Impact of past and present management practices on the land snail community of nutrient-poor calcareous grasslands

Inauguraldissertation

zur

Erlangung der Würde eines Doktors der Philosophie

vorgelegt der

Philosophisch-Naturwissenschaftlichen Fakultät

der Universität Basel

von

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Basel, 2007

Genehmigt von der Philosophisch-Naturwissenschaftlichen Fakultät auf Antrag von Prof. Dr. Bruno Baur und Prof. Dr. Andreas Erhardt

Basel, den 24. April 2007

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General introduction

Biodiversity in semi-natural grasslands

Nutrient-poor, dry calcareous grasslands in Central Europe harbour an extraordinary high diversity of plants and invertebrates (Ellenberg, 1996; Kirby, 2001; WallisDeVries et al., 2002). These semi-natural grasslands have been cultivated for hundreds of years in an extensive way, mainly by grazing and harvesting hay (Poschlod and WallisDeVries, 2002). Since the beginning of the twentieth century, increasing pressure for higher production at low cost has led to either an intensification of grassland use (increased stocking rate and/or increased use of fertilizer) or to abandonment (Hodgson et al., 2005; Strijker, 2005). These land use changes resulted in a significant decrease in biodiversity (Vickery et al., 2001; van Diggelen et al., 2005).

The high species diversity of nutrient-poor, dry calcareous grasslands has been explained by the intermediate disturbance hypothesis (Collins and Barber, 1986; Shea et al., 2004). Grazing is a form of disturbance which at light to moderate intensity results in high structural heterogeneity in the habitat (Dupré and Diekmann, 2001; Ausden et al., 2005). The different mechanisms involved include the choice of food plants (selective behaviour), trampling, inputs and outputs in the nutrient cycle and the dispersal of seeds and invertebrates (Fischer et al., 1996; Rook et al., 2004). Large herbivores had probably a considerable influence on the structure and dynamics of the landscape since the last ice age (Vera, 2000; Eriksson et al., 2002). Grazing with livestock partially took over the role of exterminated or greatly reduced populations of wild ungulates in creating and maintaining grassland patches.

Today, dry, low-nutrient grasslands are among the most endangered habitats and are of high conservation value (Van Swaay, 2002; Cremene et al., 2005). These human-made habitats harbour xerothermic plants and invertebrates adapted to dry conditions and contain numerous species whose primordial habitats (floodplains, peatlands, and rocky outcrops) have been largely destroyed (Baur et al., 1996).

Land snails as biodiversity indicators

Biodiversity of grasslands has mostly been expressed as species richness of plants. To a lesser extent, spiders and a few other insect groups (e.g. grasshoppers, carabid beetles, bees, butterflies) were used as indicators of biodiversity and to study the influence of grassland management on the biodiversity (Kruess and Tscharntke, 2002; Woodcock et al., 2005; Knop et al., 2006).

In my thesis, I used land snails as indicators for the biodiversity of dry, nutrient-poor calcareous grasslands. Gastropods are common and widespread on calcareous soils, because they can satisfy their calcium requirements for shell growth, reproduction and for other physiological processes (Wäreborn, 1970). Many snail species show distinct habitat specificity: there are species exclusively occurring in open habitat (open-land species) or species mainly found in forests (forest species; Kerney et al., 1983; Falkner et al., 2001). Nutrient-poor, dry calcareous grasslands harbour a typical gastropod community (Baur et al., 1996). Since land snails have a limited mobility, they cannot easily avoid adverse environmental conditions by displacement (Baur, 1986; Baur and Baur, 1988; Wirth et al., 1999). Furthermore, snails are especially sensitive to land use changes (Shikov, 1984; Baur and Baur, 1995). For example, the number of characteristic open-land species decreased with the successional age of abandoned steppe-like grassland in Transylvania, Romania (Cremene et al., 2005). Snail species recorded on the Red list of Switzerland provide information about the conservation value of the study site (Duelli, 1994). Appropriate management strategies can be developed by assessing the response of threatened species to particular types of grassland management. Land snails with a shell are easy to collect and most of them can easily be identified. Slugs are more difficult to identify and their activity depends largely on weather conditions (Rollo, 1991). For this reason, I did not consider any slugs in my thesis.

Pasture management in the Swiss Jura mountains

In Switzerland, most of the nutrient-poor pastures are stocked with cattle and some with sheep, horses or goats (Swiss Federal Statistical Office, 2004). The farmers mainly use manure and artificial nitrogen fertilizer to improve grassland productivity, to extend the grazing period and to increase stocking rate (Kessler and Menzi, 1997; Swiss Federal Statistical Office, 2004).

In the Jura mountains extensive grazing with low stocking rate and without use of fertilizers is a traditional form of grassland management (Strüby, 1894, 1896; Jeanrenaud, 1911; Werthemann, 1963; Imboden, 1965). Extensively managed pastures are grazed by livestock between June and September. In autumn some of these grasslands are stocked with horses for a short period as well. Shrubs and trees overgrowing the pastures are regularly removed and most of the pastures are completely or partially mown once a year between August and October for clearing.

Semi-natural grasslands are fragile because their maintenance depends on traditional farming techniques (Zamora et al., 2007). Between 1950 and 1980, 45% of the nutrient-poor, dry calcareous pastures in the Northwestern Swiss Jura mountains were converted into intensively managed pastures and a further 10% were abandoned (Zoller et al., 1986). Since the 1980s several pastures were integrated into local ecological management programs to maintain the biodiversity of traditionally used nutrient-poor, dry pastures or to enhance biodiversity by special restoration actions. Restoration efforts have mainly focused on the removal of shrub and trees in partially overgrown pastures or on the cessation of fertilization with a resulting reduction of grazing intensity in order to re-establish historical abiotic conditions and return the grassland community to its original condition.

Today, the remaining fragments of intact semi-natural grasslands are frequently surrounded by forest or intensively cultivated agricultural areas and thus isolated (Olsson et al., 2000). In the cultural landscape, boundaries are mostly human-made. The major part of forest edges adjacent to pastures are abrupt, whereas gradual forest edges are rare (di Castri et al., 1988; Brassel and Brändli, 1999). Gradual forest edges are more structured than abrupt forest edges, because the latter lack a shrub belt.

Aim of the thesis

The primary objective of this thesis is to determine how extensive pastures in the Swiss Jura mountains have to be managed to maintain and/or promote snail diversity in dry, nutrient-poor calcareous grasslands. This thesis further contributes towards assessing the effects of past and present pasture management on organisms with low mobility, such as land snails (Baur, 1986; Wirth et al., 1999).

In **chapter 1** I examined the effects of horse, cattle and sheep grazing on the diversity and abundance of terrestrial gastropods in dry, nutrient-poor grasslands. In particular, I compared the snail fauna in six extensive pastures exclusively grazed by horses, eight pastures grazed by cattle and seven by sheep.

In **chapter 2** I investigated the impact of pasture management intensity on the native land snail community. I assessed the diversity and abundance of terrestrial gastropods in eight cattle pastures without fertilizer application, in seven pastures with manure application once per year and in six pastures with manure and artificial nitrogen fertilizer application once per year. In this study, I intended to determine the maximum management intensities of pastures to avoid negative effects on the grassland snail community and to preserve the threatened snail species in dry, nutrient-poor grasslands.

Chapter 3 focuses on the effect of the management history over a period of 55 years on the present-day land snail diversity in 20 extensive pastures. In particular, I assessed the diversity and abundance of land snails in pastures covered by shrubs for 10–40 years but recently cleared, and in pastures fertilized for 15–25 years but recently extensively managed (no fertilization). As a control, I surveyed the land snail fauna in pastures which have been extensively managed throughout.

In **chapter 4** I examined the effect of different types of forest edge on the specialized open-land gastropod community of pastures. I assessed the land snail communities at six gradual and six abrupt grassland-forest edges. Gastropod species richness and abundance were recorded in 45 m-long transects running from pastures (20 m) through gradual or abrupt forest edges into the forest interior (25 m).

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Chapter 1

The effect of horse, cattle and sheep grazing on the diversity and abundance of land snails in nutrient-poor calcareous grasslands

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Basic and Applied Ecology 8: 55–65

Basic and Applied Ecology **8** (2007) 55—65

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Basic and Applied Ecology

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The effect of horse, cattle and sheep grazing on the diversity and abundance of land snails in nutrient-poor calcareous grasslands

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Received 23 August 2005; accepted 7 February 2006

KEYWORDS
Pasture management;
Livestock species;
Grazing intensity;
Gastropods;
Biodiversity

Summary

Livestock grazing is a common management practise in semi-natural grasslands in Central Europe. Different types of livestock (horses, cattle, sheep) and grazing intensity are known to affect the richness and composition of plant species. However, knowledge of grazing-dependent effects on invertebrates is limited. We examined the influence of horse, cattle and sheep grazing on the richness, abundance and composition of land snail species in 21 calcareous nutrient-poor grassland areas in the northwestern Jura Mountains, Switzerland. Grazing by different livestock species did not affect the species richness, abundance and species composition of land snails. Furthermore, the number of open-land species and the ratio of large- to small-sized snail species or individuals did not differ among the three pasture types. However, independent of livestock species, grazing intensity negatively influenced the snail fauna. Snail species richness, abundance and number of Red list species decreased with increasing grazing intensity. Grazing intensity also affected the occurrence of individual snail species (*Truncatellina cylindrica*, *Cecilioides acicula*, *Candidula unifasciata* and *Trichia plebeia*). To preserve the snail fauna in nutrient-poor grasslands, pastures can be stocked with horses, cattle or sheep. However, both maximum stocking rate (number of livestock units per hectare) and grazing duration (number of grazing days per year) must be carefully defined for the proper management of the pastures.

Zusammenfassung

Die Viehbeweidung ist eine gängige Bewirtschaftungsform in halbnatürlichen Graslandschaften in Zentraleuropa. Verschiedene Nutztierarten (Pferde, Rinder,

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1439-1791/$ - see front matter
doi:10.1016/j.baae.2006.02.003

Schafe) und die Beweidungsintensität beeinflussen die Vielfalt und Zusammensetzung der Pflanzenarten auf unterschiedliche Art und Weise. Unsere Kenntnisse über mögliche Effekte der verschiedenartigen Beweidung auf verschiedene Gruppen von Invertebraten sind aber beschränkt. Wir untersuchten den Einfluss der Pferde-, Rinder- und Schafbeweidung auf die Vielfalt, Abundanz und Zusammensetzung der Landschneckenarten in 21 Trockenrasengebiete auf nährstoffarmen, kalkreichem Boden im nordwestschweizer Jura-Gebirge. Die unterschiedlichen Beweidungsformen beeinflussten weder die Artenvielfalt, noch die Abundanz und Artenzusammensetzung der Schnecken. Auch die Anzahl Offenlandarten und die Verhältnisse der grossen zu den kleinen Schneckenarten oder -individuen unterschieden sich nicht zwischen den drei Weidetypen. Unabhängig von der Nutztierart wurde aber ein negativer Einfluss der Beweidungsintensität auf die Schneckenfauna festgestellt. Die Artenvielfalt der Schnecken, Abundanz und Anzahl Rote Liste-Arten nahmen mit zunehmender Beweidungsintensität ab. Die Beweidungsintensität beeinträchtigte auch das Vorkommen von einzelnen Schneckenarten (*Truncatellina cylindrica*, *Cecilioides acicula*, *Candidula unifasciata* und *Trichia plebeia*). Die vorliegende Studie zeigt, dass für die Erhaltung und Förderung der Schneckenfauna von Trockenrasen diese mit Pferden, Rindern oder Schafe beweidet werden können. Allerdings müssen der maximale Viehbesatz (Anzahl Grossvieheinheiten pro ha) und die Beweidungsdauer (Anzahl Tage Beweidung pro Jahr) der Weiden klar festgelegt werden.

Introduction

Nutrient-poor, dry calcareous grasslands of Central Europe developed as a result of forest clearing (Vera, 2000). Plant species from natural open habitats assembled and formed species-rich grasslands especially on dry slopes and plateaus (Ellenberg, 1996; Willmanns, 1998; Zoller, Wagner, & Frey, 1986). Since hundreds of years these grasslands have been maintained by spatially and temporally heterogeneous disturbance regimes, mainly grazing and harvesting hay (Poschlod & WallisDeVries, 2002). Extensive grassland management also promoted a high diversity of invertebrates (Baur et al., 1996; Kirby, 2001).

Since the beginning of the 20th century, increasing pressure for higher production at low cost led to an intensification of grassland use (increased stocking rate and/or increased use of fertilizer) or to abandonment (Hodgson, Grime, Wilson, Thompson, & Band, 2005; Poschlod & WallisDeVries, 2002; Strijker, 2005). These land-use changes caused a decrease in biodiversity (Van Diggelen, Sijtsma, Strijker, & Van den Burg, 2005). Today, dry nutrient-poor grasslands are among the most endangered habitats and are of high conservation value (Cremene et al., 2005; Duelli & Obrist, 2003; Van Swaay, 2002).

The high species diversity of these grasslands has been explained by the intermediate disturbance hypothesis (Collins & Barber, 1985; Connell, 1978; Shea, Roxburgh, & Rauschert, 2004). Grazing is a form of disturbance, which at light to moderate intensities results in high structural heterogeneity in the habitat (Ausden, Hall, Pearson, & Strudwick, 2005; Dupré & Diekmann, 2001; Hodgson, 1986). The different mechanisms involved include the choice of food plants (selective behaviour), trampling, inputs and outputs of nutrients and the dispersal of seeds and invertebrates (Fischer, Poschlod, & Beinlich, 1996; Rook et al., 2004).

Effects of grazing by horses, cattle and sheep on the vegetation have received considerable attention (Bullock, Hill, Dale, & Silvertown, 1994; Hart, 2001; Loucougaray, Bonis, & Bouzillé, 2004; Yunusbaev, Musina, & Suyundukov, 2003). In contrast, little is known about the influence of grazing by different livestock species on the invertebrate fauna (Carvell, 2002; Dennis, Young, & Bentley, 2001; Woodcock, Pywell, Roy, Rose, & Bell, 2005). In particular, the effect of grazing by different livestock animals and pasture management on the gastropod fauna in grasslands is mostly unknown. Gastropods are especially sensitive to land use changes and have a limited mobility (Baur, 1986; Baur & Baur, 1993; Wirth, Oggier, & Baur, 1999). There is empirical evidence of reduced species diversity and abundance of snails in pastures grazed by reindeer, cattle or sheep compared to areas without grazing (Ausden et al., 2005; Labaune & Magnin, 2002; Suominen, 1999).

In the present study, we examined the effects of horse, cattle and sheep grazing on the diversity and abundance of terrestrial gastropods in dry, nutrient-poor grasslands of the Swiss Jura Mountains. In particular, we investigated pastures managed in a traditional form with low livestock number and without use of fertilizers (extensively managed grasslands; Imboden, 1965; Jeanrenaud, 1911; Strüby, 1894, 1896; Werthemann, 1963). We addressed the following questions: (1) Does extensive grazing by different types of livestock (horses, cattle or sheep) affect the species diversity and composition, and abundance of gastropods in different ways? (2) Do other characteristics of extensively managed pastures influence the species diversity and abundance of the gastropod fauna? and (3) Are particular snail species especially sensitive to grazing by livestock?

Material and methods

Study sites

This study was carried out at 21 localities in the Swiss Jura Mountains in an area measuring 135×70 km (46°55′–47°32′N, 6°34′–8°20′E; elevations between 300 and 1100 m asl; for details see Appendix A: Table S3). The "Inventory of Dry Grasslands Sites of National Importance" (DGS) served as the basic reference for selecting the 21 pastures (Eggenberg, Dalang, Dipner, & Mayer, 2001). The area of the pastures examined ranged from 0.5 to 11.25 ha. In some cases up to 95% of the pasture's perimeter was adjacent to forest.

Six pastures were exclusively grazed by horses, eight pastures were grazed by cattle and seven by sheep (hereafter referred to as horse, cattle and sheep pasture, respectively). Some of the cattle and sheep pastures were stocked in autumn for a short period with horses as well. We did not distinguish among the various breeds of livestock since either mixed herds of the same species grazed simultaneously on a pasture or breeds of the same species were exchanged from year to year. The investigated pastures were managed with low or moderate grazing intensity (10–434 LU/ha d; see below for definition of grazing intensity). Most of the pastures were mown once a year between August and October for clearing. All the selected pastures have been extensively managed in the same way for at last 15 yr and up to the present time no fertilizer has been used.

Survey

We collected gastropods in five sampling plots (each measuring 5×5 m) in each pasture. Four sampling plots were randomly chosen using a procedure based on random numbers. The remaining sampling plot was placed in the given plot centre of the DGS-Inventory, where plant species richness had been recorded (Eggenberg et al., 2001). A GPS instrument (Garmin GPS12 Personal Navigator) was used to record the coordinates of the central point of each sampling plot. The sampling plots were at least 3 m apart from the nearest bush, 6 m from trees and 12 m from forest edge or pasture border.

We applied two methods to assess the species richness and relative abundance of terrestrial gastropods. First, one person visually searched for living snails and empty shells in each sampling plot for 20 min between 20 August and 5 October 2004. Second, we collected soil samples including dead plant material at randomly chosen spots in each sampling plot (total 0.5 l soil per plot). We dried the soil samples at 50 °C for 4 h. Then, samples were put through sieves with mesh sizes of 2, 1 and 0.2 mm and later examined under a binocular microscope. Gastropod shells were sorted out of the samples and identified according to Kerney, Cameron, and Jungbluth (1983). We did not consider slugs because their activity depends largely on weather conditions (Rollo, 1991), and the sampling methods used were not suitable to determine slug abundance (Oggier, Zschokke, & Baur, 1998).

We used the topographical map of Switzerland (scale 1:25,000) to ascertain the elevation, average degree of exposure and area of the pastures. In each pasture we also measured the soil-pH at six randomly selected points using the Hellige pH-method (AVM Process of Analysis, Freiburg, Germany). At the same points we measured the inclination of the slope using a trigonometrical method. For each pasture, soil-pH and inclination were expressed as mean value of six measurements.

By interviewing the farmers we obtained informations on livestock type, stocking rate, length of the grazing period and perimeter of the pastures. Grazing intensity was calculated as the product of the livestock units per hectare (unit defined according to the Swiss ordinance on agricultural terms and types of farming; Swiss Federal Office for Agriculture, 2004) and the number of days the pasture was stocked per year.

Snail characteristics

To examine whether gastropod species with different habitat specificity are differentially affected by grazing horses, cattle or sheep, we assigned all snail species to one of the following categories: open-land (species exclusively occurring in open habitats), forest (species mainly found in forests) or ubiquitous species (species found in different types of habitat). Detailed information on the species habitat specificity was obtained from Kerney et al., (1983) and Falkner, Obrdlík, Castella, and Speight (2001). To assess whether gastropod species of different size were affected by different livestock, we extracted data on mean adult size (shell height or shell length) from Kerney et al., (1983). The distribution of mean adult size of the species recorded was bimodal with a minimum at 5 mm. Thus, we classified snail species either as small-sized (adult size <5.0 mm) or large-sized (adult size $\geqslant 5.0$ mm).

Data analysis

In all analyses we considered the study site (21 pastures) as the unit of investigation. To examine possible differences in gastropod species richness and abundance we used analyses of covariance with pasture type as factor and grazing intensity as covariate (ANCOVA, type III model). Since the interaction between pasture type and grazing intensity was not significant in any analyses, we repeated the ANCOVA without the interaction term (Grafen & Hails, 2002). We used stepwise multiple regressions to analyse the relationships between both snail species richness and abundance and pasture characteristics (Table 1). In all analyses mean values of abiotic variables from the five sampling plots in a pasture were used. The effect of grazing intensity on the presence/absence of individual snail species was tested using a logistic regression model. For the statistical analyses we used the SPSS statistical package version 11.0. Data which did not fit normal distributions were $\log_{10}$-, square-root- or arcsin-transformed.

