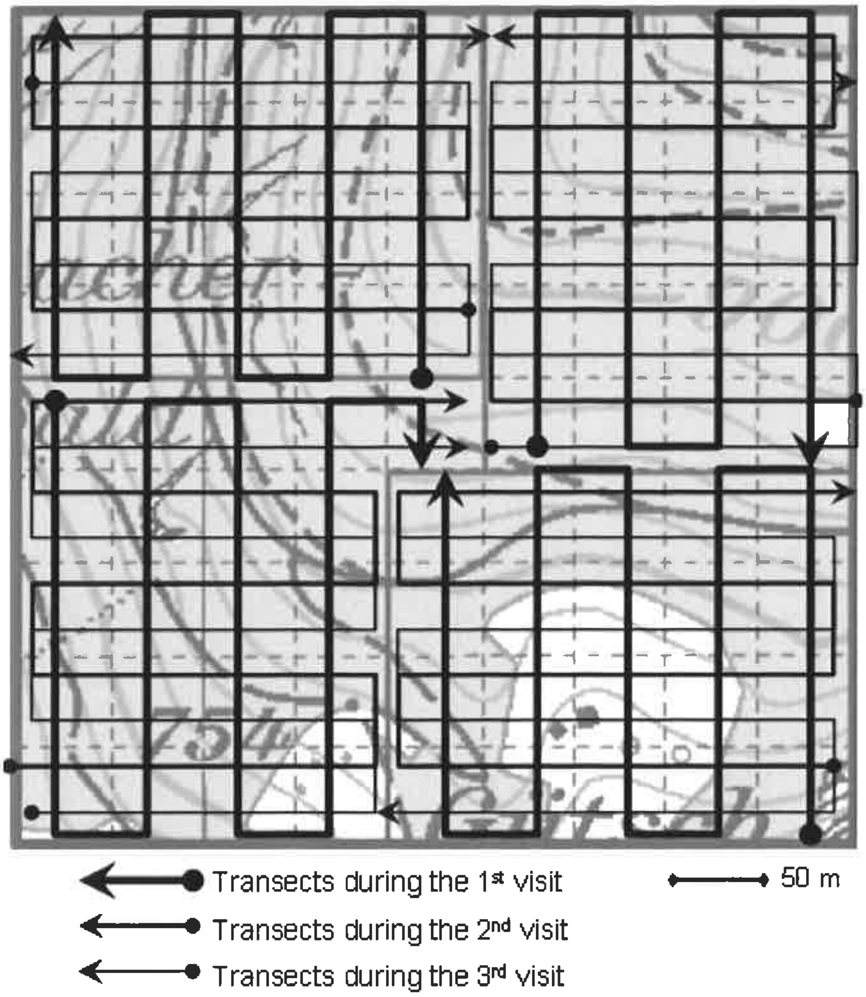


Fig. 1

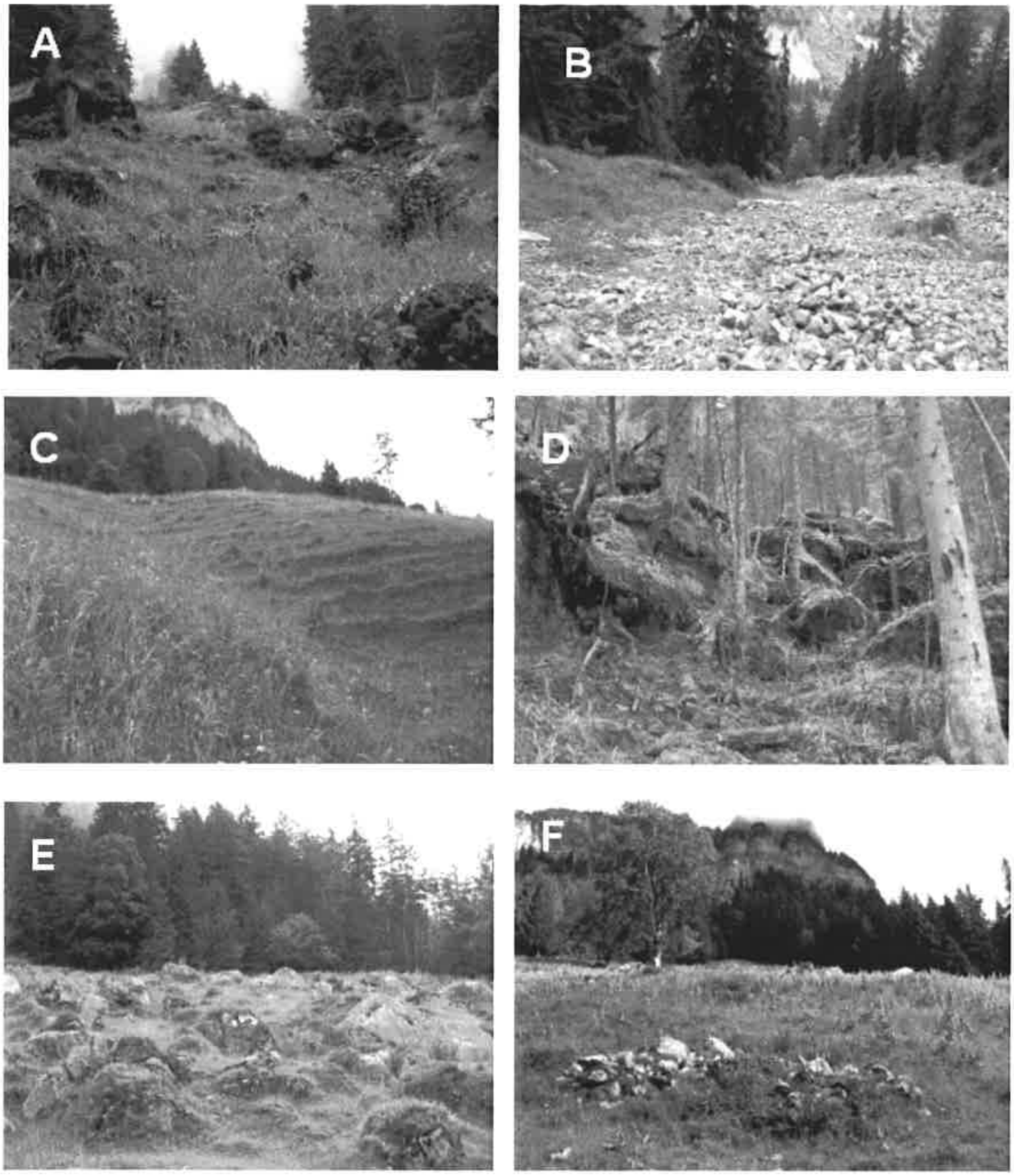


Fig. 2

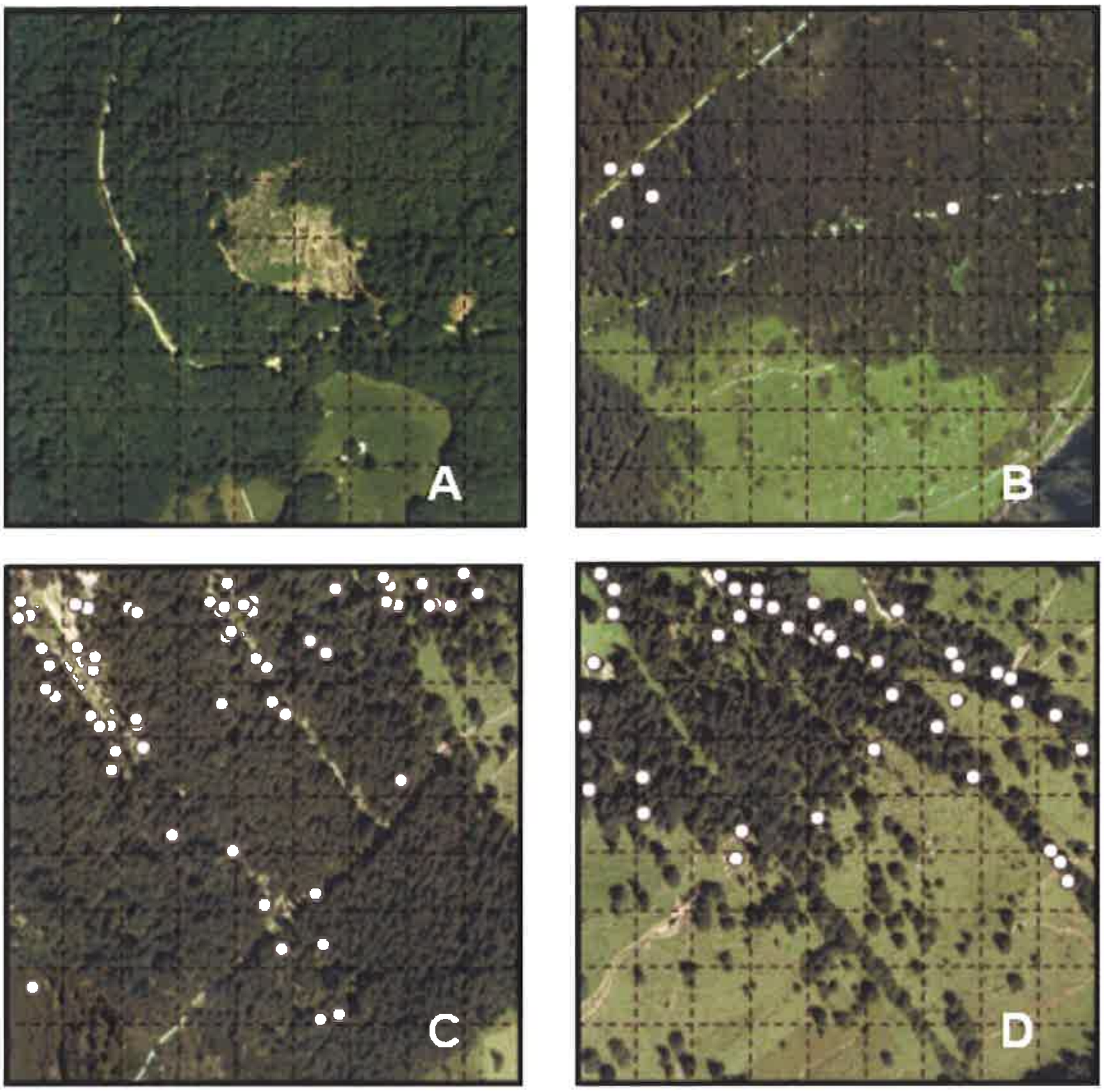


Fig. 3

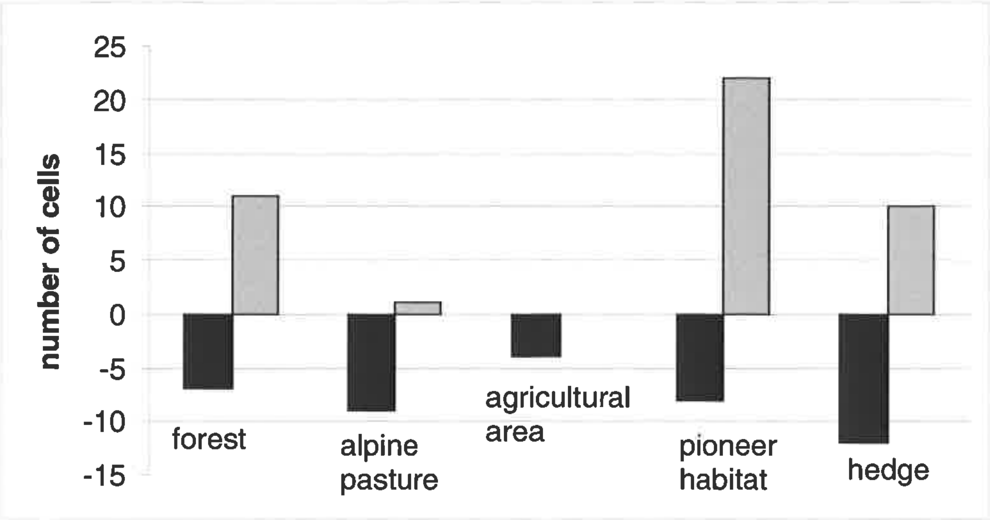
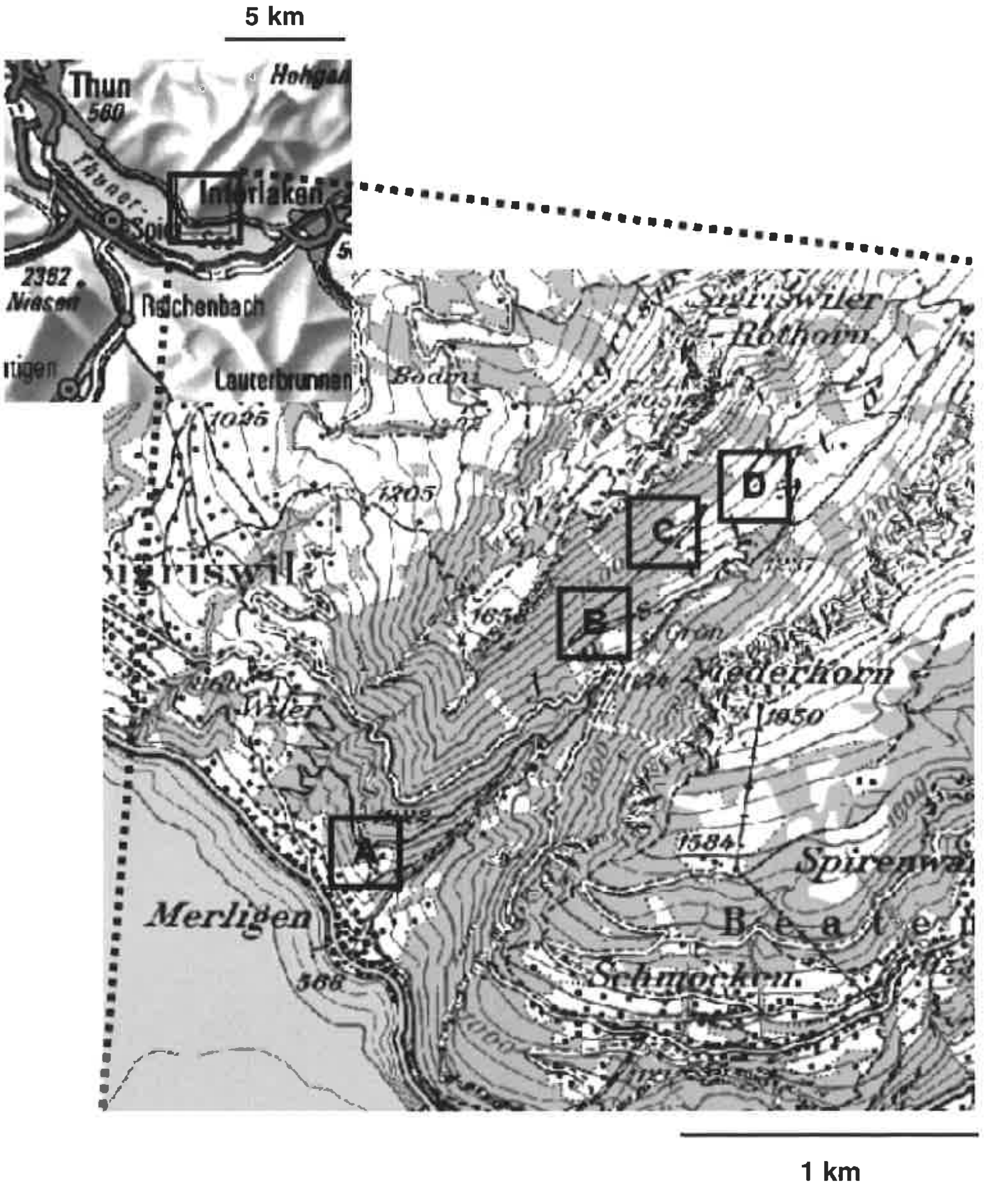

25
20
15
10
5
0
-5
-10
-15
number of cells
forest
alpine pasture
agricultural area
pioneer habitat
hedge

Fig. 4

Appendices



Appendix 1: Location of the four study plots (A – D). The small map shows the lake of Thun with the valley of interest at its north-eastern border. The larger map shows the location of the four plots.

Appendix 2: Beaufort scale

Force	mph[1]	Description	Specifications for use on land
0	Under 1	Calm	Calm; smoke rises vertical.
1	1-3	Light air	Direction of wind shown by smoke drift, but not by wind vanes.
2	4-7	Light Breeze	Wind felt on face; leaves rustle; ordinary vanes moved by wind.
3	8-12	Gentle Breeze	Leaves and small twigs in constant motion; wind extends light flag.
4	13-18	Moderate Breeze	Raises dust and loose paper; small branches are moved.
5	19-24	Fresh Breeze	Small trees in leaf begin to sway; crested wavelets form on inland waters.
6	25-31	Strong Breeze	Large branches in motion; whistling heard in telegraph wires; umbrellas used with difficulty.
7	32-38	Near Gale	Whole trees in motion; inconvenience felt when walking against the wind.
8	39-46	Gale	Breaks twigs off trees; generally impedes progress.
9	47-54	Severe Gale	Slight structural damage occurs (chimney-pots and slates removed).
10	55-63	Storm	Seldom experienced inland; trees uprooted; considerable structural damage occurs.
11	64-72	Violent Storm	Violent Storm Very rarely experienced; accompanied by wide-spread damage.
12	73 or higher	Hurricane	