To assess the similarity of snail species composition among horse, cattle and sheep pastures, we performed a hierarchical cluster analysis with simple matching coefficients (Sneat & Sokal, 1973). To examine possible differences in snail species composition among the three pasture types, we performed a correspondence analysis in Decorana with the Community Analysis Package 1.41.

Results

Pasture characteristics

The horse, cattle and sheep pastures investigated did not differ in elevation, exposure, soil-pH, inclination, area, total perimeter adjacent to woodland, tree cover, hedgerow cover and grazing intensity (ANOVA, in all cases $p>0.11$; see Appendix A: Table S3). Soil-pH was negatively correlated with the elevation of the pasture and with grazing intensity (Pearson correlation: soil-pH vs. elevation: $r=-0.62$, $n=21$, $p<0.01$; soil-pH vs. grazing intensity: $r=-0.49$, $n=21$, $p=0.02$). However,

Table 1. Variables recorded at each locality

Variable	Scale	Source	Range	Group
Elevation	Pasture	TP	360–1040 m asl	ENV
Exposure	Pasture	TP	151–199° (180° = South)	ENV
pH	Pasture	FS	5.7–8.1	ENV
Inclination	Pasture	FS	14.6–38.6°	SF
Area	Pasture	TP	0.5–11.25 ha	SF
Woodland perimeter	Pasture	FS	0–95% total perimeter adjacent to woodland	SF
Grazing intensity	Pasture	CV	10–434 LU/ha grazing days yr	FM
Tree cover	Pasture	FS	1–60%	STR
Hedgerow cover	Pasture	FS	0–30%	STR
Distance to forest edge	Sampling plot	FS	12.0–105.0 m	SF
Distance to nearest tree	Sampling plot	FS	7.0–53.4 m	SF
Distance to nearest hedgerow	Sampling plot	FS	5.1–75.0 m	SF
Stone cover	Sampling plot	FS	0–35%	STR
Old grass cover	Sampling plot	FS	0–65%	STR
Proportion of bare ground	Sampling plot	FS	0–45%	STR

Source: FS–field survey; CV–conversation; TP–topographical map. *Range*: LU–livestock units.
Group: ENV–environmental conditions; SF–spatial features; FM–farming method; STR–structural elements.

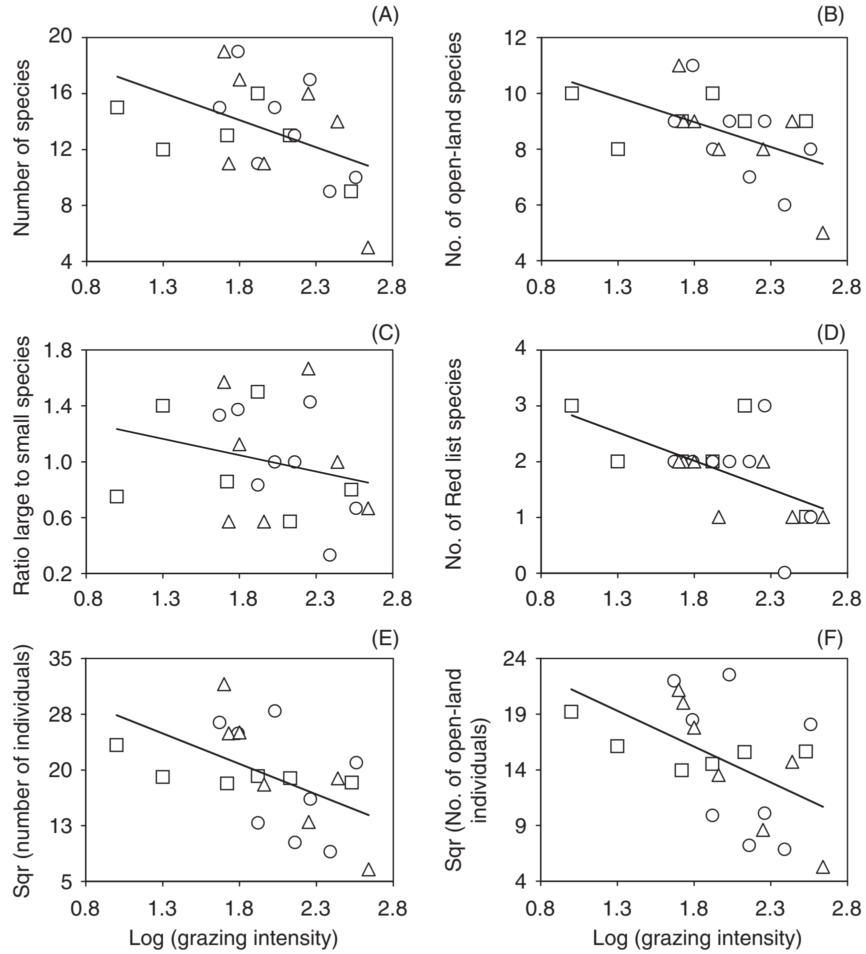

Figure 1. Relationship between number of snails species (or individuals) and grazing intensity. Pastures were grazed by horses (squares), cattle (open dots) or sheep (triangles). The regression lines are: (A) all snail species: $y = 21.08 - 3.88x$, $r^2 = 0.21$, $n = 21$, $p = 0.04$; (B) number of open-land species: $y = 12.18 - 1.78x$, $r^2 = 0.27$, $n = 21$, $p = 0.02$; (C) ratio of large- to small-sized species: $y = 1.47 - 0.23x$, $r^2 = 0.06$, $n = 21$, $p = 0.27$; (D) number of Red list species: $y = 3.85 - 1.02x$, $r^2 = 0.32$, $n = 21$, $p < 0.01$; (E) number of individuals: $y = 35.59 - 8.21x$, $r^2 = 0.28$, $n = 21$, $p = 0.01$; (F) number of open-land individuals: $y = 27.67 - 6.44x$, $r^2 = 0.27$, $n = 21$, $p = 0.02$.

no other correlations between the remaining pasture variables were found (in all cases $p > 0.05$). Moreover, the three pasture types did not differ in number of plant species recorded in the DGS-sampling plots (Kruskal-Wallis, chi-square $= 0.68$, $n = 21$, $p = 0.71$). We did not find any correlation between plant species richness and the pasture variables (Spearman rank correlation, in all cases $p > 0.13$).

Snail diversity

A total of 35 gastropod species were recorded (see Appendix A: Table S4). Snail species richness in pastures grazed by horses (13.0 ± 2.1; mean $\pm$ SD), cattle (13.6 ± 3.5) or sheep (13.3 ± 4.7) did not differ (ANCOVA, $F_{2,17} = 0.70$, $p = 0.51$; see Appendix A: Tables S3 and S5). However, grazing intensity had a significant negative effect on snail species richness ($F_{1,17} = 6.10$, $p = 0.02$). Snail species richness was not related to any of the 15 pasture variables examined in the multiple regression model, except to grazing intensity (Fig. 1A).

In all, we found 14 open-land, ten forest and eleven ubiquitous snail species (see Appendix A: Table S4). In all pastures, open-land species constituted the major proportion of the snail community (open-land species $69.7 \pm 13.6\%$, forest species $10.5 \pm 7.2\%$, ubiquitous species $19.7 \pm 8.6\%$). The number of open-land species did not differ among horse, cattle or sheep pastures (ANCOVA, $F_{2,17} = 0.05$, $p = 0.95$; see Appendix A: Tables S3 and S5). However, the number of open-land species decreased with increasing grazing intensity ($F_{1,17} = 4.96$, $p = 0.04$). No pasture variable had any effect on the number of open-land species (except grazing intensity, Fig. 1B).

Horse, cattle and sheep pastures did not differ in the ratio of large- to small-sized snail species (ANCOVA, $F_{2,17} = 0.17$, $p = 0.84$; see Appendix A: Tables S3 and S5). Furthermore, the ratio of large- to small-sized snail species was not affected by grazing intensity ($F_{1,17} = 1.48$, $p = 0.24$). The ratio of large- to small-sized snail species was positively related to percentage of stone cover, negatively to grazing intensity (Fig. 1C) and positively to distance to nearest tree (multiple regression, all three variables together, $r^2 = 0.64$, $n = 21$, $p < 0.001$).

We recorded one to three snail species considered as threatened according to the Red list of Switzerland (in one pasture no red-listed species was found; see Appendix A: Table S5). The pasture types did not differ in the number of threatened species (ANCOVA, $F_{2,17} = 0.34$, $p = 0.71$; see Appendix A: Tables S3 and S5). However, grazing intensity had a significant negative effect on the number of red-listed species ($F_{1,17} = 6.32$, $p = 0.02$). The number of red-listed snail species was negatively related to grazing intensity (Fig. 1D) and positively to woodland perimeter (multiple regression, both variables together, $r^2 = 0.49$, $n = 21$, $p < 0.01$).

The cluster analysis revealed no distinct pattern of snail species composition in horse, cattle and sheep pastures. The results of the correspondence analysis confirmed the similarity of the three pasture types in the snail species composition and abundance.

We did not find any correlation between plant species richness recorded in the DGS-sampling plots and snail species richness in the pasture (Spearman rank correlation, $r_s = -0.003$, $n = 21$, $p = 0.99$).

Snail abundance

A total of 8588 gastropod individuals were recorded (see Appendix A: Table S4). Snail abundance did not differ among pastures grazed by horses (383.0 ± 68.7 individuals per study site; mean ± SD), cattle (393.9 ± 279.5) or sheep (448.4 ± 323.1; ANCOVA, $F_{2,17} = 0.41$, $p = 0.67$; see Appendix A: Tables S3 and S5). However, grazing intensity had a significant negative effect on the number of snail individuals recorded ($F_{1,17} = 7.57$, $p = 0.01$). Snail abundance was not related to any of the 15 pasture variables examined in the multiple regression model, except grazing intensity (Fig. 1E).

In all pastures, open-land individuals constituted the major proportion of the snail community (open-land 86.9 ± 12.9% of all individuals recorded, forest 2.3 ± 3.4%, ubiquitous 10.8 ± 10.2%). The number of open-land individuals found did not differ among horse, cattle or sheep pastures (ANCOVA, $F_{2,17} = 0.04$, $p = 0.96$; see Appendix A: Tables S3 and S5). However, grazing intensity had a significant negative effect on the number of open-land snail individuals ($F_{1,17} = 5.99$, $p = 0.03$). No pasture variable had any effect on the number of open-land individuals (except grazing intensity, Fig. 1F).

Considering the ratio of large- to small-sized snails, pasture types did not differ significantly (ANCOVA, $F_{2,17} = 0.59$, $p = 0.56$) and grazing intensity had no effect on the proportion of large individuals ($F_{1,17} = 0.34$, $p = 0.56$). The ratio large- to small-sized snail individuals was positively related to inclination and woodland perimeter (multiple regression, both variables together, $r^2 = 0.59$, $n = 21$, $p < 0.001$).

Table 2. Effect of grazing intensity on the occurrence of single snail species found in pastures grazed by horses, cattle or sheep

Habitat specificity of snails	Species	Chi-squared	p	β	SE
Open-land	*Cochlicopa lubrica*	2.78	0.10	–	–
	C. lubricella	2.34	0.13	–	–
	Truncatellina cylindrica	10.98	< 0.01	−7.38	3.40
	Pupilla muscorum	3.31	0.07	–	–
	Helicella itala	0.98	0.32	–	–
	Candidula unifasciata	8.86	< 0.01	−4.93	2.41
Ubiquitous	*Punctum pygmaeum*	1.65	0.20	–	–
	Cecilioides acicula	20.69	< 0.001	−17.31	10.44
	Trichia plebeia	6.60	0.01	−3.89	1.86

The results of logistic regressions are shown.
In each case d.f. = 1 and $n = 21$.

We did not find any correlation between plant species richness recorded in the DGS-sampling plots and snail abundance in the pasture (Spearman rank correlation, $r_s = 0.32$, $n = 21$, $p = 0.15$).

Effects on individual snail species

Nine of the 35 snail species were so common that the effect of grazing intensity on their occurrence could be examined by logistic regression. Grazing intensity had a significant negative effect on the occurrence of two open-land species, *Candidula unifasciata* and *Truncatellina cylindrica*, and two ubiquitous species, *Cecilioides acicula* and *Trichia plebeia* (Table 2). *Candidula unifasciata*, *C. acicula* and *T. plebeia* belong to the species with large shells, whereas *T. cylindrica* has a small shell. *Cecilioides acicula* is a red-listed species. The occurrence of the remaining five common snail species was not significantly influenced by grazing intensity (Table 2).

Discussion

Influence of livestock type

Our study showed that species richness and abundance of land snails did not differ among pastures grazed by horses, cattle or sheep. However, grazing intensity of either livestock had a significant effect on snail species richness and abundance. Different findings have been reported in other groups of organisms. Yunusbaev et al., (2003) and Loucougaray et al., (2004) found a higher plant diversity in pastures grazed by horses than in pastures grazed by cattle or sheep, while in sheep pastures plant richness was lowest. Carvell (2002) recorded a higher diversity and abundance of bumblebees in cattle pastures than in sheep pastures, whereas Dennis et al., (2001) found a higher species richness and abundance of spiders in pastures grazed only by sheep than by both cattle and sheep. Sheep with their comparable smaller mouths can choose their food more selectively than cattle and horses (Illius & Gordon, 1987). Horses can satisfy their nutritive needs with food richer in fibres than cattle and sheep, and with their level bite they can graze closer to the ground (Duncan, 1992).

Our results could be attributed to the fact that unlike other groups of organisms (e.g. butterflies), snails are less dependent on particular species of plants for feeding, although they show food preferences (Fröberg, Baur, & Baur, 1993; Frömming, 1954). In fact, we found no relationship between snail species richness and plant species richness. However, Rouse and Evans (1994) reported a weak correlation between the diversity of the vegetation and gastropod species richness on lightly grazed sheep pastures. Gosteli (1996) suggested an association between snail and plant communities, because both may depend on similar microclimatic conditions and soil factors.

The three livestock species have a different trampling impact because of their different body mass and hoof size. In particular, the physical pressure exerted on the ground is estimated to be 0.8–0.95 kg/cm^2 in sheep and 1.2–1.6 kg/cm^2 in cattle (Spedding, 1971). However, the ratio large- to small-sized snail species found in our study did not differ among horse, cattle or sheep pastures. This indicates that the trampling impact from different livestock species may not select for a certain snail size in extensively managed pastures.

Snail diversity and abundance

Our results show a negative influence of grazing intensity on diversity and abundance of snails. An increased stocking rate can reduce or alter species diversity and abundance of several groups of arthropods (East & Pottinger, 1983; King, Hutchinson, & Greenslade, 1976; Kruess & Tscharntke, 2002a, b). On calcareous soil the promoted plant community varies in accordance with grazing intensity (Barbaro, Dutoit, Anthelme, & Corcket, 2004; Kiehl, Eischeid, Gettner, & Walter, 1996). Low to moderate grazing intensity of horses, cattle and sheep results in a highly structured vegetation, i.e. differences in plant architecture, density and growth stage (Hart, 2001; Van den Bos & Bakker, 1990). High stocking levels and longer grazing periods reduce the sward height, litter layer and soil pore volume near to soil surface. Furthermore, a high grazing intensity can also reduce the root mass and vertical depth of root growth (Pandey & Singh, 1992; Van der Maarel & Titlyanova, 1989). Species-rich snail communities depend on heterogeneous structures that provide the special microhabitats required by different species (Boycott, 1934; Cameron & Morgan-Huws, 1975; Labaune & Magnin, 2001; Labaune & Magnin, 2002). We suggest that a low structural habitat complexity effected by high grazing intensity permits fewer snail species to exist on the pasture because of a reduced availability of niches. It has been shown that low grazing pressure leads to high diversity and/or abundance in spiders, ground beetles, butterflies and small mammals (e.g., Gibson, Brown, Losito, & McGavin, 1992; Morris, 2000; Schmidt, Olsen, Bildsøe, Sluydts, & Leirs, 2005).

Most of the snails found were open-land or ubiquitous species belonging to the typical gastropod community of nutrient-poor, dry calcareous grasslands (Baur et al., 1996; Gosteli, 1996). The small number of forest snails found in the pastures may either have been passively dispersed by grazing livestock or they may have rolled down on the steep slopes from the adjacent woodland (Fischer et al., 1996).

On the pastures examined we also recorded five snail species considered as threatened according to the Red list of Switzerland (Duelli, 1994). This confirms that extensive grazing is a suitable management practise to preserve endangered gastropods in nutrient-poor grasslands.

The species composition of a snail community in a pasture may also depend on previous land use and other historical events (Cameron, Down, & Pannett, 1980; Martin & Sommer, 2004). Although our study areas have been managed the same way over the last 15 yr, earlier forms of land use might be reflected in the present snail community. Moreover, certain snail species such as *H. itala* could have been accidentally introduced into pastures in seed stock or in hay in the past (Mäder, 1939).

Sensitivity of individual snail species

In our study different snail species reacted differently to grazing intensity. We found that *C. acicula* was negatively affected by grazing intensity. This snail species is blind and lives exclusively in the soil (Falkner et al., 2001; Wächtler, 1929). It feeds mainly on fungi (Frömming, 1954). High grazing pressure may reduce the availability of this basic food resource (Bardgett et al., 2001).

In response to grazing damage, plants can build up secondary metabolites which can have a deterrent effect on grazing organisms (Bennett & Wallsgrove, 1994). High concentrations of secondary metabolites in plant material induced by high livestock grazing intensity could make the food less edible for certain snail species such as *T. cylindrica*, *C. unifasciata* and *T. plebeia*.

Implications for pasture management

From the perspective of grassland management, it is not clear which species of livestock should be employed to preserve or enhance the diversity of different groups of organisms (Rook et al., 2004). Our study suggests that for the conservation of the snail fauna on nutrient-poor, dry calcareous grasslands it is of no significance whether pastures are stocked with horses, cattle or sheep, provided the grazing intensity is low. However, where the aim is to protect the complete grassland life community the choice of livestock species can be important.

An extensive management with low grazing intensity is vital to preserve the snail diversity of nutrient-poor, dry grasslands. Similarly, other organisms (e.g. spiders, Coleoptera, Hymenoptera) benefit from maintaining a dynamic mosaic of old and young, tall and short grassland patches by low grazing intensity (Tscharntke & Greiler, 1995; WallisDeVries & Raemakers, 2001). Therefore, the maximum of grazing intensity tolerated, i.e. stocking level (number of livestock units per hectare) and grazing duration (number of grazing days per year), is a crucial factor and has to be carefully defined for an appropriate management of extensive pastures.

Acknowledgements

We thank the farmers for allowing us to work on their pastures. We are grateful to Stefan Eggenberg and the Federal Office for the Environment (FOEN) for vegetation data of the "Inventory of Dry Grasslands Sites of National Importance" (DGS), and G. Armbruster, A. Baur, K. Hövemeyer, H.-P. Rusterholz, P. Stoll and two anonymous reviewers for constructive comments on the manuscript. Financial support was received from the Bristol Foundation in Schaan (Principality of Liechtenstein).

Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.baae.2006.02.003.

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Chapter 2

Effects of management intensity on land snails in Swiss nutrient-poor pastures

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Agriculture, Ecosystems and Environment 120: 243–249

Available online at www.sciencedirect.com

ScienceDirect

Agriculture, Ecosystems and Environment 120 (2007) 243–249

Agriculture Ecosystems & Environment

www.elsevier.com/locate/agee

Effects of management intensity on land snails in Swiss nutrient-poor pastures

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Received 31 March 2006; received in revised form 17 August 2006; accepted 6 September 2006
Available online 31 October 2006

Abstract

The influence of management intensity on the richness, abundance and composition of land snail species was examined in 21 calcareous, nutrient-poor cattle pastures in the northwestern Jura mountains, Switzerland. Grazing intensity was positively correlated with the extent of fertilization of the pastures. Pastures without fertilizer application and with low grazing intensity harboured more snail species and more threatened snails than pastures with annual addition of manure or pastures with manure and nitrogen fertilizer and higher grazing intensity. Fewer snail individuals, open-land species and open-land individuals were found on pastures with high than on pastures with low management intensity. To preserve the threatened snail species in dry, nutrient-poor grasslands, a network of pastures should be managed without fertilization and grazing intensity should not exceed 180 LU ha^{-1} d (product of livestock units per hectare and grazing days).

Keywords: Pasture; Fertilization; Grazing intensity; Gastropods; Biodiversity

1. Introduction

The impact of pasture management intensity on different groups of organisms varies considerably. Some competitive plant species and exotic species of mites and springtails increase their abundance under conditions of fertilization and high grazing intensity, whereas species richness and abundance of the majority of native plants, ants, grasshoppers, beetles and birds decrease (van Wingerden et al., 1992; Verhulst et al., 2004; Oliver et al., 2005). Little is known about the effect of pasture management intensity on the gastropod fauna. Gastropods are especially sensitive to land use changes and have limited mobility (Baur, 1986; Wirth et al., 1999). For example, the number of characteristic open-land species decreased with successional age of abandoned steppe-like grassland in Transylvania, Romania (Cremene et al., 2005). Climatic warming due to extensive urban development in the surroundings of Basel, Switzerland, might have caused the local extinction of the land snail *Arianta arbustorum* (Baur and Baur, 1993). There is empirical evidence of reduced species diversity and abundance of snails in pastures grazed by reindeer, cattle or sheep compared to areas without grazing (Suominen, 1999; Labaune and Magnin, 2002; Ausden et al., 2005). Furthermore, snail species richness is lower in fertilized than unfertilized meadows (Gosteli, 1996). As human-made habitats, calcareous grasslands contain numerous species whose primordial habitats (floodplains, peatlands, and rocky outcrops) have been largely destroyed (Baur et al., 1996).

In Switzerland, farmers mostly use manure and artificial nitrogen fertilizer to improve grassland productivity, to extend the grazing period and to increase livestock number (Swiss Federal Statistical Office, 2004). In the present study, the effect of pasture management intensity on the native gastropod community was examined in the Swiss Jura mountains. In particular, the diversity and abundance of terrestrial gastropods were assessed in cattle pastures without fertilizer application, with manure application once per year and in pastures with manure and artificial nitrogen

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0167-8809/$ – see front matter
doi:10.1016/j.agee.2006.09.008

fertilizer application once per year. The following questions were addressed: (1) How do different levels of management intensity affect the species richness, abundance and composition of the gastropod community? (2) Do other characteristics of cattle pastures influence the species diversity and abundance of the gastropod community? (3) Are particular snail species especially sensitive to the intensity of pasture management?

2. Material and methods

This study was carried out at 21 localities in the Swiss Jura mountains in a region measuring 90 km × 32 km (47°15′–47°33′ N, 7°08′–8°20′ E; elevations between 360 and 1040 m a.s.l.). The area of the pastures examined ranged from 1.25 to 11.25 ha.

Eight pastures were unfertilized, seven pastures were fertilized once per year with manure (up to 25 m^3/ha) and six pastures once per year with manure (up to 25 m^3/ha) and artificial nitrogen fertilizer (25 kg/ha; hereafter referred to as extensive, low-intensive and intensive pasture, respectively). Extensive pastures were stocked mostly with steers between June and September (47–365 LU ha^{-1} d, for definition of grazing intensity, see below), and low-intensive and intensive pastures with mother cows or milk cows between April and October (100–869 LU ha^{-1} d, respectively, 440–1410 LU ha^{-1} d). In autumn some of the pastures were stocked with horses for a short period. Five of the eight extensive pastures, six of the seven low-intensive and five of the six intensive pastures were mown between August and October for clearing. All examined pastures had been managed in the same way for at least 15 years.

2.1. Survey

Gastropods were collected in five sampling plots (each measuring 5 m × 5 m) in each pasture. The sampling plots were randomly chosen using a procedure based on random numbers. A GPS instrument (Garmin GPS12 Personal Navigator) was used to record the coordinates of the central point of each sampling plot. The sampling plots were at least 3 m apart from the nearest bush, 6 m from trees, and 12 m from forest edge or pasture border.

Two methods were applied to assess the species richness and relative abundance of terrestrial gastropods. First, one person searched for living snails and empty shells in each sampling plot for 20 min between 21 April and 29 May 2005. Second, soil samples were collected including dead plant material at randomly chosen spots in each sampling plot (in total 0.5 l soil per plot). The soil samples were dried at 60 °C for 24 h. Then, samples were put through sieves with mesh sizes of 2, 1 and 0.2 mm and later examined under a binocular microscope. Gastropod shells were sorted out of the samples and identified according to Kerney et al. (1983). Slugs were not considered because their activity depends largely on weather conditions (Rollo, 1991), and the sampling methods used were not suitable to determine slug abundance (Oggier et al., 1998).

The topographical map of Switzerland (scale 1:25,000) was used to ascertain the elevation, average degree of exposure and area of the pastures. In each pasture the soil-pH was measured at six randomly selected points using the Hellige pH-method (AVM Process of Analysis, Freiburg, Germany). At the same points the inclination of the slope was measured using a trigonometrical method. The distance from the sampling plot's centre to (1) the nearest forest, (2) the nearest tree and (3) the nearest hedgerow was also measured, and the cover of stones, old grass and bare ground were estimated. The cover of old grass (dry grass not considered by grazing cattle) was recorded in each sampling plot toward the end of the grazing season between 23 August and 19 September 2005.

Information on type and rate of fertilization, livestock type, stocking rate, length of the grazing period and perimeter of the pastures was obtained by interviewing the farmers. Grazing intensity was calculated as the product of the livestock units (LU, unit defined according to the Swiss ordinance on agricultural terms and types of farming; Swiss Federal Office for Agriculture (2004); milk cow = 1, mother cow = 0.8, steer > 2 years old = 0.6, steer 1–2 years old = 0.4, calf of mother cow = 0.17) per hectare, and the number of days the pasture was stocked per year.

2.2. Snail characteristics

Snail species were assigned to one of the following categories: open-land (species exclusively occurring in open habitat), forest (species mainly found in forests) or ubiquitous species (species found in different types of habitat). Detailed information on the species habitat specificity was obtained from Kerney et al. (1983) and Falkner et al. (2001). To assess whether gastropod species of different size were affected by management intensity, data on mean adult size (shell height or shell length) were extracted from Kerney et al. (1983). The distribution of mean adult size of the species recorded was bimodal with a minimum at 5 mm. Thus, snail species were classified either as small-sized (adult size < 5.0 mm) or large-sized (adult size ≥ 5.0 mm).

2.3. Data analysis

The study area (21 different pastures) was considered as the unit of investigation in all analyses. One-way analysis of variance (ANOVA) was applied to examine possible differences in pasture characteristics, gastropod species richness and abundance among extensive, low-intensive and intensive pastures. In case of significant difference, pairwise comparisons of means were conducted using Fisher's LSD test. Spearman rank correlation was calculated to examine a possible correlation between fertilization type and grazing intensity of the pastures. Stepwise multiple regression models were used to examine the relationships between both snail species richness and abundance and various pasture characteristics. For each pasture, soil-pH was expressed as median and the other abiotic variables as mean values. Fisher's exact test was used to examine a possible influence of fertilization on the occurrence of single snail species. The effect of grazing intensity on the presence/absence of single snail species was tested using logistic regression models. Statistical analyses were performed using the SPSS statistical package Version 11.0. Data which did not fit normal distributions were $\log_{10}$-, square-root- or arcsin-transformed.

3. Results

The extensive, low-intensive and intensive pastures examined differed in grazing intensity (ANOVA, $F_{2,18} = 16.79, p < 0.001$). Grazing intensity was low in the extensive pastures (154.5 ± 107.5 LU ha^{-1} d, mean $\pm$ S.D.), moderate in low-intensive pastures (486.7 ± 303.0 LU ha^{-1} d) and high in the intensive pastures (1020.0 ± 403.4 LU ha^{-1} d; Fisher's LSD test, extensive pasture versus low-intensive: $p = 0.01$, extensive versus intensive: $p < 0.001$, low-intensive versus intensive: $p < 0.01$). Grazing intensity was positively correlated with the extent of fertilization of the pastures (Spearman rank correlation, $r_s = 0.79$, $n = 21$ $p < 0.001$).

The three pasture types did not differ in elevation, exposure, soil-pH, area, total perimeter adjacent to woodland and tree cover (ANOVA, in all cases $p > 0.17$). However, the three pasture types differed in inclination (ANOVA, $F_{2,18} = 3.78$, $p = 0.04$). Intensive pastures were less steep than extensive pastures and low-intensive pastures (Fig. 1A). Inclination between extensive and low-intensive pastures did not differ. The three pasture types also differed in hedgerow cover (ANOVA, $F_{2,18} = 6.27$, $p < 0.01$). Extensive pastures contained more hedgerows than low-intensive pastures and intensive pastures (Fig. 1B). Hedgerow cover did not differ between low-intensive and intensive pastures.

A total of 28 gastropod species were recorded. For all the snail species found as empty shells, also living snails were collected in the same pastures. Snail species richness differed among pasture types (ANOVA, $F_{2,18} = 6.09$, $p = 0.01$). Extensive pastures harboured more snail species (14.0 ± 3.0; mean $\pm$ S.D.) than low-intensive (9.7 ± 2.5; Fisher's LSD test, $p = 0.02$) and intensive pastures (8.5 ± 3.9; $p < 0.01$). However, snail species richness did not differ between low-intensive and intensive pastures ($p = 0.50$). Snail species richness of the 21 pastures was negatively related to grazing intensity (Table 1). The stepwise multiple regression further revealed that snail species richness was also positively related to stone cover.

In all, we found 13 open-land, 7 forest and 8 ubiquitous snail species. In all pastures, open-land species constituted the major proportion of the snail community (open-land species $72.4 \pm 14.7\%$, forest species $6.8 \pm 7.2\%$, ubiquitous species $20.8 \pm 11.8\%$). The number of open-land species differed among pasture types (ANOVA, $F_{2,18} = 3.88$, $p = 0.04$). Extensive pastures harboured marginally more open-land snail species than low-intensive and more open-land snail species than intensive pastures (Fisher's LSD test, $p = 0.06$, and $p = 0.02$). In contrast, the number of open-land species did not differ between low-intensive and intensive pastures ($p = 0.48$). The number of open-land species of the 21 pastures was negatively related to grazing intensity (Table 1).

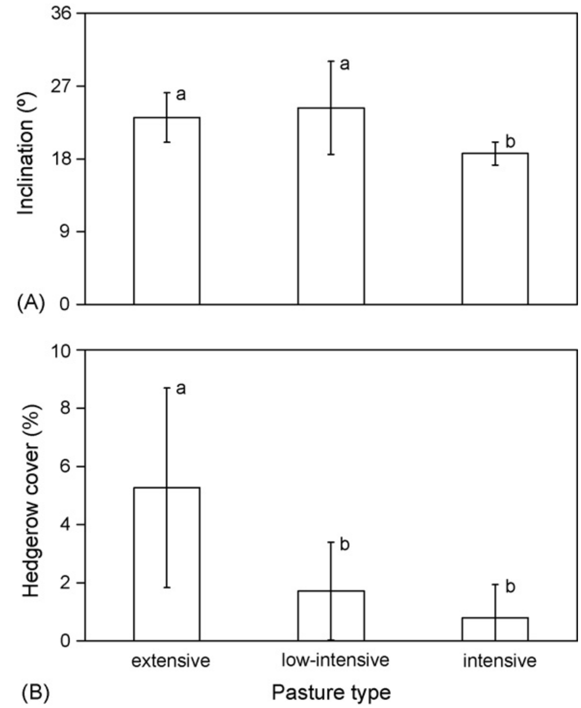

Fig. 1. Inclination (A) and hedgerow cover (B) in the three pasture types (mean $\pm$ S.D.). Significant differences ($p < 0.05$) between pasture types are indicated by different letters (based on pairwise comparisons using Fisher's LSD test).

The three pasture types did not differ in the ratio of large- to small-sized snail species (ANOVA, $F_{2,18} = 2.88$, $p = 0.08$). Thus, independent of shell size, the different snail species were similarly influenced by different pasture types. The ratio of large- to small-sized snail species was negatively affected by grazing intensity (Table 1). The stepwise multiple regression further revealed that the ratio of large- to small-sized snail species was positively related to woodland perimeter.

One to three snail species considered as threatened according to the Red List of Switzerland were recorded (in three low-intensive and three intensive pastures no red-listed species were found). The pasture types differed significantly in the number of threatened species (ANOVA, $F_{2,18} = 10.50$, $p < 0.01$). Extensive pastures harboured more red-listed species than low-intensive and intensive pastures (Fisher's

Table 1
Stepwise multiple regression analysis results with diversity and abundance of snails as dependent variables and 15 pasture variables as independent variables

Dependent variable / Independent variable	β	S.E.	t	p
Number of snail species				
Intercept	–	–	6.96	<0.001
Grazing intensity	−0.18	0.07	−2.57	0.019
Stone cover	24.93	10.65	2.34	0.031
Entire model: $r^2 = 0.56$, $n = 21$, $p = 0.001$				
Number of open-land snail species				
Intercept	–	–	12.49	<0.001
Grazing intensity	−0.12	0.03	−3.53	0.002
Entire model: $r^2 = 0.40$, $n = 21$, $p = 0.002$				
Ratio of large- to small-sized snail species				
Intercept	–	–	3.84	0.001
Grazing intensity	−0.01	0.01	−2.53	0.021
Woodland perimeter	0.32	0.14	2.32	0.032
Entire model: $r^2 = 0.59$, $n = 21$, $p = 0.000$				
Number of Red List species				
Intercept	–	–	4.07	0.001
Grazing intensity	−0.05	0.02	−3.14	0.006
Stone cover	6.47	2.61	2.48	0.023
Entire model: $r^2 = 0.63$, $n = 21$, $p = 0.000$				
Abundance of snails				
Intercept	–	–	18.38	<0.001
Stone cover	4.56	1.22	3.73	0.001
Entire model: $r^2 = 0.42$, $n = 21$, $p = 0.001$				
Abundance of open-land snail species				
Intercept	–	–	14.15	<0.001
Stone cover	4.84	1.33	3.63	0.002
Entire model: $r^2 = 0.41$, $n = 21$, $p = 0.002$				
Ratio of large- to small-sized snail individuals				
Intercept	–	–	6.95	<0.001
Grazing intensity	−0.02	0.00	−3.63	0.002
Entire model: $r^2 = 0.41$, $n = 21$, $p = 0.002$				

LSD test, in both cases $p < 0.01$). However, the number of threatened species did not differ between low-intensive and intensive pastures ($p = 0.61$). The number of red-listed snail species of the 21 pastures was negatively affected by grazing intensity (Table 1). Two or three threatened snail species were found in seven of eight pastures with grazing intensity up to 180 LU ha^{-1} d, whereas one red-listed species at most was recorded in the 13 pastures with higher grazing intensity. The stepwise multiple regression further revealed that the number of threatened species was positively related to stone cover (Table 1).

A total of 5200 gastropod individuals were recorded. Considering single pastures 0.01–21.5% (8.6 ± 6.6%; mean ± S.D.) of the individuals recorded were alive. The proportion of living snails did not differ between the three pasture types (ANOVA, $F_{2,18} = 0.10$, $p = 0.89$). Snail abundance decreased from extensive (431.9 ± 322.5 individuals per study area) to low-intensive (141.4 ± 53.4) and intensive pastures (125.8 ± 70.2; ANOVA, $F_{2,18} = 4.37$, $p = 0.03$). The number of individuals in extensive pastures was marginally higher than in low-intensive and higher than in intensive pastures (Fisher's LSD test, $p = 0.07$, and $p = 0.01$). However, snail abundance did not differ between low-intensive and intensive pastures ($p = 0.35$). Snail abundance of the 21 pastures was also positively related to stone cover (Table 1).

In all pastures, open-land individuals constituted the major proportion of the snail community (open-land 83.3 ± 15.0% of all individuals recorded, forest 1.3 ± 2.4%, ubiquitous 15.3 ± 13.8%). The number of open-land individuals found differed among pasture types (ANOVA, $F_{2,18} = 3.81$, $p = 0.04$). The abundance of open-land species in extensive pastures was marginally higher than in low-intensive and higher than in intensive pastures (Fisher's LSD test, $p = 0.08$, and $p = 0.02$). The abundance of open-land species did not differ between low-intensive and intensive

Table 2
Effect of grazing intensity on the occurrence of single snail species found in extensive, low-intensive and intensive pastures

Habitat specificity of snails	Species	Chi-squared	p	β	S.E.
Open-land	*Cochlicopa lubrica*	0.05	0.82	–	–
	Cochlicopa lubricella	9.02	0.003	−0.17	0.07
	Truncatellina cylindrica	4.60	0.03	−0.11	0.06
	Pupilla muscorum	1.88	0.17	–	–
	Vitrina pellucida	4.89	0.03	−0.15	0.09
	Helicella itala	12.78	0.000	−0.30	0.13
Forest	*Aegopinella nitens*	2.99	0.08	–	–
Ubiquitous	*Punctum pygmaeum*	0.38	0.54	–	–
	Cecilioides acicula	1.10	0.29	–	–
	Trichia plebeia	0.15	0.70	–	–
	Helix pomatia	11.33	0.001	−0.39	0.22

The results of logistic regressions are shown. In each case d.f. = 1 and $n = 21$.

pastures ($p = 0.42$) and was positively related to the extent of stone cover in the 21 pastures (Table 1).

The three pasture types marginally differed in the ratio of large- to small-sized snail individuals (ANOVA, $F_{2,18} = 3.50$, $p = 0.05$) which was negatively related to grazing intensity in the 21 pastures (Table 1).

Eleven of the 28 snail species occurred in 5 pastures at least and in 18 pastures at most. The type of pasture influenced the occurrence of *Helicella itala*, a red-listed species. Individuals of *H. itala* were found in seven of the eight unfertilized pastures, but in none of the 13 fertilized pastures (low-intensive and intensive pastures combined; Fisher's exact test, $p < 0.001$). In contrast, the occurrence of the other 10 common snail species (*Cochlicopa lubrica*, *Cochlicopa lubricella*, *Truncatellina cylindrica*, *Pupilla muscorum*, *Aegopinella nitens*, *Punctum pygmaeum*, *Vitrina pellucida*, *Cecilioides acicula*, *Trichia plebeia* and *Helix pomatia*) did not differ between unfertilized and fertilized pastures (Fisher's exact test, in all cases $p > 0.10$).

Logistic regression models were calculated to examine the effect of grazing intensity on the occurrence of the 11 common snail species. Grazing intensity had a significant negative effect on the occurrence of four open-land species (*C. lubricella*, *T. cylindrica*, *H. itala* and *V. pellucida*) and one ubiquitous species (*H. pomatia*, a red-listed species; Table 2). The predicted probability of occurrence of 50% in the model was achieved at 92 LU ha^{-1} d for *V. pellucida*, at 130 LU ha^{-1} d for *H. pomatia*, at 217 LU ha^{-1} d for *H. itala*, at 358 LU ha^{-1} d for *C. lubricella* and at 374 LU ha^{-1} d for *T. cylindrica* (Fig. 2). *Cochlicopa lubricella*, *H. itala*, *V. pellucida* and *H. pomatia* belong to the large-sized species, whereas *T. cylindrica* has a small shell. The occurrence of the remaining six common snail species was not influenced by grazing intensity (Table 2).