1) miles per hour (10 m above ground)

Appendix 3: Cloud cover

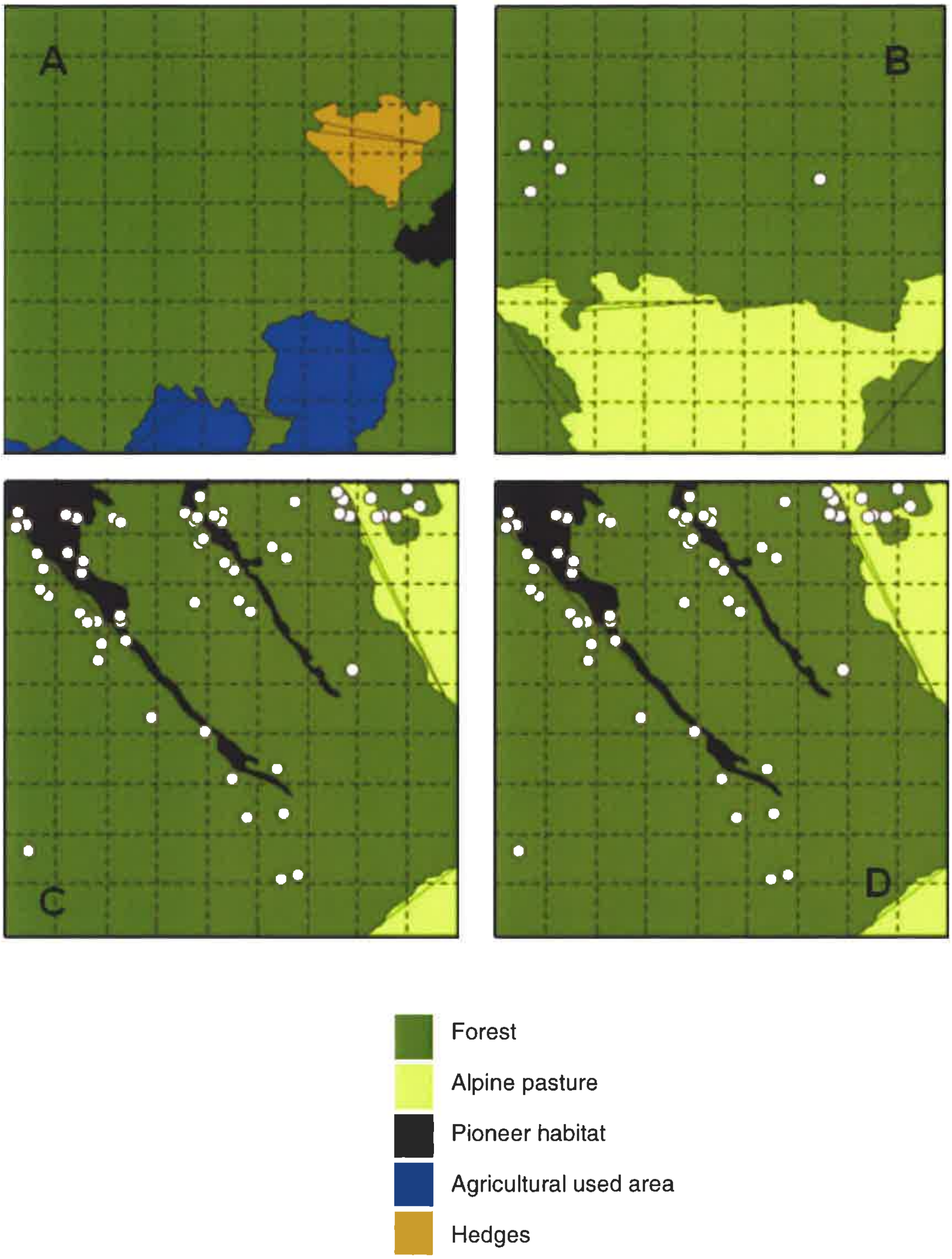
Since 1971 Meteoswiss measures cloud cover by splitting up the sky into 8 patches and counting how many patches are covered with clouds. I used only 6 different categories for this covariate:

Category	Cloud cover	Specifications
1	0/8	cloudless
2	1-2/8	bright
3	3/8	slightly clouded
4	4-6/8	clouded
5	7/8	strongly clouded
6	8/8	overcast

Appendix 4: Criteria for small-scale structures assignment.