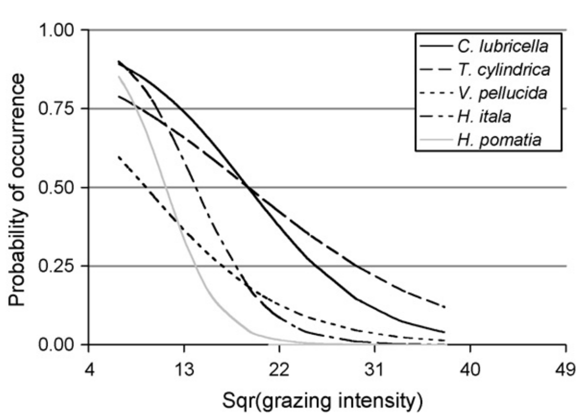

Fig. 2. Incidence functions of the five snail species whose occurrence in the pastures is affected by grazing intensity.

4. Discussion

This study showed that management intensity of pastures had a negative effect on the species richness of snails. Application of fertilizer in dry, nutrient-poor calcareous grasslands increases total of vegetation biomass (Willems et al., 1993). Higher biomass and denser vegetation structure further reduce light penetration (Bobbink, 1991). The microclimate in low-intensive and intensive pastures is probably characterized by longer periods of low temperature and higher moisture near the soil surface than in extensive pastures. This could be especially detrimental for thermophile snail species occurring in nutrient-poor, calcareous grasslands (e.g. *T. cylindrica*, *H. itala*) which need drier and warmer microclimatic conditions than mesophile species (e.g. *C. lubrica*, *T. plebeia*; Falkner et al., 2001). In fact, Cameron and Morgan-Huws (1975) found that xerophile snail species are favoured by short vegetation.

Species-rich snail communities depend on heterogeneous structures that provide a variety of microhabitats (a wide range of temperature and humidity conditions, different food resources and refuges above and below ground) for the different species (Labaune and Magnin, 2001). Most probably a decrease in structural habitat complexity by high management intensity allows fewer snail species to coexist in the pasture because the number of niches available is reduced.

The ratio of large- to small-sized snail species and that of large- to small-sized individuals was negatively influenced by grazing intensity. Thus, species with large shells are more strongly affected by grazing intensity than species with small shells. Higher grazing intensity implies increased treading by cattle and consequently more compact soil (Greenwood and McKenzie, 2001). This could impede large snails from taking shelter in the soil, whereas small snails would be able to creep in fissures of compacted soil. Therefore, snails with large shells can be more easily crushed by cattle than snails with small shells.

Manuring might be detrimental to particular snail species, especially *H. itala*, which could not be found in any pasture fertilized with manure. Substances occurring in cattle manure (i.e. ammonia, benzoic acid, sulfide) are highly toxic for earthworms (Curry, 1976). Heavy application of cattle manure can rapidly reduce earthworm and nematode species diversity and abundance (Zajonc, 1975; Dmowska and Kozlowska, 1988).

The investigated extensive and low-intensive pastures were slightly steeper than the intensive pastures. In steep slopes cattle moved frequently along gateways, resulting in an increased structural heterogeneity of the habitat. Thus, extensive pastures on slopes could provide additional microhabitats to various snail species (Labaune and Magnin, 2001). Hedgerow cover was higher in extensive pastures than in low-intensive and intensive pastures. However, it is rather unlikely that hedgerows may affect the snail fauna in the pastures examined because hedgerow cover did not exceed 10% of the area of any pasture.

Stone cover positively influenced the species diversity and abundance of snails. Stones provide an additional microhabitat and their lichen and cyanobacteria cover represent a further food resource to some specialized snail species (Baur et al., 1994). Moreover, pasture areas with high stone cover, and consequently low plant cover, are less frequently visited by cattle than sites with high plant cover. Therefore, trampling pressure by cattle might be reduced in areas with high stone cover, which in turn may result in an increased snail survivorship. Furthermore, stones prevent cattle from evenly grazing the sward and so contribute to the development of humid microsites with tall vegetation. This could be of vital importance for snails in periods following a grazing session with high stocking rate, when the soil surface in pastures is homogeneously covered with short vegetation providing no shelter from sun radiation.

4.1. Implications for pasture management

This study showed that pasture management of low intensity preserves snail diversity. Today, dry nutrient-poor grasslands are among the most endangered habitats and are of high conservation value (Baur et al., 1996; Cremene et al., 2005). Therefore, a network of pastures with low management intensity is necessary to maintain snail diversity. To preserve the threatened snail species in dry, nutrient-poor grasslands, the management intensity has to be defined. Based on the results of this study, no fertilizer should be applied and grazing intensity of pastures should not exceed 180 LU ha^{-1} d. To avoid any negative effects of grazing intensity on individual snail species, grazing intensity should be even lower (not exceeding 92 LU ha^{-1} d). The levels suggested coincide with the proposed management intensity for maintaining diurnal butterfly diversity in low productive and in dry, nutrient-poor pastures (Gonseth, 1994). At low management intensity, it is of no significance for the conservation of the specialized snail fauna, whether pastures are stocked with horses, cattle or sheep (Boschi and Baur, in press).

Acknowledgements

We thank the farmers for allowing us to work on their pastures. We are grateful to the Offices of Agriculture, respectively, of Land-Use Planning of the cantons Aargau, Basel-Landschaft, Jura and Solothurn for their collaboration in organising appropriate study areas, and G. Armbruster, A. Baur, H.-P. Rusterholz, P. Stoll, S. Zschokke and two anonymous reviewers for constructive comments on the manuscript. We gratefully acknowledge financial support from the Bristol Foundation in Schaan (Principality of Liechtenstein).

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Chapter 3

Past pasture management affects the land snail diversity in nutrient-poor calcareous grasslands

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Submitted for publication

Abstract

Changes in agriculture (intensification or abandonment) have resulted in a dramatic reduction of semi-natural grasslands in Central Europe in the twentieth century. Recent management actions aim to restore overgrown and formerly fertilized nutrient-poor grasslands. Former land use is known to influence the present-day vegetation. Similar information is not available for animals with low dispersal ability. We investigated the effect of pasture management history over a period of 55 years on the present-day land snail diversity in 20 dry, nutrient-poor grasslands in the Swiss Jura mountains. Snails were recorded in pastures left unmanaged for 10–40 years but recently cleared from overgrowing shrubs, in pastures fertilized for 15–25 years but recently managed extensively (no fertilizer), and in pastures which have been extensively managed throughout (= control). Past shrub cover had a negative effect on the total number of snail species and individuals, the number of open-land species and individuals and the number of red-listed individuals. Former use of fertilizer reduced red-listed species and individuals and changed the snail community. Three species (*Vitrina pellucida*, *Helicella itala* and *Abida secale*) were found less frequently in formerly fertilized pastures than in extensive pastures. Our results show that changes in pasture use for a period of 10–40 years alter the land snail fauna. To recover species losses by former intensification or abandonment, corridors connecting intact dry, nutrient-poor grasslands are suggested.

Keywords

Land use history; Shrub cover; Management intensity; Fertilization; Gastropods; Biodiversity

Zusammenfassung

Im Laufe des zwanzigsten Jahrhunderts haben Veränderungen in der Bewirtschaftung der Grasländer (Intensivierung oder Brachlegung) zu einem dramatischen Rückgang der halbnatürlichen Grasländer in Zentraleuropa geführt. Seit einigen Jahren wird versucht, verbuschte und ehemals gedüngte Trockenrasen mit geeigneten Massnahmen in ihren ursprünglichen Zustand zurückzuführen. Verschiedene Studien zeigen, dass die heutige Vegetation durch die frühere Landnutzung beeinflusst wird. Ähnliche Kenntnisse über Tiere mit geringem Ausbreitungsvermögen fehlen. Wir untersuchten den Einfluss unterschiedlicher Bewirtschaftungsformen während 55 Jahren auf die heutige Schneckenfauna in 20 nährstoffarmen Trockenrasen im Schweizer Jura-Gebirge. Die Schneckenfauna wurde in Weiden untersucht, die während 10–40 Jahren nicht mehr gepflegt, vor kurzer Zeit aber von den dabei entstandenen Büschen befreit wurden und in Weiden, die während 15–25 Jahren gedüngt, aber seit mindestens vier Jahre wieder extensiv (ohne Düngereinsatz) bewirtschaftet wurden. Als Kontrolle dienten Weiden, die immer extensiv bewirtschaftet wurden. Die zwischenzeitliche Verbuschung reduzierte die Anzahl Schneckenarten und -individuen, die Anzahl Offenlandarten und -individuen und die Anzahl Rote Liste-Individuen. Die zwischenzeitlich intensivere Weidebewirtschaftung reduzierte die Anzahl Rote Liste-Arten und Individuen, und veränderte die Artenzusammensetzung der Schneckengesellschaft. Drei Arten (*Vitrina pellucida*, *Helicella itala* and *Abida secale*) wurden weniger häufig in den ehemals gedüngten Weiden als in den extensiven Weiden gefunden. Unsere Ergebnisse zeigen, dass Änderungen in der Weidenbewirtschaftung während 10–40 Jahren die Schneckenfauna langfristig verändern. Die renaturierten Weiden sollten durch Korridore mit intakten, nährstoffarmen Trockenweiden verbunden werden, damit die lokal ausgestorbenen Schneckenarten diese Flächen wieder besiedeln können.

Introduction

Maintaining biodiversity in agricultural areas is one of the major challenges for biodiversity conservation in Central Europe. Traditional rural biotopes, particularly semi-natural grasslands, have been recognised as regional biodiversity hotspots (Cremene, Groza, Rakosy, Schileyko, Baur et al., 2005). As human-made habitats, dry, nutrient-poor calcareous grasslands harbour also numerous species whose primordial habitats (floodplains, peatlands, and rocky outcrops) have been largerly destroyed (Baur, Joshi, Schmid, Hänggi, Borcard et al., 1996). However, semi-natural grasslands are fragile because their maintenance depends on traditional farming techniques (Zamora, Verdú & Galante, 2007). During the twentieth century, increasing pressure for higher production at low costs has led to either an intensification of grassland use (increased stocking rate and/or increased use of fertilizer) or to abandonment (Strijker, 2005). These two processes lead to a reduction of the area of semi-natural grassland. The remaining fragments of semi-natural grassland are frequently surrounded by intensively managed farmland and/or forest. Besides reduction in area and habitat fragmentation, the history of land use has been found to be an important factor determining the present-day composition of plant communities in semi-natural grasslands (Lunt & Spooner, 2005). Various plant species respond rapidly to habitat alterations, whereas others show a considerable time lag in their response (Eriksson & Ehrlén, 2001). In the latter species, this could cause delayed extinction, but may also permit recovery when the habitat quality is improved.

The impact of the management history of semi-natural grasslands on the present-day species richness and species composition has been exclusively investigated in vascular plants (Cousins & Eriksson, 2001; Alard, Chabrerie, Dutoit, Roche & Langlois, 2005). However, the history of land use may also influence other groups of organisms with low dispersal abilities. We examined the effect of pasture management history over a period of 55 years on the present-day land snail community in the Swiss Jura mountains. Gastropods have a limited mobility and are especially sensitive to land use changes (Shikov, 1984; Baur & Baur, 1995).

In the Swiss Jura mountains extensive grazing with a low number of livestock and without the use of fertilizers is a traditional form of grassland management (i.e. Strüby, 1894; Werthemann, 1963). These calcareous grasslands harbour a high species diversity of plants and invertebrates (Baur et al., 1996). Between 1950 and

1980, 45% of all nutrient-poor, dry calcareous pastures in the Northwestern Swiss Jura mountains were converted into intensively managed pastures and further 10% were abandoned (Zoller, Wagner & Frey, 1986). Since the 1980s several pastures were integrated in local ecological management programs to maintain the biodiversity of traditionally used nutrient-poor, dry pastures or to enhance biodiversity by special restoration actions. Previous studies showed that management intensity of pastures, i.e. fertilization and grazing intensity, had a negative effect on both species richness and abundance of land snails (Boschi & Baur, 2007a, b). However, pastures grazed by horses, cattle and sheep did not differ in land snail fauna when grazing intensity was low.

In the present study, we assessed the diversity and abundance of land snails in pastures covered by shrubs for 10–40 years but recently cleared, and in pastures fertilized for 15–25 years but recently extensively managed (no fertilization). As a control, we examined the land snail fauna in pastures which have been extensively managed throughout. In particular, we addressed the following questions: (1) Does a former shrub cover for 10–40 years influence the species richness, abundance and species composition of gastropods in nutrient-poor calcareous pastures? (2) Does former fertilization for 15–25 years alter the snail fauna of nutrient-poor calcareous pastures? And (3) are single snail species differently affected by formerly overgrown and/or fertilized pastures?

Material and methods

Study sites and management history

This study was carried out at 20 localities in the Swiss Jura mountains in a region measuring 29 x 37 km (47°15'–47°29' N, 7°25'–7°55' E; elevations between 340 and 1222 m a.s.l.). The area of the study sites examined ranged from 1.2 ha to 66.0 ha.

Six pastures were partially overgrown by shrubs between 1951 and 1994 (Table 1). During this period the pastures were stocked with cattle, but no mowing and further removal of shrubs occurred. Since 1991, however, growing shrubs and trees were regularly removed in all six pastures. In the first half of the twentieth century the pastures were lightly fertilized with Thomas phosphate meal or dung every third year or even less frequently. In the past 50 years no fertilizer was applied. These pastures are hereafter referred to as shrub cleared pastures.

We assessed changes in shrub cover of the pastures using aerial photographs made in 1951–1953, 1970, 1982, 1987–1988, 1994 and 2000 by the Swiss Federal Office of Topography. To correctly identify shrub on the aerial photographs, we considered only vegetation structures which showed visible shadows. The crown cover of shrubs and trees was estimated following the scale of Huss (1984). Information of the type of management and condition of the pastures in the period 1896–1963 was extracted from Strüby (1894, 1896), Werthemann (1963) and Imboden (1965). Information on pasture management for the past 40 years was obtained from the Office of Agriculture and the Office of Land Use Planning of the cantons Basel-Landschaft and Solothurn and from the farmers.

Six pastures were fertilized once per year with manure (up to 25 m^3/ha) or nitrogen fertilizer (up to 25 kg/ha) and more intensively grazed (up to 568 $LU.ha^{-1}.d$, for definition of grazing intensity see below) for 15 or more years in the past 40 years. Before this period of intensification the pastures were lightly fertilized with Thomas phosphate meal or dung every third year or even less frequently. Between 1993 and 2001 these pastures were integrated into local ecological management programs which do not allow any fertilization and consequently, lead to a reduced grazing intensity. Shrubs were regularly removed on the pastures between 1951 and 1994 (Table 1). These pastures are hereafter referred to as formerly fertilized pastures.

We considered another eight extensive pastures as control sites (hereafter referred to as extensive pastures). These pastures did not receive any fertilizer in the past 50 years. In the first half of the twentieth century, however, they were lightly fertilized with Thomas phosphate meal or dung every third year or even less frequently. Shrubs were regularly removed between 1951 and 1994 (Table 1).

The 20 pastures examined were stocked with steers and in a few cases with mother cows or milk cows between the middle of May and October. In autumn some of the pastures were stocked with horses for a short period.

Survey

We collected gastropods in five sampling plots (each measuring 5 m x 5 m) in each pasture (in an area up to 10 ha). The sampling plots were randomly chosen using a procedure based on random numbers. We used a GPS instrument (Garmin GPS12 Personal Navigator) to record the coordinates of the central point of each sampling plot. The sampling plots were at least 3 m apart from the nearest bush, 6 m from any tree, and 12 m from forest edges or pasture borders.

In shrub cleared pastures we collected snails in five sampling plots situated in areas where shrubs were not removed between 1951 and 1994 and in five plots where shrubs were removed in the same period. In the comparisons of the three pasture types, data of the sampling plots situated in areas covered by shrubs were considered. Within shrub cleared pastures, data of sampling plots in formerly shrub-covered and shrub-free areas were compared.

We applied two methods to assess the species richness and relative abundance of terrestrial gastropods. First, one person searched for living snails and empty shells in each sampling plot for 20 min between 24 August and 8 October 2005. Second, we collected soil samples including dead plant material at randomly chosen spots in each sampling plot (in total 0.5 l soil per plot). We dried the soil samples at 60 °C for 24 h. Then, samples were put through sieves with mesh sizes of 2, 1 and 0.2 mm and later examined under a binocular microscope. Gastropod shells were sorted out of the samples and identified according to Kerney, Cameron & Jungbluth (1983). We did not consider slugs because their activity depends largely on weather conditions (Rollo, 1991), and the sampling methods used were not suitable to determine slug abundance (Oggier, Zschokke & Baur, 1998).

We used the topographical map of Switzerland (scale 1:25 000) to ascertain the elevation, average degree of exposure and area of the pastures. The isolation index of the single pastures was calculated from edge-to-edge according to Krauss, Steffan-Dewenter & Tscharntke (2003) considering all dry grassland areas of national importance within a radius of 3 km (Eggenberg, Dalang, Dipner & Mayer, 2001). In each pasture the inclination of the slope was measured at six randomly selected points using a trigonometrical method. We also measured the distance from the sampling plot's centre to (1) the nearest forest, (2) the nearest tree and (3) the nearest hedgerow, and estimated the cover of stones, old grass (dry grass not considered by grazing cattle) and bare ground. We collected a soil sample using a soil corer of 5.7 cm diameter and 10 cm depth in each sampling plot. The samples from the five plots of each pasture were combined for soil analyses: the percentage of carbon (C) and nitrogen (N), the content (in mg per 100 g soil) of calcium (Ca), phosphor (P_2O_5), potassium (K_2O), magnesium (Mg), copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn), the C/N ratio (C/N) and the soil pH in water (pH).

By interviewing the farmers we obtained information on livestock type, stocking rate, length of the grazing period and perimeter of the pastures. Grazing intensity was calculated as the product of the livestock units (LU, unit defined according to the Swiss ordinance on agricultural terms and types of farming; Swiss Federal Office for Agriculture, 2004; milk cow = 1, mother cow = 0.8, steer > 2 years old = 0.6, steer 1–2 years old = 0.4, calf of mother cow = 0.17) per hectare, and the number of days the pasture was stocked per year.

Snail characteristics

To examine whether gastropod species with different habitat specificity have been differentially affected by former pasture management, we assigned all snail species to one of the following categories: open-land (species exclusively occurring in open habitat), forest (species mainly found in forests) or ubiquitous species (species found in different types of habitat). Detailed information on the species habitat specificity was obtained from Kerney et al. (1983) and Falkner, Obrdlík, Castella & Speight (2001). Species considered as threatened are recorded on the Red list of Switzerland (Duelli, 1994). To assess whether gastropod species of different size were affected by former pasture management, we extracted data on mean adult size (shell height or shell length) from Kerney et al. (1983). The distribution of mean adult size of the species recorded was bimodal with a minimum at 5 mm. Thus, we classified snail species either as small-sized (adult size < 5.0 mm) or large-sized (adult size ≥ 5.0 mm).

Data analysis

The study site (20 different pastures) was considered as the unit of investigation in all analyses comparing the three pasture types. We applied one-way analysis of variance (ANOVA, type III model) to examine possible differences in habitat characteristics among pasture types. Sequential Bonferroni corrections of the significance level were used for multiple comparisons of environmental variables (Holm, 1979). Stepwise discriminant analysis was used to examine whether the three pasture types can be separated on the basis of environmental variables. Stepwise multiple regressions were performed to analyse the relationships between pasture characteristics and both snail species richness and abundance. As soil pH appeared to influence both snail species richness and abundance we used analyses of covariance with pasture type as factor and soil pH as covariate (ANCOVA, type III model). If the interaction between pasture type and soil pH was not significant, we repeated the ANCOVA without the interaction term (Grafen & Hails, 2002). In cases of significant differences among pasture types, we used Fisher's LSD test for pairwise comparisons of means.