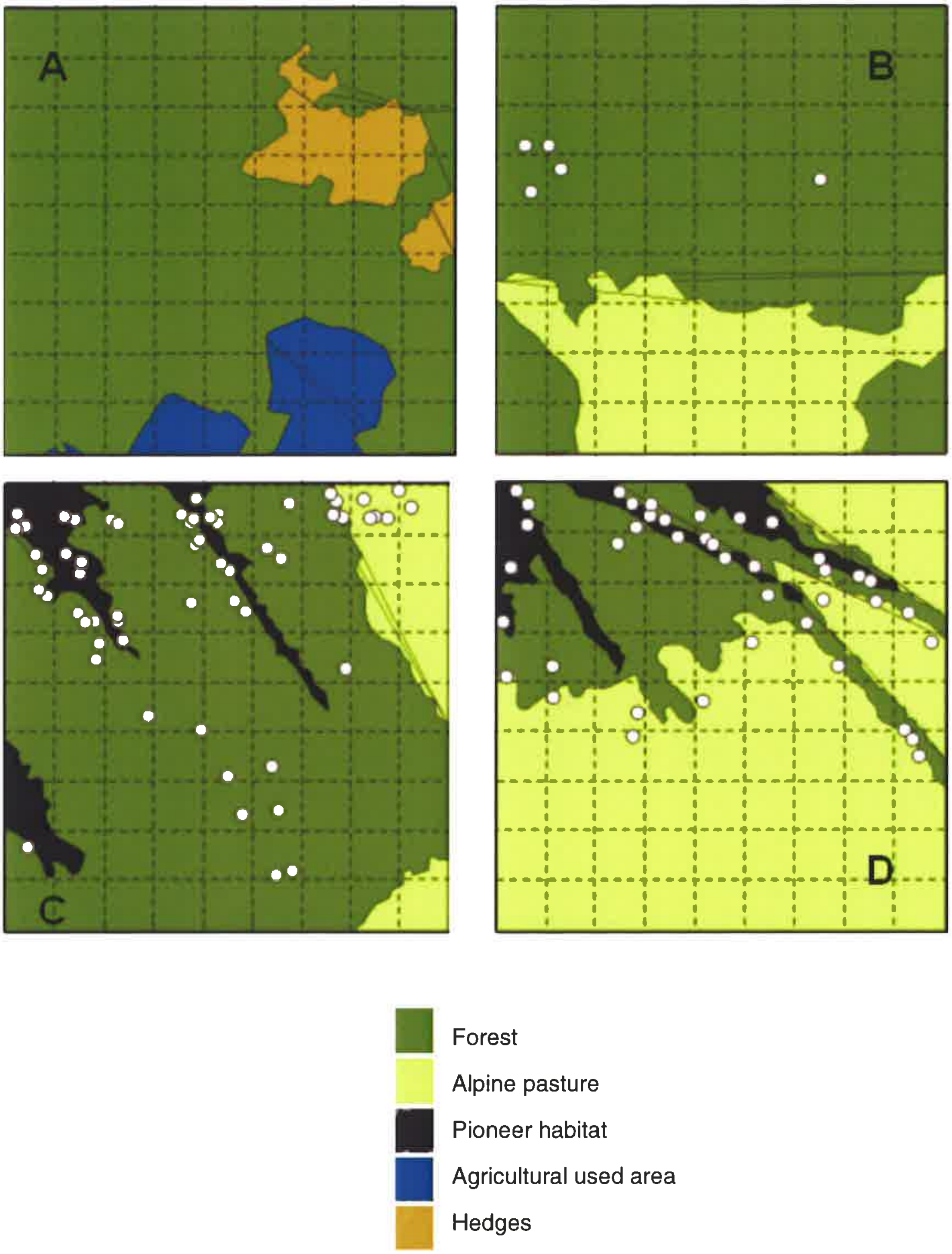
Variable	Criteria
Stabilised scree	- Stones don't move by walking on them. - > 2 stones can be reached with hands by a person resting at a place. - Half of the stones are small enough to move them by hand. - Visible cracks between stones and soil.
Instable scree	- > 2 stones can be reached with hands by a person resting at a place. - Stones move by walking on them.
Scree absent	- < 2 stones can be reached with hands by a person resting at a place.
Craggy boulders	- Boulders are too big to be moved by hand. - Visible cracks between boulders and soil. - < 5 foot steps between 2 boulders.
Homogenous boulders	- Boulders are too big to be moved by hand. - No visible cracks between boulders. - < 5 foot steps between 2 boulders.
Stone cairns	- > 1 stone cairn per cell.

1960



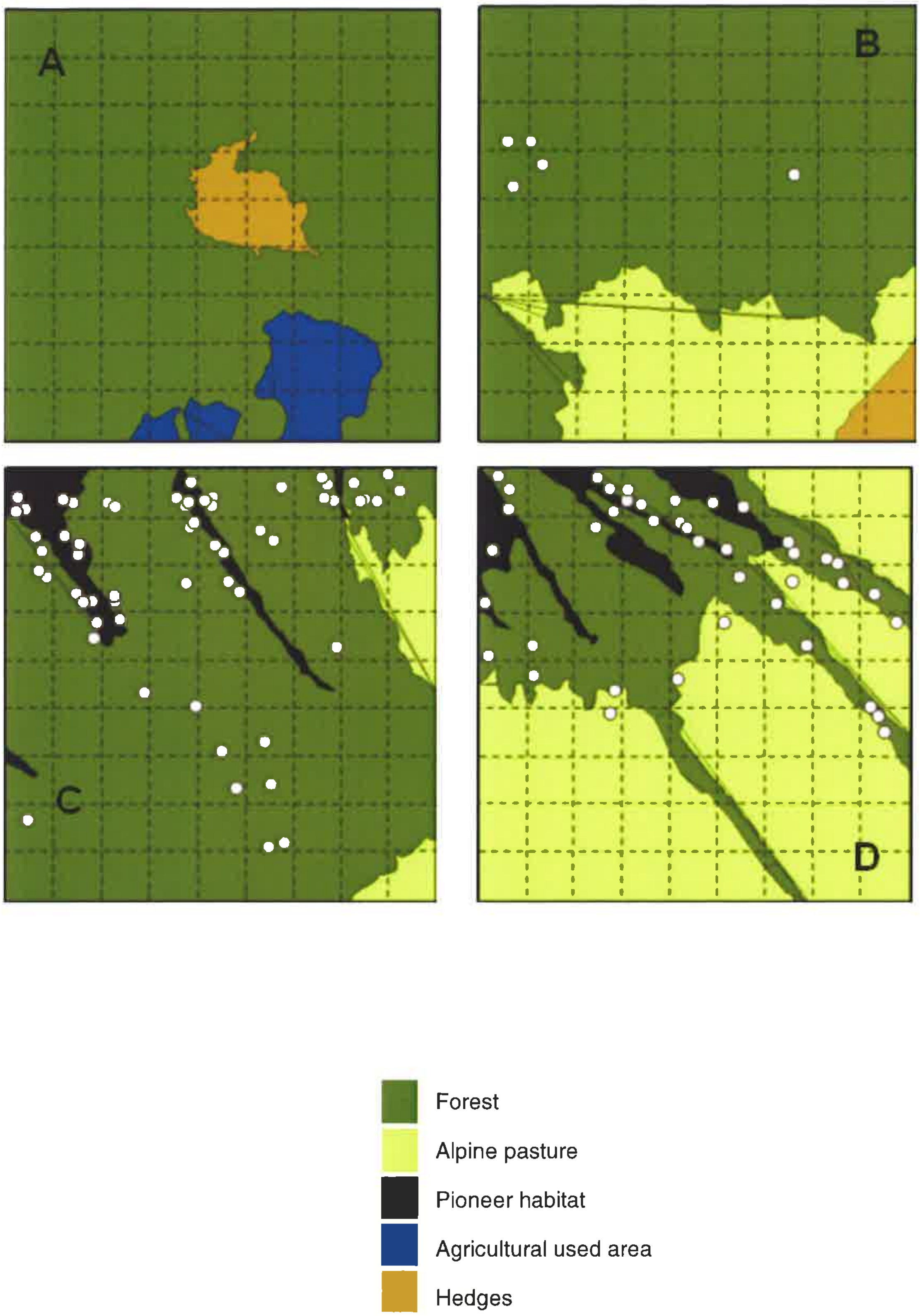
Appnedix 5: Habitat composition in the year 1960. This layer contains the variables forest, alpine pasture, agricultural area, pioneer site and hedge.