We calculated Spearman rank correlations to examine possible correlations between snail species richness, abundance and the time elapsed since the removal of shrubs (in shrub cleared pastures) and the cessation of fertilization (in formerly fertilized pastures). As year of shrub removal in a pasture we determined the mean between the year of the aerial photograph with high shrub cover and the year of the photograph showing a dramatic reduction in shrub cover. Fisher's exact test was used to examine a possible influence of management history on the occurrence of individual snail species. In shrub cleared pastures, we applied paired t-tests to compare snail species richness, abundance and habitat characteristics of areas formerly covered by shrubs with areas free of shrubs throughout. We performed detrended canonical correspondence analyses (DCA) to examine possible differences in snail species composition among the three pasture types (Leps & Smilauer, 2003).

Statistical analyses were performed using the SPSS statistical package version 11.0, MacBonferroni and CANOCO 4.5. Data which did not fit normal distributions were $\log_{10}$-, square-root- or arcsin-transformed.

Results

Snail species richness

Shrub cleared, formerly fertilized and extensive pastures did not differ in any of the environmental variables examined (see Appendix A: Table 3). However, stepwise discriminant analysis revealed a first discriminant function based on the variables exposition, elevation, isolation and soil pH which separated fertilized pastures from the two other pasture types (Eigenvalue = 4.82, Canonical Correlation = 0.91, Chi-square = 33.03, df = 8, $p < 0.001$). The second discriminant function was not significant ($p = 0.13$). Stepwise multiple regression models with the environmental variables revealed that snail species richness, the number of open-land species and the number of red-listed species in the 20 study sites were positively related to soil pH of the pastures (Table 2). Furthermore, the total snail species richness and abundance were positively related to the isolation index.

A total of 32 gastropod species (14 open-land, seven forest and eleven ubiquitous species) were recorded in the 20 pastures. Open-land species constituted the major proportion of the snail community (open-land species 64.9 ± 11.1%, forest species 5.8 ± 6.8%, ubiquitous species 29.3 ± 7.8%, mean ± SD of 20 pastures). One to four snail species considered as threatened according to the Red list of Switzerland were recorded in the 20 pastures (in one formerly fertilized pasture no red-listed species was found).

Snail species richness differed among pasture types (ANCOVA, $F_{2,16} = 9.05$, $p < 0.01$; Fig. 1A). Moreover, soil pH had a significant positive effect on the number of snail species ($F_{1,16} = 16.86$, $p < 0.01$; Fig. 1A). Shrub cleared pastures harboured fewer snail species than extensive pastures (Fisher's LSD test, $p = 0.04$; Fig. 1A). Furthermore, we recorded fewer snail species in formerly fertilized pastures than in extensive pastures ($p < 0.01$). However, snail species richness did not differ between shrub cleared and formerly fertilized pastures ($p = 0.37$). The number of open-land species did not differ among pasture types (ANCOVA, $F_{2,16} = 1.91$, $p = 0.18$; Fig. 1B). However, soil pH had a significant positive effect on open-land species richness ($F_{1,16} = 5.42$, $p = 0.03$; Fig. 1B).

The three pasture types differed significantly in the number of threatened species (ANCOVA, $F_{2,16} = 7.49$, $p < 0.01$; Fig. 2A), but the number of red-listed species was not affected by soil pH ($F_{1,16} = 1.95$, $p = 0.18$). Shrub cleared pastures harboured marginally fewer red-listed species than extensive pastures (Fisher's LSD test, $p = 0.06$; Fig. 2A). Furthermore, the number of threatened species was lower in formerly fertilized pastures than in extensive pastures ($p < 0.01$). However, the number of threatened species did not differ between shrub cleared and formerly fertilized pastures ($p = 0.11$). The three pasture types differed marginally in the ratio of large- to small-sized snail species (ANCOVA, $F_{2,16} = 3.18$, $p = 0.07$), but this ratio was not affected by soil pH ($F_{1,16} = 1.47$, $p = 0.24$).

In shrub cleared pastures, the number of snail species, open-land species and red-listed species and the ratio of large- to small-sized species were not correlated with the time elapsed since shrub removal (Spearman rank correlation, in all cases $p > 0.55$). Furthermore, in formerly fertilized pastures, the number of snail species, open-land species and red-listed species and the ratio of large- to small-sized species were not correlated with the time elapsed since the cessation of fertilization (in all cases $p > 0.76$).

The DCA ordination based on the abundance data of each snail species revealed an overlapping area of 42% between the polygons of shrub cleared and extensive pastures (Fig. 3). In contrast, overlapping areas of only 1% and 2% were found between the polygons of formerly fertilized and extensive pastures and between the polygons of formerly fertilized and shrub cleared pastures. The first axis (Eigenvalue = 0.212) explained 27.9% of the variance in snail species data (together with the second and third axis 43.5%).

Snail abundance

A total of 11948 gastropod individuals were recorded in the 20 pastures. In all pastures, open-land individuals constituted the major proportion of the snail community (open-land 76.6 ± 19.1% of all individuals recorded, forest 0.8 ± 2.2%, ubiquitous 22.6 ± 18.0%; mean ± SD). A stepwise multiple regression model with the environmental variables revealed that the number of open-land snail individuals was positively related to the soil pH of the pastures examined (Table 2).

Total snail abundance did not differ among pasture types (ANCOVA, $F_{2,16} = 0.75$, $p = 0.49$). Moreover, soil pH did not affect total snail abundance ($F_{1,16} = 0.01$, $p = 0.92$). However, shrub cleared, formerly fertilized and extensive pastures differed in the number of open-land individuals (ANCOVA, $F_{2,16} = 7.41$, $p < 0.01$; Fig. 1C). Furthermore, soil pH and the interaction between pasture type and soil pH had a significant positive effect on the number of open-land snail individuals ($F_{1,16} = 36.06$, $p < 0.001$ and $F_{2,16} = 7.80$, $p < 0.01$; Fig. 1C). Shrub cleared pastures harboured marginally fewer open-land individuals than extensive pastures (Fisher's LSD test, $p = 0.08$; Fig. 1C). However, the abundance of open-land species did not differ between formerly fertilized and extensive pastures, and between formerly fertilized and shrub cleared pastures ($p = 0.16$ and $p = 0.74$).

The three pasture types differed in the number of red-listed snail individuals (ANCOVA, $F_{2,16} = 12.77$, $p < 0.001$; Fig. 2B). Soil pH had a marginally positive effect on the abundance of threatened snails ($F_{1,16} = 3.60$, $p = 0.08$). Shrub cleared pastures harboured fewer threatened snail individuals than extensive pastures (Fisher's LSD test, $p = 0.03$; Fig. 2B). Furthermore, the number of red-listed individuals was lower in formerly fertilized pastures than in extensive pastures and in shrub cleared pastures ($p < 0.001$ and $p = 0.04$). The three pasture types did not differ in the ratio of large- to small-sized snail individuals (ANCOVA, $F_{2,16} = 2.29$, $p = 0.13$). Furthermore, the ratio of large- to small-sized snail individuals was not affected by soil pH ($F_{1,16} = 0.39$, $p = 0.54$).

In shrub cleared pastures, total snail abundance, the number of open-land individuals, the number of red-listed individuals and the ratio of large- to small-sized snail individuals were not correlated with the time elapsed since shrub removal (Spearman rank correlation, in all cases $p > 0.33$). Moreover, in formerly fertilized pastures, total snail abundance, the number of open-land individuals and that of red-listed individuals were not correlated with the time elapsed since the cessation of fertilization (Spearman rank correlation, in all cases $p > 0.54$). However, the ratio of large- to small-sized snail individuals was positively correlated with the time elapsed since the cessation of fertilization ($r_s = 0.99$, $n = 6$, $p < 0.001$).

Effects on individual snail species

Twelve of the 32 snail species occurred at least in five pastures and at most in 15 of the 20 pastures examined (= common species). *Abida secale*, an ubiquitous species, occurred marginally less frequently in shrub cleared pastures than in extensive pastures (Fisher's exact test, $p = 0.098$). The occurrence of the other eleven common snail species (*Cochlostoma septemspirale, Cochlicopa lubrica*, *Cochlicopa lubricella*, *Truncatellina cylindrica*, *Pupilla muscorum*, *Nesovitrea hammonis*, *Vitrina pellucida, Helicella itala, Cecilioides acicula*, *Trichia plebeia* and *Helix pomatia*) did not differ between the two pasture types (in all cases $p > 0.32$).

Vitrina pellucida and *H. itala*, two open-land snail species, and *A. secale* were found less frequently in formerly fertilized pastures than in extensive pastures (Fisher's exact test, $p = 0.03$, $p < 0.01$ and $p = 0.02$). *Helicella itala* is a red-listed species. Furthermore, *H. pomatia*, a red-listed but ubiquitous species, occurred marginally less frequently in formerly fertilized than in extensive pastures ($p = 0.054$). The other eight common snail species did not differ in frequency of occurrence between the formerly fertilized and extensive pastures (in all cases $p > 0.11$).

Snail diversity and abundance within shrub cleared pastures

Within shrub cleared pastures, areas formerly covered by shrubs did not differ from shrub-free areas for at least 55 years in any of the soil variables examined (in all cases $p > 0.004$, the critical significance level after Bonferroni correction).

Pasture areas formerly covered by shrubs tended to harbour fewer snail species than shrub-free areas ($t_5 = 2.15$, $p = 0.08$). Furthermore, fewer open-land snail species were recorded in areas formerly covered by shrubs than in shrub-free areas ($t_5 = 2.80$, $p = 0.04$; Fig. 4A). The number of threatened species and the ratio of large- to small-sized snail species did not differ between formerly shrub-covered and shrub-free areas ($t_5 = 2.00$, $p = 0.10$ and $t_5 = 0.12$, $p = 0.91$).

Within pasture, total snail abundance in areas formerly covered by shrubs was lower than in shrub-free areas ($t_5 = 8.00$, $p < 0.001$; Fig. 4B). Furthermore, formerly shrub-covered areas harboured fewer open-land individuals and red-listed individuals than shrub-free areas ($t_5 = 4.86$, $p < 0.01$; $t_5 = 4.37$, $p < 0.01$; Fig. 4C and D). The ratio of large- to small-sized snail individuals, however, did not differ between formerly shrub-covered areas and shrub-free areas ($t_5 = 0.84$, $p = 0.44$).

Discussion

Our study shows that changes in pasture management over the last 55 years influenced the present-day snail community of dry, nutrient-poor calcareous grasslands. Formerly shrub-covered but now restored pastures harboured fewer snail species and individuals, fewer open-land species and individuals and fewer red-listed individuals than extensive pastures. An increased management intensity over a period of 15–25 years had a negative effect on the number of both red-listed species and individuals and altered the snail community. The present-day grazing intensity of the pastures examined was relatively low (less than 180 $LU.ha^{-1}.d$ in 18 of the 20 pastures). A previous study showed that threatened snail species in dry, nutrient-poor grasslands are not affected at low levels of grazing intensity (Boschi & Baur, 2007b).

In shrub cleared pastures, the former shrub and tree cover protected the soil from intensive solar radiation and wind (Geiger, Aron & Todhunter, 2003). As a consequence, the relative humidity of both the soil and the air above the ground is higher and the temperature lower than in shrub-free pastures. Furthermore, the daily fluctuations of air humidity and temperature are reduced in shrub-covered pastures (Morecroft, Taylor & Oliver, 1998). These microclimatic conditions might be less favourable for thermophile snail species of dry grasslands (e.g. *T. cylindrica* and *H. itala*; Falkner et al., 2001). However, shrub cover was patchy in these pastures allowing some open-land snails to survive until shrub removal. Moreover, some individuals could subsequently have been transported by cattle from shrub-free to formerly shrub-covered pasture areas (Fischer, Poschlod & Beinlich, 1996).

Formerly fertilized pastures were managed more intensively over a period of 15 years or even longer. Management intensity of pastures is characterized by a combination of fertilization and grazing intensity which can negatively influence the snail fauna in different ways. Application of fertilizer in nutrient-poor calcareous grasslands increases biomass of plants which further reduces light penetration to the ground (Bobbink, 1991). During the previous period of intensive management, the microclimate in formerly fertilized pastures was characterized by an increased moisture near the soil surface. These conditions might have been unfavourable for xerothermic snail species. Moreover, species-rich snail communities depend on heterogeneous structures that provide a variety of microhabitats (a wide range of temperature and humidity conditions, different food resources and refuges above and below ground) for different species (Labaune & Magnin, 2001). A decrease in structural habitat complexity as a consequence of former fertilizer application and intensive grazing resulted in the local extinction of snail species with specific habitat requirement. In particular, *V. pellucida* and *H. itala*, which were found less frequently in formerly fertilized than extensive pastures, might have been affected by the former high management intensity and *H. itala* especially by the application of fertilizer (Boschi & Baur, 2007b).

The ratio of large- to small-sized snail individuals was positively correlated with the time elapsed since the cessation of fertilization in formerly fertilized pastures. However, the ratio did not differ between formerly fertilized and extensive pastures. Boschi & Baur (2007b) found that snail species with large shells were more affected by grazing intensity than species with small shells. Large-sized snail individuals are assumed to benefit from lower grazing intensity after cessation of fertilization, especially from a decreased trampling by cattle.

Our study showed that snail species richness, and both the number of open-land species and individuals increased with increasing soil pH. The influence of soil pH on species richness and abundance of snails is consistent with other studies (Wäreborn, 1970). Furthermore, there was a significant interaction between pasture type and soil pH on the number of open-land snail individuals. The accumulation of leaf litter in formerly shrub-covered pastures could have caused an increase in soil acidity. Vegetation changes can affect soil pH within a decade (Farley & Kelly, 2004). However, the litter of only some specific plant species influences the soil pH (Falkengren-Grerup, ten Brink & Brunet, 2006). In contrast, former fertilization does not seem to influence the present-day soil pH as former shrub cover does. Frequent application of manure and/or artificial nitrogen fertilizer without addition of chalk reduces the soil pH (Silvertown, Poulton, Johnston, Edwards, Heard et al., 2006). However, in the present study formely fertilized pastures were only lightly fertilized, with no apparent impact on soil pH.

In most cases, the snail community of shrub cleared pastures, and especially that of formerly fertilized pastures did not recover after shrub removal or cessation of fertilization. On one hand, the length of time for recolonisation could have been too short for snails, since they have a limited dispersal ability (Baur & Baur, 1988; Baur & Baur, 1995). On the other hand, the isolation of the pastures examined may reduce the probability of immigration of snails. In fact, we found a negative effect of isolation on the snail species richness and abundance. The extent of isolation of a pasture from the remaining grassland in the surrounding landscape is actually considered as one of the key factors influencing the species richness, distribution and abundance of individuals within habitat fragments (Saunders, Hobbs & Margules, 1991).

General implications

Most management plans aim to preserve the whole community, in particular the threatened or rare plant and animal species, of calcareous grasslands using different regimes of mowing, grazing and shrub clearing. Because the study sites are rather isolated, the recolonisation is reduced and the snail community may not recover from periods of shrub cover and intensive management (Muller, Dutoit, Alard & Grévilliot, 1998). The situation of formerly fertilized pastures seems to be analogous to ecological compensation areas which contributed little to regional species richness, in particular to the conservation of threatened invertebrate species (Kleijn, Berendse, Smit, Gilissen, Smit et al., 2004). Therefore, extensive pasture management of formerly fertilized pastures should be complemented with the creation and maintenance of new semi-natural areas and the preservation of a network of intact semi-natural grasslands.

Acknowledgements

We thank the farmers giving access to their pastures. We are grateful to both the Offices of Agriculture and Land Use Planning of the cantons Basel-Landschaft and Solothurn for their collaboration in organising appropriate study areas, and G. Armbruster, A. Baur, H.-P. Rusterholz and P. Stoll for constructive comments on the manuscript. Financial support was received from the Bristol Foundation in Schaan (Principality of Liechtenstein).

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Table 1. Temporal changes in the cover of shrubs and trees (median; range in parenthesis), year of the shrub removal and year since the cessation of fertilization on the pastures examined.

Pasture type	ID	Cover of shrubs and trees (%)						Shrub removal / cessation of fertilization
		1951–53	1970	1982	1987–88	1994	2000	(yr)
Shrub cleared	S1	1 (-)	0 (-)	0 (-)	90 (-)	2 (-)	5 (-)	1991
	S2	80 (-)	0 (0–10)	1 (-)	0 (0–15)	0 (0–1)	0 (0–5)	1961
	S3	70 (10–70)	60 (30–70)	80 (80–90)	60 (10–80)	20 (0–20)	1(1–10)	1991
	S4	40 (40–50)	50 (50–80)	80 (70–80)	80 (0–80)	0 (0–1)	1 (0–1)	1991
	S5	1 (1–10)	5 (-)	0 (-)	70 (70–90)	1 (0–30)	1 (-)	1991
	S6	70 (-)	0 (0–2)	5 (0–5)	2 (0–2)	2 (0–2)	2 (0–2)	1961
Formerly fertilized	F1	10 (-)	10 (-)	0 (-)	0 (-)	0 (-)	0 (-)	1999
	F2	1 (-)	1 (-)	0 (-)	0 (-)	0 (-)	0 (-)	2001
	F3	0 (0–30)	0 (0–20)	0 (0–20)	0 (0–20)	0 (0–20)	0 (0–10)	2001
	F4	5 (0–20)	0 (-)	0 (-)	0 (0–5)	0 (0–5)	0 (0–5)	1994
	F5	1 (1–10)	1 (-)	1 (1–10)	1 (-)	1 (-)	1 (-)	1993
	F6	0 (-)	0(-)	0 (-)	0 (-)	0 (-)	0 (-)	1998
Extensive	E1	1 (1–15)	1 (-)	1 (1–20)	1 (1–10)	1 (1–10)	3 (3–10)	-
	E2	0 (-)	0 (-)	0 (-)	0 (-)	1 (-)	1 (-)	-
	E3	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	-
	E4	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	-
	E5	0 (-)	1 (1–20)	3 (0–3)	1 (1–25)	1 (1–20)	5 (0–10)	-
	E6	5 (1–15)	5 (1–10)	5 (1–10)	1 (1–10)	0 (0–10)	10 (0–10)	-
	E7	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	-
	E8	1 (-)	1 (-)	0 (-)	0 (-)	1 (1–10)	1 (1–10)	-

Table 2. Results of stepwise multiple regression analyses with diversity and abundance of snails as dependent variables and pasture variables as independent variables.

Dependent variable Independent variable	β	SE	Cumulative r^2	t	p
- Number of snail species					
Intercept	-	-	-	–4.01	0.001
Soil pH	6.32	1.18	0.37	5.35	< 0.001
Isolation index	0.01	0.00	0.56	2.37	0.030
Woodland perimeter	3.77	1.68	0.67	2.25	0.039
- Number of open-land snail species					
Intercept	-	-	-	–1.46	0.162
Soil pH	2.27	0.79	0.31	2.86	0.010
- Number of red-listed species					
Intercept	-	-	-	–4.34	0.001
Exposure	0.03	0.00	0.27	4.38	< 0.001
Soil pH	1.55	0.38	0.54	4.10	0.001
Area	0.61	0.27	0.65	2.26	0.038
- Abundance of snails					
Intercept	-	-	-	–1.63	0.121
Isolation index	0.39	0.14	0.31	2.85	0.011
- Abundance of open-land snail species					
Intercept	-	-	-	0.17	0.867
Soil pH	9.64	2.20	0.50	4.41	< 0.001
N content	–428.54	177.26	0.62	–2.42	0.027

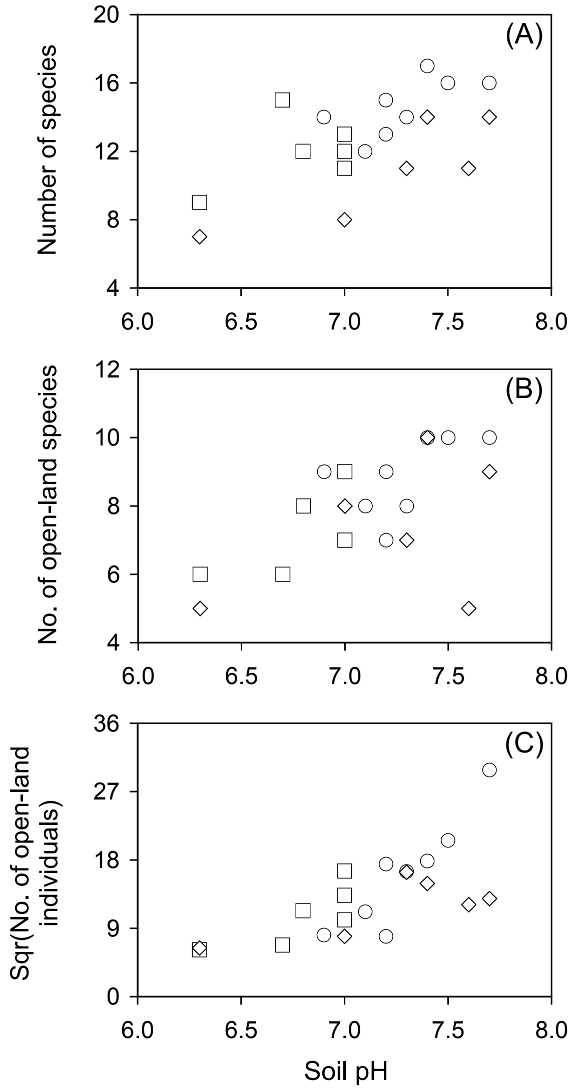

Fig. 1. Relationship between snail species richness (A), the number of open-land species (B) and the number of open-land individuals (C) and soil pH. Shrub cleared pastures are indicated by squares, formerly fertilized pastures by diamonds and extensive pastures by open dots. Statistics are presented in the text.

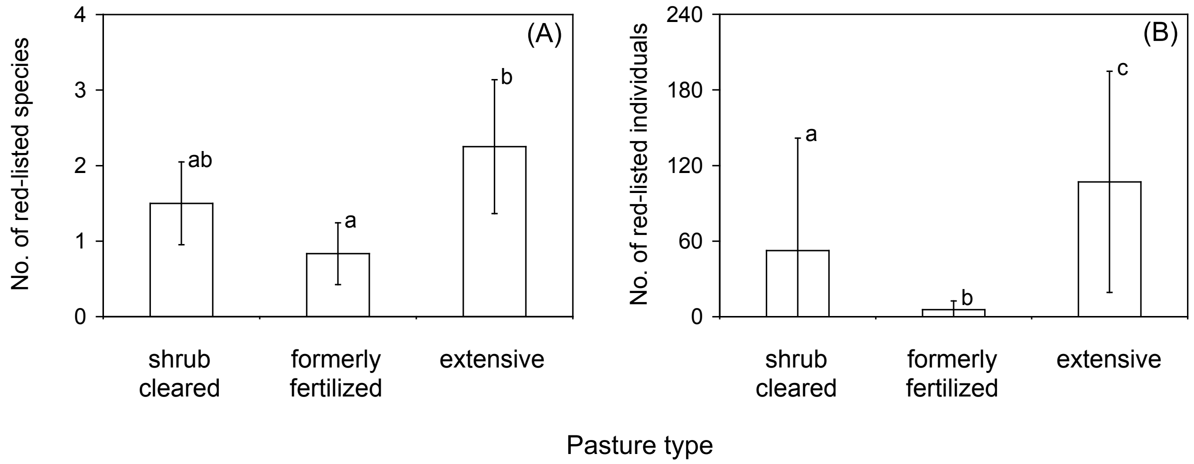

Fig. 2. Number of red-listed species (A) and individuals (B) in the six shrub cleared pastures, six formerly fertilized and eight extensive pastures (mean ± SD). Significant differences ($p < 0.05$) between pasture types are indicated by different letters (based on pairwise comparisons using Fisher's LSD test).

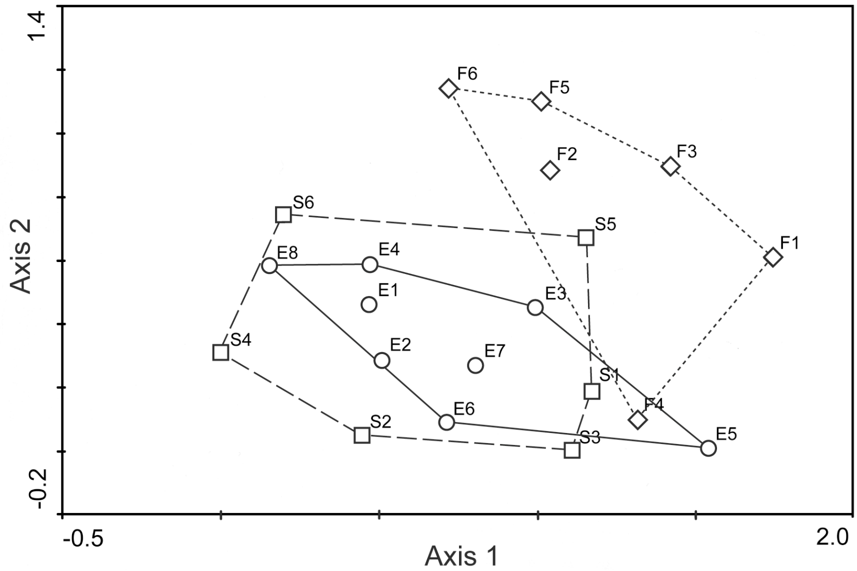

Fig. 3. Ordination diagram based on detrended correspondence analysis of snail species composition in shrub cleared (squares), formerly fertilized (diamonds) and extensive pastures (open dots). The polygons represent the boundaries of the different pasture types. ID's of the pastures as in Table 1.

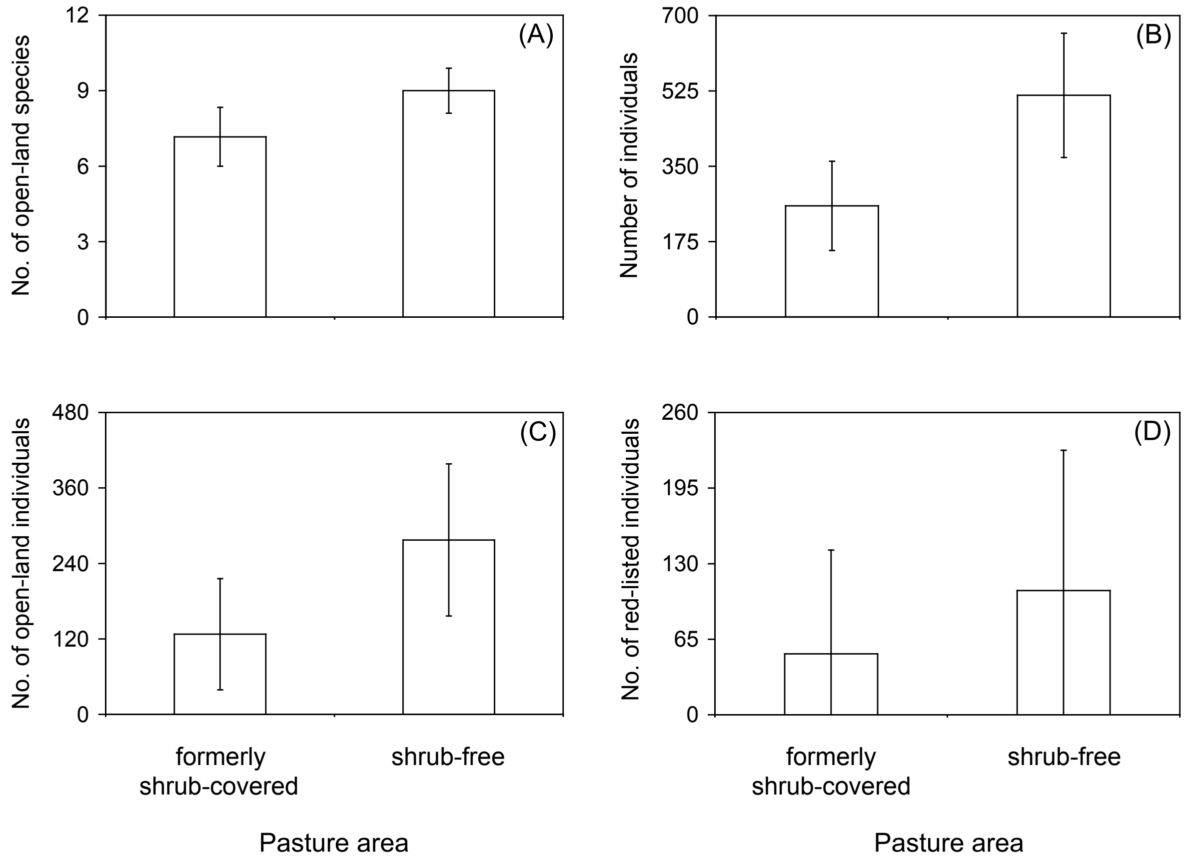

Fig. 4. Number of open-land species (A), total number of individuals (B), number of open-land individuals (C) and red-listed individuals (D) recorded in formerly shrub-covered and shrub-free areas in shrub cleared pastures (mean ± SD, n = 6 in each case).

Appendix A

Table 3. Characteristics of the six shrub cleared, six formerly fertilized and eight extensive pastures investigated in the Swiss Jura mountains. Five samples per pasture were pooled and the mean ± SD among pastures of the same type was calculated. p adjusted using Holm's (1979) sequentially rejective multiple Bonferroni procedure. In each case d.f. = 2 and n = 20.

Environmental variables	Pasture type			ANOVA		Sequential critical p
	Shrub cleared	Formerly fertilized	Extensive	F	p	
Elevation (m a.s.l.)	843 ± 214	536 ± 178	928 ± 228	6.27	0.009	0.002
Exposure (°)	177 ± 30	139 ±.20	170 ± 19	4.79	0.022	0.003
Inclination (°)	23.9 ± 5.4	22.4 ± 5.6	26.8 ± 3.1	1.66	0.220	0.003
Area (ha)	29.3 ± 22.1	12.8 ± 15.8	17.1 ± 10.7	2.11	0.152	0.003
Isolation index (km.ha)	20.2 ± 14.1	4.5 ± 4.3	21.0 ± 19.2	4.86	0.021	0.002
Woodland perimeter (%)	79.3 ± 16.2	50.2 ± 30.8	72.0 ± 14.7	1.90	0.179	0.003
Present tree cover (%)	3.3 ± 1.5	5.5 ± 5.9	4.2 ± 6.4	0.22	0.805	0.017
Present hedgerow cover (%)	2.0 ± 1.4	2.5 ± 2.1	3.3 ± 3.5	0.02	0.981	0.025
C (%)	4.7 ± 0.6	4.6 ± 0.2	5.0 ± 0.3	1.65	0.222	0.004
N (%)	2.0 ± 0.2	2.1 ± 0.1	2.0 ± 0.1	1.05	0.371	0.007
Ca (mg / 100 g soil)	495.3 ± 270.8	731.0 ± 282.2	674.1 ± 174.5	1.60	0.230	0.004
P_2O_5 (mg / 100 g soil)	3.4 ± 1.6	3.8 ± 2.0	4.3 ± 0.4	1.19	0.330	0.006
K_2O (mg / 100 g soil)	19.8 ± 3.9	19.0 ± 6.5	16.6 ± 3.4	0.85	0.445	0.008
Mg (mg / 100 g soil)	22.3 ± 6.4	26.3 ± 3.9	26.6 ± 5.3	1.42	0.268	0.004
Cu (mg / 100 g soil)	0.10 ± 0.07	0.06 ± 0.05	0.05 ± 0.02	0.85	0.445	0.010
Fe (mg / 100 g soil)	5.9 ± 7.9	5.2 ± 10.9	1.0 ± 1.0	1.46	0.260	0.004
Mn (mg / 100 g soil)	21.6 ± 9.9	13.2 ± 14.9	16.9 ± 9.9	1.12	0.350	0.006
Zn (mg / 100 g soil)	0.72 ± 0.34	0.48 ± 0.41	0.68 ± 0.58	0.57	0.578	0.012
C/N ratio	2.4 ± 0.5	2.2 ± 0.1	2.5 ± 0.3	1.38	0.278	0.005
Soil pH	6.8 ± 0.3	7.2 ± 0.5	7.3 ± 0.2	3.59	0.050	0.003
Present grazing intensity ($LU.ha^{-1}.d$)	108.0 ± 41.7	105.5 ± 16.2	142.4 ± 135.9	0.02	0.981	0.050

Chapter 4

The effect of different types of forest edge on the land snail communities of adjacent, nutrient-poor calcareous grasslands

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Submitted for publication

Abstract

Semi-natural, nutrient-poor dry grasslands harbour numerous plant and invertebrate species. These grasslands are increasingly threatened because of land use intensification or abandonment. The remaining fragments of nutrient-poor grassland are frequently surrounded by forest or intensively cultivated agricultural areas. Effects of adjacent habitats may further reduce the size of grassland fragments. We examined the effects of gradual and abrupt forest edges on the snail community of extensive pastures in the Swiss Jura mountains. Gastropod species richness and abundance were assessed in 45 m-long transects running from pastures (20 m) through gradual or abrupt forest edges into the forest interior (25 m). The two types of forest edge influenced the snail communities in the adjacent pastures in a different way. In pastures, at a distance of 10 m from gradual forest edges, more open-land snail species were found than at the corresponding distance from abrupt forest edges. Furthermore, ecotones of gradual forest edges harboured more open-land individuals than those of abrupt forest edges. In general, snail species richness and abundance of individuals were larger in the ecotone than in the grassland or forest interior. The snail communities in the pastures were distinct from those in the ecotones and forest interior independent of the type of forest edge. The shadowing of trees and alterations of the microclimate close to the forest edge may reduce the actual size of grassland remnants. Hence, a regular removal of encroaching shrubs and the maintenance of gradual forest edges may contribute to the preservation of species-rich open-land snail communities in small semi-natural grassland fragments.

Introduction

Maintaining biodiversity in agricultural areas is one of the major challenges for biodiversity conservation in Central Europe (WallisDeVries et al. 2002). Traditional rural habitats, particularly semi-natural grasslands, have been recognised as regional biodiversity hotspots (van Swaay 2002, Cremene et al. 2005). As human-made habitats, dry, nutrient-poor calcareous grasslands harbour also numerous species whose primordial habitats (floodplains, peatlands, and rocky outcrops) have been largerly destroyed (Baur et al. 1996). However, semi-natural grasslands are fragile because their maintenance depends on traditional farming techniques (Zamora et al. 2007). During the twentieth century, increasing pressure for higher production at low costs has led to either an intensification of grassland use (increased stocking rate and/or increased use of fertilizer) or to abandonment (Hodgson et al. 2005, Strijker 2005). Both processes lead to a reduction of the area of semi-natural grassland.

Remaining fragments of semi-natural grassland are frequently surrounded by forest or intensively cultivated agricultural areas and thus isolated (Olsson et al. 2000). The zone of transition between different adjacent ecological systems is called the ecotone (di Castri et al. 1988). Within a natural system, the change in organism composition across the ecotone is rarely abrupt and there is usually some interchange between the habitats resulting from dispersal. Moreover, in some groups of organisms, there are species which are specialized for ecotone structures (e.g. in Neuroptera, Duelli et al. 2002). Hence, ecotones typically exhibit larger species diversity and often larger abundance of species than adjacent ecological systems (Ries et al. 2004). In particular, ecotones harbour a higher number of spider, carabid and bird species than adjacent habitats (Bedford and Usher 1994, Berg and Pärt 1994, Downie et al. 1996).

Ecotone research concentrates mostly on forest edge effects on forest communities, whereas studies including the effects on grasslands are rare (e.g. Magura 2002). Edge effects indicate negative influences of a habitat boundary on the abiotic conditions in the interior of a habitat, or on species that use interior habitat (Groom et al. 2006). Differences in structural complexity and biomass of the two adjacent ecosystems result in differences in microclimate and other abiotic factors, such as light intensity and air speed near forest edges (Matlack 1993). Many of these parameters are also more variable near the edge than in the habitat interior. Therefore, forest edges make the functional core area of a grassland remnant smaller than its actual area (Laurance and Yensen 1991). Small grassland fragments may no longer provide open-land conditions, and as a result may undergo dramatic changes in the natural composition of open-land communities (Saunders et al. 1991).

The boundaries between grassland and forest can be abrupt, gradual, sharp or form a “mosaic” of the two ecosystems (di Castri et al. 1988). In the cultural landscape, boundaries are mostly human-made. Although the structure of grassland-forest edge is of great importance for diversity and abundance of farmland birds, it is not known whether a certain type of forest edge is more appropriate than others to maintain the diversity of invertebrates in small grassland fragments (Berg and Pärt 1994). The response of animals to forest edges depends upon their habitat preference, body size, mobility, behavioural characteristics and life history (Ingham and Samways 1996). However, there are no studies available on the influence of forest edges on organisms living in grasslands with limited mobility, such as gastropods (Baur 1986, Baur and Baur 1988, Wirth et al. 1999).

In the Swiss Jura mountains extensive grazing with a low number of livestock and without the use of fertilizers is a traditional form of grassland management (Werthemann 1963, Imboden 1965). These calcareous grasslands harbour a high species diversity of plants and invertebrates (Baur et al. 1996). Between 1950 and 1980, 45% of all nutrient-poor, dry calcareous pastures in the Northwestern Swiss Jura mountains were converted into intensively managed pastures and a further 10% were abandoned (Zoller et al. 1986). The fragmentation and isolation of nutrient-poor grassland remnants resulted in a significant decline of specialist plant species within a short period (Fischer and Stöcklin 1997). Similar declines are assumed in specialized invertebrates inhabiting these grasslands (Niemelä and Baur 1998).

To examine the effect of different types of forest edge on the specialized open-land gastropod community of nutrient-poor grasslands, we assessed the diversity and abundance of land snails at six gradual and six abrupt forest edges in the Northwestern Swiss Jura mountains. In particular, we addressed the following questions: (1) Do gradual and abrupt forest edges affect the spatial distribution, diversity and abundance of open-land and forest species in different ways? (2) Are typical open-land and typical forest species differently affected by the two types of forest edge? And (3) are species diversity and abundance of land snails increased in the grassland-forest ecotone?

Material and methods

Study sites

This study was carried out at 12 localities in the Swiss Jura mountains in a region measuring 33 x 15 km (47°19'–47°27'N, 7°19'–7°48'E; elevations between 475 and 972 m a.s.l.). At each locality a grassland-forest edge situated on a SSE–SSW slope (inclination 19.4–33.9°) was examined. The pastures ranged in size from 1.7 to 41.0 ha and were partly or entirely surrounded by mixed deciduous forest dominated by beech (*Fagus sylvatica*). Tree species at the forest edges included also *Sorbus aria*, *Acer campestre*, *Pinus sylvestris*, *Quercus petraea* and *Picea abies* as well as bushes of *Crataegus monogyna*, *Rosa* sp., *Ligustrum vulgare*, *Prunus spinosa* and *Viburnum lantana*. The nutrient-poor, dry calcareous grasslands belong to the Teucrio-Mesobrometum association (Ellenberg 1996). The pastures were unfertilized and stocked with a low density of steers or mother cows between June and September (Boschi and Baur 2007). All examined pastures have been managed in the same way for at least 15 years.

Survey design

At each study site three parallel transect lines of sampling plots (measuring 1 m x 1 m) were established 20 m apart from each other. Transect lines were placed perpendicular to the forest edge extending from the pasture (20 m) through the forest edge into the interior of the forest (25 m). The length of the transect line was determined by the width of the extensively managed pastures. In the Swiss Jura mountains the majority of extensive pastures are narrow strips (50–175 m wide) surrounded by forest, intensively managed agricultural areas and settlements. On each transect line 10 sampling plots were placed at distances of 5 m. Four plots were placed in the pasture, one exactly at the forest edge (close to the first stem of bush or tree) and five in the forest interior (Fig. 1).