1975

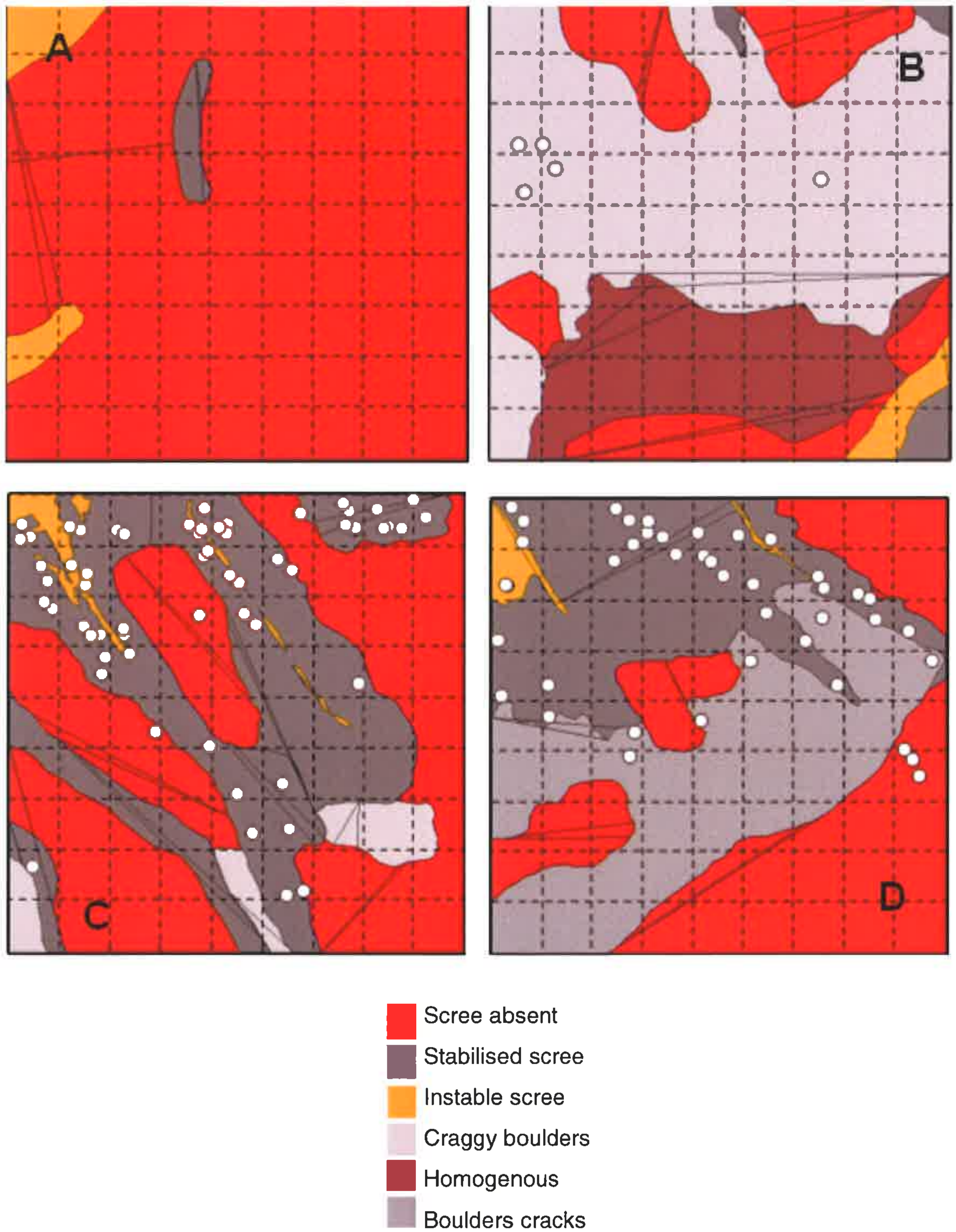


Appendix 6: Habitat composition in the year 1975.

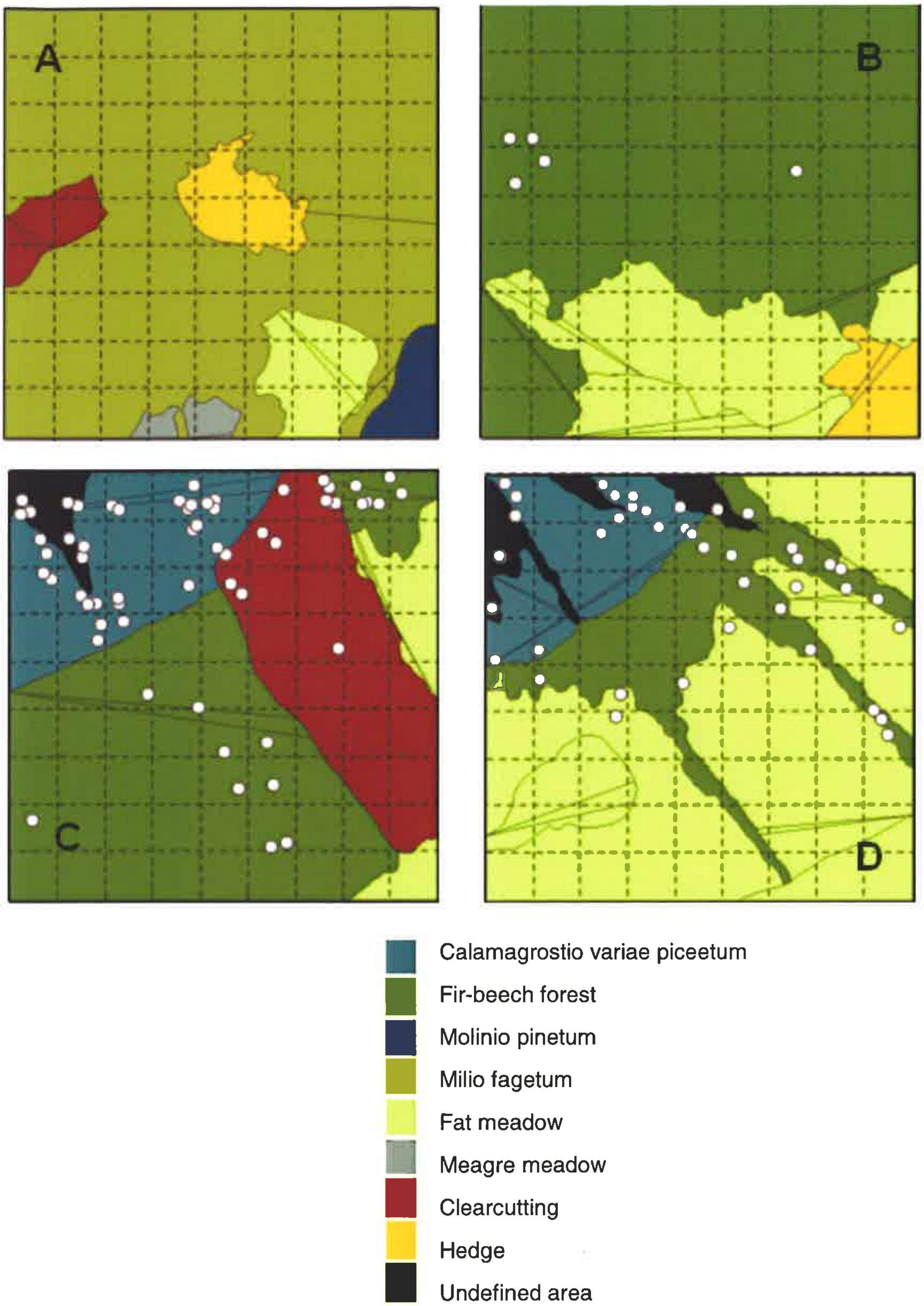
1998



Appendix 7: Habitat composition in the year 1998.



Appendix 8: Habitat composition in the four plots. The variables included in this layer describe structures of the soil.



Appendix 9: Habitat composition in the four study plots. This layer consists of variables registered in the year 2005. Each white dot represents a record.

Appendix 10: Variables used in the current data set

Site covariates (ψ)	measure	character
Altitude	m. a. s. l.	continuous
Inclination	%	continuous
pH	degree of acidity	continuous
Exposition	deflection from N in ° 1)	continuous
Fat meadow	0= no;1= yes	categorical
Meagre meadow	0= no;1= yes	categorical
Pasturing	0= no;1= yes	categorical
Mowing	0= no;1= yes	categorical
Fertilisation	0= no;1= yes	categorical
Fir- beech- forest	0= no;1= yes	categorical
Calamagrostio variae piceetum	0= no;1= yes	categorical
Milio fagetum	0= no;1= yes	categorical
Molinio pinetum	0= no;1= yes	categorical
Forest	0= no;1= yes	categorical
Clearcutting	0= no;1= yes	categorical
Instable scree	0= no;1= yes	categorical
Stabilised scree	0= no;1= yes	categorical
Scree absent	0= no;1= yes	categorical
Stone cairns	0= no;1= yes	categorical
Homogenous boulders	0= no;1= yes	categorical
Craggy boulders	0= no;1= yes	categorical

1) Deflection was calculated with the formula

$$Exposition = \frac{1-\cos\left(\left(\frac{\pi}{180}\right)*\left(Exposition\_map-30\right)\right)}{2}$$

Sampling covariates (p)	measure 1)	character
Length of transects	m/1000	continuous
Time of the search	hh.mm/10000 (like 06:13->0.0613)	continuous
Temperature	°C/100	continuous
Sampling method	0=by sight;1=turning cover	categorical
Humidity	%/100	continuous
Precipitation	0=no;1=yes	categorical
Wind	Value after Beaufort scale/10	categorical
Cloud cover	Value after Appendix 2 /10	categorical
Date of the search	Days after begin of fieldwork/1000	continuous