All 12 forest edges examined faced towards south. Six of them were gradual with a strip of bushes ranging from 1.1 to 7.4 m (hereafter referred to as gradual forest edge). These bushes are expanding from the formerly abrupt forest edge and thereby are overgrowing the pasture. The other six forest edges showed an abrupt change from forest to grassland vegetation (hereafter referred to as abrupt forest edge). Soil pH in water, determined at two forest edges (0–10 cm depth), was similar in the pasture (pH = 7.8), at the edge (7.7) and in the forest interior (7.5).

Sampling methods

We collected gastropods in the sampling plots between 19 April and 7 June 2006. Two methods were applied to assess the species richness and relative abundance of terrestrial gastropods. First, one person visually searched for living snails and empty shells in each sampling plot for 15 min. Second, we collected soil samples including dead plant material at randomly chosen spots in each sampling plot (total 0.25 l soil per plot). We dried the soil samples at 50 °C for 4 h. Then, samples were put through sieves with mesh sizes of 2, 1 and 0.2 mm and later examined under a binocular microscope. Gastropod shells were sorted out of the samples and identified according to Kerney et al. (1983). We did not consider slugs because their activity depends largely on weather conditions (Rollo 1991), and the sampling methods used were not suitable to determine slug abundance (Oggier et al. 1998).

Snail characteristics

Snail species were assigned to one of the following categories: open-land (species exclusively occurring in open habitat), forest (species mainly found in forests) or ubiquitous species (species found in different types of habitat). Detailed information on the species habitat specificity was obtained from Kerney et al. (1983) and Falkner et al. (2001). Species considered as threatened are recorded on the Red list of Switzerland (Duelli 1994).

Data analysis

The study sites (n = 12 grassland-forest edges) were considered as unit of investigation in all analyses comparing snail species richness and abundance of gradual and abrupt forest edges. We used t-test to examine possible differences in snail species richness and abundance between gradual and abrupt forest edges. Chi-square test was applied to compare proportions of snails species and individuals with different habitat specificity at single distances from forest edge and to examine habitat preference of common species. We considered a species as common if it occurred in at least eight of the 12 study sites and if altogether more than 30 individuals were found. The spatial distribution of individuals of common species was compared with a uniform distribution assuming equal numbers of snails in each sampling plot in pasture, ecotone and forest interior. The width of each of these ecological zones was determined by comparing the proportions of snail species and individuals with particular habitat specificity (obtained from the literature) at gradual and abrupt forest edges using 5 m steps (see results). With our set up of sampling plots we would expect to find 40% of the individuals in the pasture, 30% in the ecotone and 30% in the forest interior (null hypothesis of uniform distribution; Fig. 1). *Abida secale*, *Orcula dolium* and *Vitrea subrimata*, which are restricted to rocky habitats, were excluded from this analysis. Sequentially Bonferroni correction of the significance level was used for multiple comparisons of distributions of single snail species (Holm 1979).

To examine possible differences in snail species composition among the three ecological zones and between gradual and abrupt forest edges, we used detrended canonical correspondence analyses (DCA; Leps and Smilauer 2003).

Statistical analyses were performed using the SPSS statistical package version 11.0, MacBonferroni and CANOCO 4.5. Data which did not fit normal distributions were $\log_{10}$-, square-root- or arcsin-transformed.

Results

A total of 19379 gastropod individuals belonging to 52 species (13 open-land, 23 forest and 16 ubiquitous species) were recorded. Five of the 52 snail species (9.6%) are considered as threatened according to the Red list of Switzerland. In the pasture at distances ≥ 5 m from the forest edge, 35 snail species were found. Forty-five species were recorded in the forest interior at distances of 0–10 m from the forest edge and 38 species at distances > 10 m from the forest edge.

Effects of forest edges along transect lines

Comparing gradual and abrupt forest edges at different distances from the edge, the proportion of open-land, forest and ubiquitous snail species changed depending on the position of the sampling plots (Fig. 2). In the pasture at distances of 15–20 m from the forest edge, the snail community consisted of 67.8 ± 11.3% (mean ± SD) open-land species, 6.6 ± 7.8% forest species and 25.6 ± 9.4% ubiquitous species. In the forest interior at distances of > 5 m from the forest edge, there were 6.8 ± 5.6% open-land species, 78.3 ± 7.9% forest species and 14.9 ± 6.9% ubiquitous species. Transect lines covering gradual and abrupt forest edges did not differ in the proportion of open-land, forest and ubiquitous species, except in the pasture at a distance of 10 m and marginally at a distance of 15 m from the forest edge ($\chi^2_2 = 8.80$, $p = 0.01$ and $\chi^2_2 = 5.57$, $p = 0.06$; all other comparisons, $p > 0.18$; Fig. 2A and B). At gradual forest edges a higher proportion of open-land species and a lower proportion of forest species were found at distances of 10 and 15 m from the edge than at abrupt forest edges (Fig. 2A and B).

Considering the number of snail individuals, pastures at distances of 10–20 m from the forest edge contained 86.6 ± 11.5% open-land snail individuals, 1.8 ± 2.8% forest individuals and 11.6 ± 10.4% ubiquitous individuals. The forest interior at distances > 10 m from the edge harboured 1.9 ± 1.9% open-land snail individuals, 85.3 ± 9.8% forest individuals and 12.8 ± 9.3% ubiquitous individuals. Gradual forest edges differed in the proportion of open-land, forest and ubiquitous individuals from abrupt forest edges at distances of 0–10 m in the forest ($\chi^2_2 = 10.33$, $p < 0.01$, $\chi^2_2 = 8.07$, $p = 0.02$ and $\chi^2_2 = 6.52$, $p = 0.04$; all other comparisons, $p > 0.13$; Fig. 2C and D). Gradual forest edges harboured more open-land individuals and fewer forest individuals than abrupt forest edges (Fig. 2C and D). Based on these abundances, three ecological zones can be defined along the transect lines: pasture (at a distance > 0 m from the forest edge), ecotone (0–10 m in the forest) and forest interior (at a distance > 10 m from the forest edge).

Grassland-forest ecotone

Snail species richness did not differ between gradual forest edges and abrupt forest edges both in the pasture and ecotone (in both cases, $p < 0.21$; Fig. 3A). In contrast, fewer snail species were found in the forest interior with gradual edge than in the forest interior with abrupt edge ($t_{10} = 2.57$, $p = 0.03$; Fig. 3A). Pastures, ecotones and forest interiors contained similar proportions of threatened snail species irrespective of the type of forest edge (in all cases, $p > 0.59$).

Total snail abundance did not differ between gradual forest edges and abrupt forest edges in the pasture ($t_{10} = 0.12$, $p = 0.91$; Fig. 3B). However, fewer snail individuals were found at gradual edges than at abrupt edges both in the ecotone and forest interior ($t_{10} = 2.80$, $p = 0.02$ and $t_{10} = 3.68$, $p < 0.01$; Fig. 3B). Pastures, ecotones and forest interiors harboured similar proportions of threatened snail individuals irrespective of the type of forest edge (in all cases $p > 0.16$).

The DCA ordination based on the abundance data of each snail species revealed a distinct separation of the snail communities in the pastures from those in the ecotone and forest interior (Fig. 4). Snail communities in the ecotone were similar to those of the forest interior. In neither ecological zone, snail communities at gradual forest edges were separated from snail communities at abrupt forest edges. The first axis (Eigenvalue = 0.697) explained 34.7% of the variance in snail species data (together with the second and third axis 48.4%).

Habitat preference of single snail species

Twenty-four of the 52 snail species (46.2%) were common species (Table 1). Eight snail species, including the red-listed *Helicella itala,* preferred the open-land rather than the ecotone or the forest (Table 1). Another twelve snail species, including the red-listed *Acicula lineata*, occurred mainly in the ecotone and forest interior. *Punctum pygmaeum* and *Trichia plebeia* showed no preference for any of the three ecological zones. Interestingly and in contrast to data from the literature, the open-land species *Vitrina pellucida* was most frequently found in the ecotone. Furthermore, *Helix pomatia*, according to the literature an ubiquitous species, preferred the open-land and ecotone rather than the forest.

The proportion of snail individuals found in pasture, ecotone and forest interior did not differ between gradual and abrupt forest edges for either common snail species, except for *Trichia plebeia*. In this species a higher proportion of individuals was recorded in pastures and a lower proportion both in the ecotone and forest interior at gradual than at abrupt edges ($\chi^2_2 = 10.33$, $p < 0.001$, the critical significance level after Bonferroni correction; all other comparisons $p > 0.003$).

Discussion

The present study showed that gradual and abrupt forest edges differed in the proportions of open-land snail species and individuals occurring in the adjacent pastures. In the pastures, at a distance of 10 m from gradual forest edges more open-land species were found than at the corresponding distance from abrupt forest edges. Furthermore, gradual forest edges harboured more open-land individuals in the ecotone than abrupt forest edges. The snail communities of the pastures were clearly distinct from those of the ecotones and forest interior at both types of forest edge. In accordance with previous studies considering spider, carabid beetle and bird diversity we found a higher snail species richness in the ecotone than in the adjacent ecological zones (Bedford and Usher 1994, Berg and Pärt 1994, Downie et al. 1996).

Shrubs and trees provide shade and protection against wind. Consequently, the air and soil humidity above the ground is lower and the temperature higher in the pasture than in the ecotone and forest interior (Geiger et al. 2003). Furthermore, the daily fluctuations of air humidity and temperature are reduced in the ecotone and forest interior (Morecroft et al. 1998). Based on abiotic variables, estimates of ecotone width reached 50 m into the interior of forests (Matlack 1993). The width of the edge zone may vary, primarily determined by the size of the adjacent habitats and the degree of difference between the habitat types. Moreover, the orientation of the edge may influence the width of the ecotone (Fraver 1994).

Abiotic factors in close proximity to gradual forest edges with an open tree canopy differ from those at abrupt forest edges with a dense tree canopy (Murcia 1995). Since solar radiation penetrates deeper and stronger into gradual forest edges, air and soil temperature is higher and the relative humidity lower at gradual than at abrupt forest edges (Chen et al. 1995). Furthermore, the microclimate is probably more variable and the decomposition rates of leaf litter and woody debris are higher at gradual than at abrupt forest edges.

The snail community in the pasture mainly consisted of thermophile species that require dry and warm conditions typical for nutrient-poor, calcareous grasslands (Baur et al. 1996, Falkner et al. 2001). The microclimatic conditions in the ecotone and forest interior are unfavourable for these snail species. Mesophilous snail species, which preferentially occur in habitats of intermediate humidity, find most suitable microclimatic conditions in the ecotone and forest interior. Interestingly, the microclimatic conditions in the pasture close to gradual forest edges appear to be more favourable for open-land snail species than those close to abrupt forest edges. Forest species, however, occurred less frequently close to gradual forest edges than close to abrupt forest edges. This is probably a result of a reduced shading by the relatively open tree canopy close to gradual forest edges compared with the dense tree canopy at abrupt forest edges. Magnin and Tatoni (1995) suggested that a forest snail community can establish when tree cover exceeds a 50% threshold.

Habitat structures in pastures consist mainly of grass and herbs, in the ecotone and forest interior of stems of trees and bushes, leaf litter and dead wood. Food preferences for specific plant species influence the occurrence and abundance of certain weevil species across grassland-forest edges (Horváth et al. 2000). Although some land snail species show distinct food preferences, the majority of the snail species are polyphagous (Frömming 1954, Fröberg et al. 1993). However, numerous snail species have narrow habitat requirements (e.g. various forest snail species live in leaf litter and feed on decaying leaves). Therefore, the availability of food and shelter combined with microclimatic conditions may influence the composition of the snail community across grassland-forest edges.

The habitat preferences found in the common snail species of the present study coincide with those of the literature (Kerney et al. 1983, Falkner et al. 2001), the only exceptions were *Vitrina pellucida* and *Helix pomatia*. The open-land species *V. pellucida* was mainly found in the ecotone. This snail species prefers moister conditions than most of the other open-land species (Falkner et al. 2001). However, the low abundance of *V. pellucida* recorded in the pastures could also be the result of its low tolerance to grazing. High grazing intensity reduces plant density, sward height and litter layer, and hence decreases the heterogeneity in vegetation structure and indirectly humidity above surface (King and Hutchinson 1976). Moreover, this snail species has a fragile shell that could easily be crushed by cattle. In fact, Boschi and Baur (2007) found that *V. pellucida* was the most sensitive snail species to increased grazing intensity in pastures. In the present study, *H. pomatia*, an ubiquitous species according to the literature, preferred open-land and ecotone and avoided forest interior. Pollard (1975) found *H. pomatia* in open woodland facing towards south. In our study sites, the forest interior consisted of dense stands of trees which might be less suitable for *H. pomatia*.

Surprisingly, a relatively large number of individuals of the open-land species *Helicella itala* was found in the ecotone. This indicates that the ecotone could complement the open-land habitat of this threatened and red-listed species. All common forest snail species were also found in the ecotone. The microclimatic conditions of the ecotone did probably not very much differ from those in the forest interior. Moreover, the soil surface features in the ecotone, characterized by herbs, shrubs, leaf litter and dead wood, could fulfill the requirements of forest snails. In this habitat, forest snail species might be stronger competitors for food and shelter than open-land species. However, interspecific competition has only rarely been shown to influence terrestrial gastropod communities (Baur and Baur 1990).

Implications for management of grassland-forest edges

Remnants of nutrient-poor semi-natural grassland – a highly threatened habitat type with numerous endangered plant and invertebrate species – are frequently surrounded by forest. It has been assumed that the actual area of the grassland remnants is further reduced by shadowing of trees and altered microclimatic conditions close to the forest edge. This study showed that the typical open-land snail community occurs at a distance of ≥ 5 m from forest edges facing towards south, whereas from the edge into forest interior the snail community is dominated by forest species. Shrubs encroaching in the pasture reduce the habitat for the specialized open-land species. Hence, the regular removal of overgrowing shrubs is important for maintaining an intact open-land snail community in small semi-natural grassland fragments.

The grassland-forest ecotone appears to be a suitable habitat for a few open-land snail species and could therefore function as a source for recolonisation of pastures under restoration. From this point of view, gradual forest edges should be promoted. Therefore, we recommend creating and/or maintaining gradual forest edges through regular management practices both in the ecotone and forest interior. In particular, the stocking level of trees should be gradually reduced to a crown cover of 30% over a distance of 35 m from the forest interior up to the forest edge and shrubs should be periodically cut (Dipner 2006).

Acknowledgements

We thank the farmers for allowing us to work on their pastures and A. Baur, H.-P. Rusterholz and P. Stoll for constructive comments on the manuscript. We gratefully acknowledge financial support from the Bristol Foundation in Schaan (Principality of Liechtenstein).

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Table 1. Abundance in pasture, ecotone and forest interior and habitat preference of the 24 common snail species. Data from gradual and abrupt forest edges (n = 6 in both cases) are combined.

Species	Habitat specificity[1]	No. of individuals			Chi-square test[2]		Habitat preference[3]
		Pasture	Ecotone	Forest interior	χ^2	p	
Cochlicopa lubricella	O	156	1	0	131.0	< 0.001	open-land
Truncatellina cylindrica	O	514	17	0	399.4	< 0.001	open-land
Vertigo pygmaea	O	425	8	0	343.6	< 0.001	open-land
Pupilla muscorum	O	357	3	0	297.9	< 0.001	open-land
Vallonia costata	O	901	17	0	728.4	< 0.001	open-land
Vallonia pulchella	O	101	0	0	86.0	< 0.001	open-land
Vallonia excentrica	O	619	6	1	483.1	< 0.001	open-land
Vitrina pellucida	O	51	73	24	13.7	< 0.01	ecotone
Helicella itala[4]	O	1715	422	22	913.3	< 0.001	open-land
Cochlostoma septemspirale	F	217	1316	1896	1131.7	< 0.001	ecotone, forest
Acicula lineata[4]	F	1	44	99	76.6	< 0.001	ecotone, forest
Carychium tridentatum	F	44	98	179	66.2	< 0.001	ecotone, forest
Acanthinula aculeata	F	11	135	165	122.5	< 0.001	ecotone, forest
Ena obscura	F	3	60	47	58.5	< 0.001	ecotone, forest
Discus rotundatus	F	8	222	304	101.7	< 0.001	ecotone, forest
Aegopinella pura	F	2	71	97	79.8	< 0.001	ecotone, forest
Aegopinella nitens	F	18	97	109	63.0	< 0.001	ecotone, forest
Cochlodina fimbriata	F	1	30	56	15.1	< 0.001	ecotone, forest
Cochlodina laminata	F	1	43	42	39.7	< 0.001	ecotone, forest
Perforatella incarnata	F	3	73	69	62.8	< 0.001	ecotone, forest
Helicodonta obvoluta	F	10	179	253	139.4	< 0.001	ecotone, forest
Punctum pygmaeum	U	491	442	353	5.8	0.05*	none
Trichia plebeia	U	127	92	59	5.5	0.06*	none
Helix pomatia[4]	U	36	32	3	16.4	< 0.001	open-land, ecotone

* p above the critical significance level after Bonferroni correction (Holm 1979). In each case d.f. = 2.

[1] According to the literature (see methods): O = Open-land, F = Forest, U = Ubiquist.

[2] Chi-square tests were used to test deviations from the null hypothesis of uniform distribution among the three ecological zones (40% in pasture, 30% in ecotone, 30% in forest interior).

[3] Habitat preference is determined by a significant deviation from a uniform distribution among the three ecological zones.

[4] Recorded on the Red list of Switzerland (Duelli 1994).

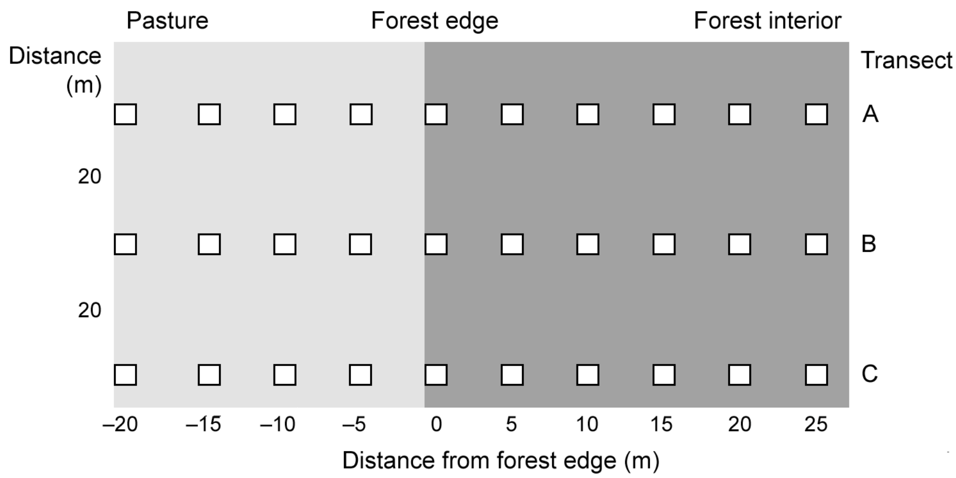

Fig. 1. Spatial arrangement of sampling plots (1 m x 1 m) along the three transect lines (A–C) at a forest edge. Distances are not drawn to scale.

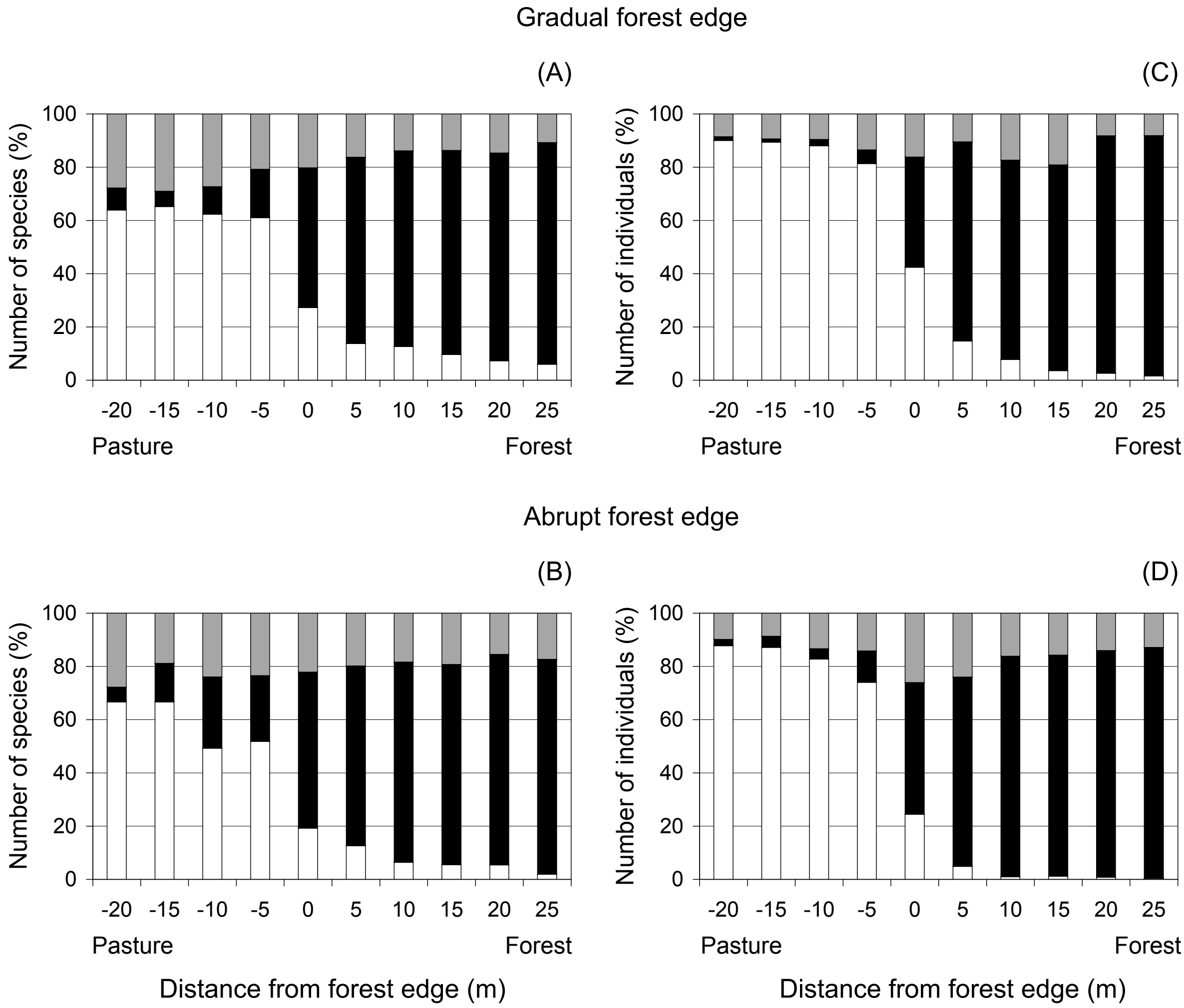

Fig. 2. Percentages of habitat-specific snail species and individuals at gradual (A, C) and abrupt forest edges (B, D). White areas of bars refer to open-land species, black to forest species and gray to ubiquitous species. Mean values of six forest edges are shown for each distance.

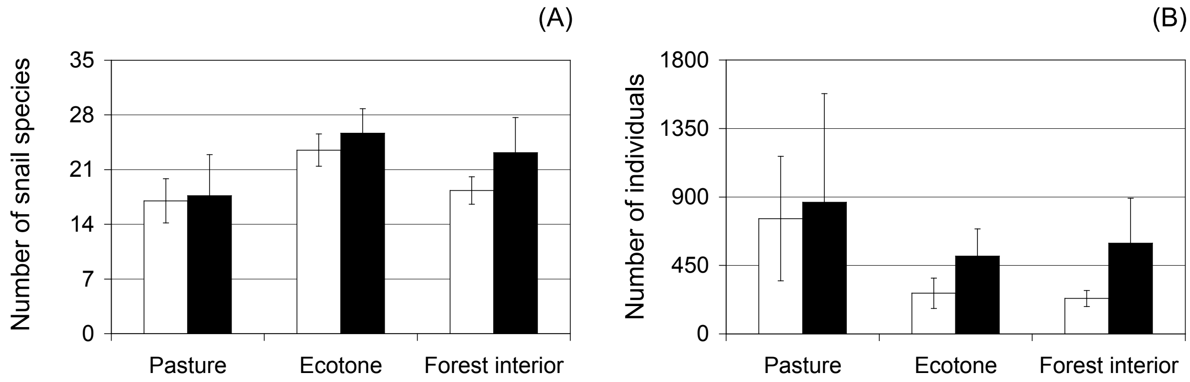

Fig. 3. Total number of snail species (A; mean ± SD) and individuals (B) at six gradual forest edges (white bars) and six abrupt forest edges (black bars).

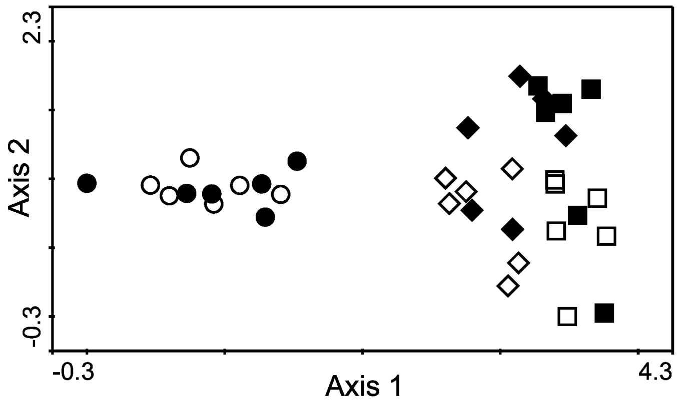

Fig. 4. Ordination diagram based on detrended correspondence analysis of snail species composition in the pasture (dots), ecotone (diamonds) and forest interior (squares). Open symbols refer to gradual forest edges (n = 6), filled symbols to abrupt forest edges (n = 6).

General discussion

Implications for pasture management and outlook

The aim of this thesis was to assess how extensive pastures in the Swiss Jura mountains have to be managed to maintain and/or promote snail diversity in dry, nutrient-poor calcareous grasslands. I investigated the effect of different forms of pasture management in the past and present on the land snail communities.

The results show that to preserve the snail fauna in dry, nutrient-poor grasslands, pastures can be stocked with horses, cattle or sheep (**chapter 1**). Woodcock et al. (2005) found that long-term sheep pastures harboured higher proportions of phytophagous beetle species than cattle pastures. For the conservation of bumblebees, however, cattle grazing has been shown to be preferable to sheep grazing (Carvell, 2002). These different findings are only apparently inconsistent with one another. Grazing at low intensity by horses, cattle or sheep promotes and maintains species-rich, but different plant communities (Oates, 1995; Rook et al., 2004). The type of plant community in a pasture is probably not important for snails. Gastropods are usually generalist feeders, although food specialists occur (Frömming, 1954; Fröberg et al., 1993). In contrast, phytophagous beetles and bumblebees are more specific in their food requirements and prefer the plant community occurring in extensive sheep pastures or in extensive cattle pastures respectively (Carvell, 2002; Woodcock et al., 2005). Therefore, for the management of semi-natural grasslands, the choice of livestock species is probably important for the protection of invertebrates with specific plant species or plant community preferences.

Independent of livestock type, grazing intensity has to be low to maintain the typical grassland snail community (**chapter 1**). In particular, to maintain the threatened snail species in dry, nutrient-poor grasslands, no fertilizer should be applied and grazing intensity should not exceed 180 $LU.ha^{-1}.d$ (product of livestock units per hectare and grazing days; **chapter 2**). To avoid any negative effects of grazing intensity on individual snail species, grazing intensity should be even lower (not exceeding 92 $LU.ha^{-1}.d$). The recommended levels of grazing intensity coincide with the proposed management intensity for maintaining diurnal butterfly diversity in low productive and dry, nutrient-poor pastures (Gonseth, 1994). However, other organism groups belonging to the grassland community could be even more sensitive to grazing intensity than land snails and butterflies. Hence, the level of tolerance to grazing intensity should be assessed for further invertebrates occurring in semi-natural grasslands.

Other pasture management issues could also influence the snail community. For example, the beginning of a grazing season on a pasture, the number of grazing events per paddock during the grazing season and the time between successive grazing events. So far, there are no studies on the influence of these issues on invertebrates occurring in semi-natural grasslands. Finally, mowing and grazing of grasslands could also affect the snail community in different ways. Zurbrügg and Frank (2006) found a higher species richness and abundance of bugs in meadows than in pastures, whereas butterfly communities did not differ between mown and grazed semi-natural grasslands (Saarinen and Jantunen, 2005).

The actual size of the semi-natural grassland remnants may be reduced by shadowing of shrubs and/or trees and altered microclimatic conditions close to the forest edge (**chapter 4**). Hence, the regular removal of overgrowing shrubs is an important management practice for maintaining an intact open-land snail community in small grassland fragments. The fact that a drastic reduction of open-land species and an increase of forest species already occurs close to the first shrubs or trees of south-facing gradual forest edges, corroborates the negative effect of past shrub cover of pastures during 10–40 years on the present-day grassland snail communities assessed in **chapter 3**.

Regular removal of shrubs in the pastures should be complemented by management practices at the forest edge, especially in small grassland fragments. The results of **chapter 4** indicate that the microclimatic conditions on the pasture appeared to be more favourable for open-land snail species close to gradual forest edges than close to abrupt forest edges. So far, it is not known whether open-land species of other invertebrate groups are affected by the structure of forest edge in a similar way as open-land snails. However, a higher species diversity of arthropods was found at structured forest edges than at abrupt forest edges (Hänggi and Baur, 1998; Duelli et al., 2002). Therefore, I recommend creating and/or maintaining gradual forest edges through regular management practices in the forest adjacent to the pasture. In particular, trees should be gradually reduced to a crown cover of 30% over a distance of 35 m from the forest interior up to the forest edge and shrubs should be periodically cut (Dipner, 2006).

Past shrub cover and higher management intensity of pastures for a period of 10–40 years during the last 55 years altered the snail community of dry, nutrient-poor grasslands (**chapter 3**). This indicates the necessity to consider former pasture management in studies on the effect of actual management practices on the present-day grassland community. Besides the recent management history of the last 55 years, previous land use may also be reflected in the current composition of snail communities (Cameron et al., 1980; Martin and Sommer, 2004). Moreover, special historical events might have an impact on the present-day snail fauna in pastures. For example, certain snail species such as *Zebrina detrita* and *Helicella itala* could have been accidentally introduced into pastures in seed stock or in hay (Mäder, 1939). Hence, to understand the diversity of land snails in a specific pasture, it is important to analyse the management history of the area.

The impact of the recent management history of pastures on present-day snail fauna found in **chapter 3** has consequences for the development of effective management strategies for promoting grassland biodiversity. Knowledge of past pasture management allows us to identify grasslands under restoration and specifically connect them with intact dry, nutrient-poor grasslands to recover species losses by former shrub cover or management intensification. Connection could be improved by the creation and maintenance of new semi-natural areas. An exchange of livestock between intact pastures and pastures under restoration during the grazing season could further contribute to improve the connectivity of isolated pastures, as snails and other invertebrates can be passively transported by livestock (Fischer et al., 1996).

Maintaining and promoting the diversity of species in grassland is one of the main objectives of Swiss agricultural policy. One approach to promote biodiversity is the development of quality criteria for farming methods and habitat types (Swiss Federal Office of Agriculture, 2004). To assess the quality of grasslands, it is necessary to measure the biodiversity. A single indicator for the entire biodiversity is theoretically and practically impossible (e.g. Lawton et al., 1998; Duelli and Obrist, 2003). Species richness and the composition of several organism groups should be recorded as an estimate of the biodiversity of grasslands (Vessby et al., 2002; Cremene et al., 2005; Oertli et al., 2005). Büchs (2003) suggest the development of sets of indicators, which allow a monitoring of biodiversity trends in agro-ecosystems. In **chapter 2** the presence of five snail species (*Cochlicopa lubricella, Truncatellina* *cylindrica, Vitrina pellucida, Helicella itala* and *Helix pomatia*) indicates an appropriate pasture management intensity for maintaining snail diversity. These snail species belong to the typical dry, nutrient-poor grassland community (**chapters 1**, **2**, **3** and **4**; Baur et al., 1996). Hence, I propose to include these snail species in the set of indicators used for evaluating the conservation value of pastures in the Swiss Jura mountains.

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Summary

Nutrient-poor, dry calcareous grasslands in Central Europe harbour an extraordinary high diversity of plants and invertebrates. Consequently, they are of high conservation value. However, changes in agriculture (intensification or abandonment) have resulted in a dramatic reduction of semi-natural grasslands in the twentieth century. Today, dry grasslands are among the most endangered habitats. Furthermore, these grasslands are frequently fragmented and surrounded by forest or intensively cultivated agricultural areas.

Semi-natural grasslands are fragile because their maintenance depends on traditional farming techniques. In order to avoid any loss of species by inappropriate land use, it is important to assess the responses of threatened species to particular types of grassland management. Although different types of present and past pasture management are known to affect the species richness and composition of plant communities, knowledge of the effects on invertebrates is limited. In particular, no studies exist on the influence of different types of pasture management on animals with limited mobility, such as gastropods.

In the present thesis, I examined the effects of different pasture management practices on the snail community in dry, nutrient-poor grasslands of the Swiss Jura mountains, where extensive grazing with low stocking rate and without use of fertilizers is a traditional form of grassland management. I assessed the snail communities in extensive pastures grazed by horses, cattle or sheep, in cattle pastures with different management intensity and in extensive pastures with different management history in the last 55 years. Furthermore, gastropod species richness and abundance were examined in transects running from extensive pastures through gradual or abrupt forest edges into the forest interior.

Grazing by different livestock species did not affect the species richness, abundance and species composition of land snails. However, independent of livestock species, snail species richness, abundance and number of red-listed species decreased with increasing grazing intensity. Furthermore, cattle pastures without fertilizer application and with low grazing intensity harboured more snail species and more threatened snails than pastures with annual addition of fertilizer and higher grazing intensity. Management intensity had also a negative influence on individual snail species (*Cochlicopa lubricella, Truncatellina cylindrica*, *Vitrina pellucida*, *Helicella itala* and *Helix pomatia*). Former changes in pasture use for a period of 10–40 years altered the present-day snail fauna. Past shrub cover had a

negative effect on the total number of snail species and individuals, the number of open-land species and individuals and the number of red-listed individuals. Former use of fertilizer and higher grazing intensity reduced red-listed species and individuals and altered the snail community. The grassland snail communities of the pastures changed distinctly to forest communities at the first bushes or trees of edges towards forest interior irrespective of the type of forest edge. In pastures, at a distance of 10 m from gradual forest edges, more open-land snail species were found than at the corresponding distance from abrupt forest edges. Furthermore, ecotones of gradual forest edges harboured more open-land individuals than those of abrupt forest edges.

For the conservation of grassland land snail communities, it does not matter whether pastures are stocked with horses, cattle or sheep, provided the grazing intensity is low. To preserve the threatened snail species in dry, nutrient-poor grasslands, a network of pastures should be managed without fertilization and grazing intensity should not exceed 180 LU.ha^{-1}.d (product of livestock units per hectare and grazing days). Furthermore, to recover the typical grassland snail community in shrub cleared pastures or former fertilized pastures, the connection between intact pastures and grasslands under restoration should be improved by creating and maintaining new semi-natural areas and by exchanging livestock among these areas during the grazing season. Since shadowing of trees and alterations of the microclimate close to the forest edge may reduce the actual size of small grassland fragments, encroaching shrubs should be regularly removed and gradual forest edges created and maintained.

Dank

Zuallererst möchte ich der Bristol-Stiftung, Zürich, für das Vertrauen die sie mir gegeben hat, danken. Ihre finanzielle Unterstützung hat mir ermöglicht diese Dissertation durchzuführen.

Bruno Baur danke ich für seine fachliche Betreuung. Ich konnte sehr von seiner Erfahrung in der Schnecken-Forschung und von seinen umfassenden Kenntnissen in der Statistik profitieren. Ebenfalls danke ich ihm für die vielen Korrekturen der Manuskripte.

Ich möchte mich bei allen folgenden kantonalen Institutionen und deren Mitarbeiterinnen und Mitarbeiter bedanken, die mir bei der Organisation geeigneter Untersuchungsgebiete und mit den notwendigen Bewilligungen geholfen haben: Hansruedi Reimann, Abteilung Landwirtschaft, Kanton Aargau; Dieter Rudin und Susanne Kaufmann, Landwirtschaftliches Zentrum Ebenrain; Paul Imbeck, Amt für Raumplanung, Kanton Basel-Landschaft; Laurent Gogniat, Office des eaux et de la protection de la nature, Kanton Jura; Hans Bienz und Rolf Glünkin, Amt für Raumplanung, Kanton Solothurn; Jean Fahrni, Service de l'agriculture, Kanton Neuenburg; sowie alle kontaktierten Ackerbaustellen. Dank gebührt auch Stephan Eggenberg, Atelier für Naturschutz und Umweltfragen, Christophe Hunziker, Bureau d'étude Environnement, und das Bundesamt für Umwelt für ihre Hilfsbereitschaft und das zur Verfügung stellen der Daten aus dem „Inventar der Trockenwiesen und -weiden nationaler Bedeutung“ (TWW). Für die Mithilfe bei der graphischen Darstellung der TWW-Daten mit dem geographischen Informationssystem (GIS) danke ich Claude Steck.

Dankbar bin ich allen Bauern, die mir wichtige Informationen bezüglich der Bewirtschaftung der Weiden gegeben haben und auf ihren Weiden arbeiten liessen.

Ich danke Georg F. J. Armbruster für das zur Verfügung stellen seiner Referenzsammlung der Schneckengehäusen und für seine Hilfe mit der Bestimmung der unsicheren Fälle. Für das Nachbestimmen der Zweifelsfälle danke ich auch Margret Gosteli, Naturhistorisches Museum Bern. Christoph Oberer danke ich für seine Einführung in die Schneckenwelt.

Ebenso danke ich Peter Stoll für seine Hilfe bei schwierigen statistischen Fragen und die Durchsicht meiner Manuskripte. Für die konstruktive Kritik zu den Manuskripten danke ich auch Anette Baur und Hans-Peter Rusterholz. An dieser Stelle möchte ich noch Helen C. Landolt für ihre sprachliche Korrekturen in Englisch danken.

Für die gute Stimmung unter den Doktorandinnen und Doktoranden und die Hilfe bei vielen wichtigen Kleinigkeiten danke ich Kathrin Blassmann, Daniel Bloch, Tessa Hegetschweiler, Ursula Monzeglio und Deborah Renz.

Ich danke Gabriela Ammann für ihre Gastfreundschaft in Basel, sowie allen die mich während dieser Zeit moralisch unterstützt haben.

Zuletzt einen ganz herzlichen Dank an die ehemalige Professur für Natur- und Landschaftsschutz der ETH Zürich. Dort hatte ich die Idee zum Thema meiner Dissertation und konnte sie zum Projektantrag weiterentwickeln. Einen speziellen Dank gilt an Karl Martin Tanner, der mich ganz am Anfang und in weiteren entscheidenden Phasen meiner Doktorarbeit unterstützt und geholfen hat. Besonders danke ich ihm für die anregenden Diskussionen und für die Zeit, die er sich immer für mich genommen hat. Ebenfalls danke ich Klaus C. Ewald und Ruth Rupp für ihre tolle Unterstützung.

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