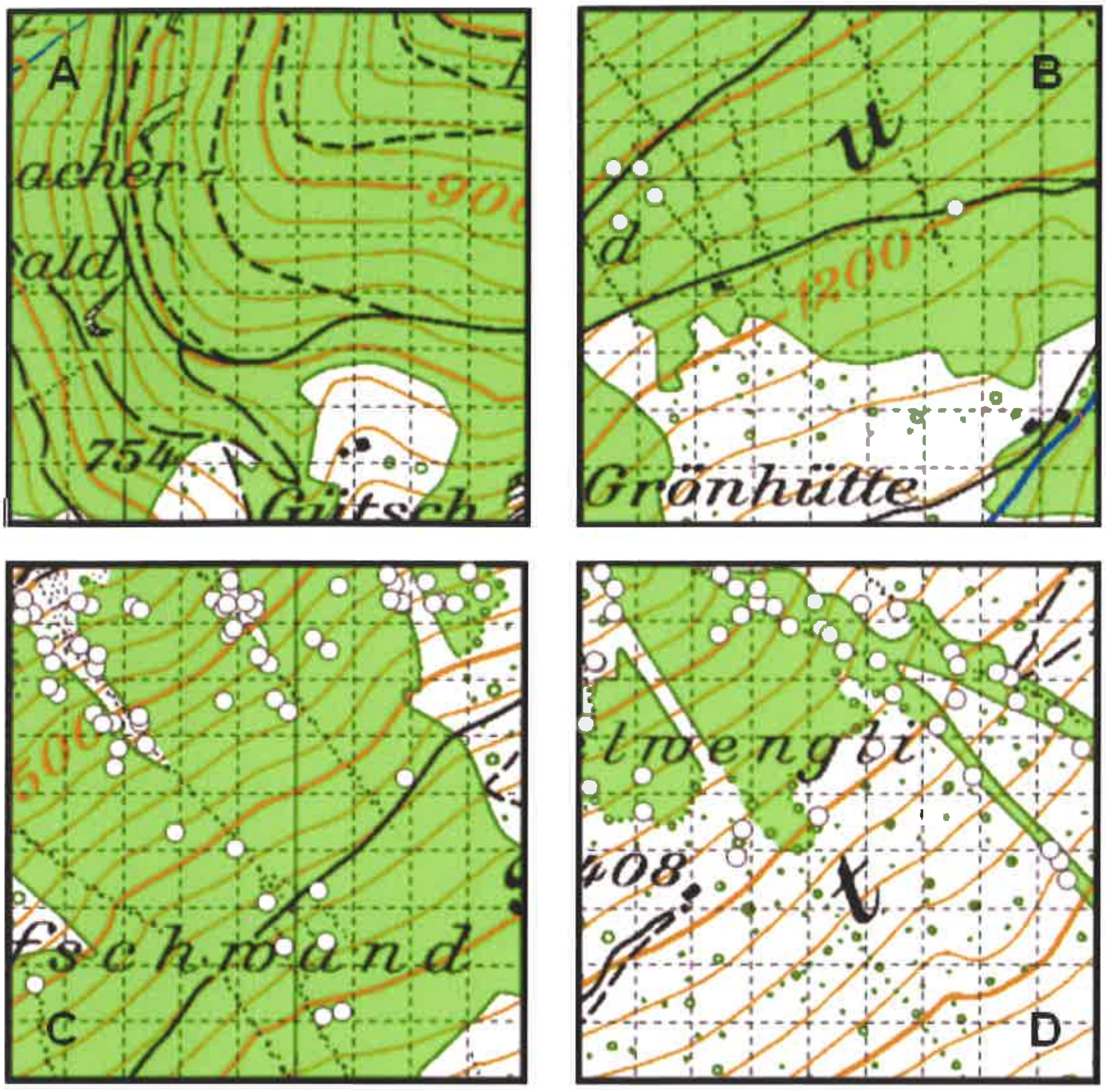
1) values should be between 0 and 1 to process them with PRESENCE.

Appendix 11: Variables of the historical data set

Site covariates (ψ)	**measure**	**character**
Forest in 1998	0=no;1=yes	categorical
Alpine pasture in 1998	0=no;1=yes	categorical
Agricultural area in 1998	0=no;1=yes	categorical
Pioneer habitat in 1998	0=no;1=yes	categorical
Hedge in 1998	0=no;1=yes	categorical
Forest in 1975	0=no;1=yes	categorical
Alpine pasture in 1975	0=no;1=yes	categorical
Agricultural area in 1975	0=no;1=yes	categorical
Pioneer habitat in 1975	0=no;1=yes	categorical
Hedge in 1975	0=no;1=yes	categorical
Forest in 1960	0=no;1=yes	categorical
Alpine pasture in 1960	0=no;1=yes	categorical
Agricultural area in 1960	0=no;1=yes	categorical
Pioneer habitat in 1960	0=no;1=yes	categorical
Hedge in 1960	0=no;1=yes	categorical
Changes of landscape	0=no;1=yes	categorical
Change of forest between 1960 and 1975	0=no;1=yes	categorical
Change of alpine pasture between 1960 and 1975	0=no;1=yes	categorical
Change of pioneer habitat between 1960 and 1975	0=no;1=yes	categorical
Change of forest between 1975 and 1998	0=no;1=yes	categorical
Change of alpine pasture between 1975 and 1998	0=no;1=yes	categorical
Change of pioneer habitat between 1975 and 1998	0=no;1=yes	categorical
Age of forest	1)	categorical
Age of alpine pasture	1)	categorical
Age of agricultural area	1)	categorical
Age of pioneer habitat	1)	categorical
Age of hedge	1)	categorical

1) Age was calculated by counting the time periods during which this variable was present in a cell and dividing it by 10. Since there were 3 time periods the age of a variable could be 0; 0.1; 0.2 or 0.3.

Sampling covariates (p)	**measure**	**character**
Time of the search	hh.mm/10000 (like 06:13->0.0613)	continuous
Temperature	°C/100	continuous
Sampling method	0=by sight;1=turning cover	categorical
Humidity	%/100	continuous
Precipitation	0=no;1=yes	categorical
Wind	Value after Beaufort scale/10	categorical
Cloud cover	Value after Appendix 2 /10	categorical
Date of the search	Days after begin of fieldwork/1000	continuous



Appendix 12: Distribution of the detected salamanders within the 4 study plots. Each dot represents one record. Dashed lines figure the 50 x 50 m raster grid (81 cells per plot).