Soil pH and plant diversity shape land snail communities in intensively-managed montane and subalpine meadows

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Faculty of Science, University of Bern

Handed in by
Gerard Martínez De León

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Supervised by
PD Dr. Jean-Yves Humbert
Prof. Dr. Raphäel Arlettaz

Abstract

Grassland management practices in mountainous regions are often constrained by complex topography and a lack of accessibility for agricultural machinery but little is known about the response of invertebrate communities to the intensification of farming with respect to natural environmental contexts. This study explored the factors influencing the composition of land snail communities in intensively-managed mountain meadows in the SW Swiss Alps (Valais). Land snails were chosen because of their low mobility, making them suitable indicators of small-scale habitat conditions. Variables related to topography, soil properties, vegetation, surrounding landscape and agricultural management were recorded in situ or obtained from interviews with farmers. Generalised linear mixed models were used to analyse the effects of these variables on snail density, species richness and the occurrence of red-listed species, while community composition was investigated using a multivariate model-based approach. Soil pH was the most important factor at our study sites, with high pH values being indicative of a limestone substrate that facilitates the monopolisation of this mineral for shell formation. Snail density and species richness decreased with elevation, probably as a result of shorter periods of activity. Plant diversity favoured the abundance of most snail species, suggesting a higher structural complexity or more diverse food supplies. Remarkably, grassland intensification did not seem to affect snail density, but a 45% loss in species richness is observed in plots having undergone farming intensification in the long run. Based on these results, we recommend maintaining a good proportion of extensively-managed grasslands in areas devoted to pasturing or hay production in order to support the most sensitive species that typically disappear with management intensification.

Key words: Alps; Community composition; Conservation; Fertilisation; Intensive management; Mountain grassland; Snails

Introduction

Semi-natural grasslands are among the most ecologically diverse habitats in temperate regions, harbouring many more species than the natural vegetation that would occur if they were not managed (Grime, 1973; MacDonald et al., 2000). Nonetheless, traditionally managed grasslands have been disappearing in the last decades because of land-use changes, driven by the demands of higher yields at low costs. In mountain regions, management practices are becoming more intensive in sites where accessibility is easy and machinery use feasible, while abandonment is undergoing in hardly accessible and less profitable areas (e.g. Tasser & Tappeiner, 2002; Zimmermann, Tasser, Leitinger, & Tappeiner, 2010). Enhancing hay production comes at the cost of grassland biodiversity erosion (Beckmann et al., 2019; Humbert, Dwyer, Andrey, & Arlettaz, 2016). The addition of fertilisers promotes higher yields, mostly by favouring few fast-growing plants while losing small sized species in a more homogeneous and shaded understory (Hautier, Niklaus, & Hector, 2009; Socher et al., 2012). Overall invertebrate abundance could potentially benefit from the increase in primary production (Ebeling et al., 2013; Siemann, 1998), but several species are lost with the associated intensification of the mowing regime (i.e. earlier and more frequent cuts; Buri, Arlettaz, & Humbert, 2013; Marini, Fontana, Klimek, Battisti, & Gaston, 2009; Uchida & Ushimaru, 2014), the loss of diverse floral resources (Hudewenz et al., 2012), and the alteration of the habitat structure and microclimate (Kampmann et al., 2008; Marini, Fontana, Battisti, & Gaston, 2009; Schwab, Dubois, Fried, & Edwards, 2002). Yet, because of the constraints imposed by their complex topography, mountain meadows are generally smaller, less frequently fertilized and mown (Kampmann et al., 2008; Marini, Fontana, Klimek, et al., 2009). In this context, a less hostile matrix with a higher proportion of low-input grasslands allows for greater dispersal and a better preserved species pool (Knop, Herzog, & Schmid, 2011), so montane biodiversity is generally not as eroded as in the more intensified lowland grasslands (Dietschi, Holderegger, Schmidt, & Linder, 2007). Despite being key components of grassland ecosystem functioning (e.g. De Deyn, Raaijmakers, Zoomer, Bezemer, & Putten, 2003; Stein et al., 2010), more knowledge on invertebrates is necessary to better evaluate the impact of management intensification on mountain biodiversity (Humbert et al., 2016). So far it is known that each taxon has a particular response to management intensification: some groups are found to be especially sensitive (e.g. orthopterans; Marini, Fontana, Scotton, & Klimek, 2008); whereas others are even more abundant under a moderate management regime (e.g. carabids, leafhoppers and spiders; Andrey, Humbert, & Arlettaz, 2016; Grandchamp et al., 2005; Lessard-Therrien et al., 2018).

Using an experimental approach, Dani (2017) demonstrated that average land snail abundance was boosted after 5 years of management intensification, but so did its variance. Environmental factors can potentially explain most of this variation in intensively managed meadows, but their influence needs to be properly assessed in this particular habitat (see Baur et al., 2014, where this issue is addressed in several other alpine habitats). In the same experiment (Dani, 2017), snail species evenness tended to decline with increasing management intensity. This effect could be exacerbated with time exposure, as more sensitive species may show a delayed response to these new conditions, becoming rarer over time and eventually disappearing locally (Hylander & Ehrlén, 2013). In fact, in Switzerland, land snail communities in grasslands have become more homogeneous in recent years, most likely due to the spread of generalist species coupled with the loss of rarer, specialist species (BDM Coordination Office, 2014). Snail communities in meadows with a long-term intensive management are thus expected to be more species-poor than those in meadows that have been managed intensively for a shorter time.

The aim of this study was to investigate which factors influence the composition of land snail communities in montane and subalpine intensively managed meadows. Terrestrial gastropods (i.e. land snails and slugs) constitute a species-rich group, with 197 species occurring in Switzerland (Rüetschi, Stucki, Müller, Vicentini, & Claude, 2012). Most of them are generalist feeders (Kiss, 2017; Richardson, 1975) that can potentially alter the composition of plant communities in grasslands (Allan & Crawley, 2011). Snails and slugs are frequent prey for upper trophic levels, particularly for many birds, small mammals, reptiles, and even arthropods (Goodhart, 1958; Nyffeler & Symondson, 2001; Pedersen, Jensen, & Toft, 2009; Rosin, Lesicki, Kwiecinski, Skorka, & Tryjanowski, 2017). They are especially sensitive to habitat changes and fragmentation because of their extremely low mobility and high habitat specialization of many species (Baur et al., 2014; Nicolai & Ansart, 2017; Stoll et al., 2009), so they are potentially good indicators of small-scale habitat conditions. Their conservation status calls for more research, given that 20% of the species found in Europe are threatened, and another 10% are data deficient. A better understanding of the ecological determinants of gastropod diversity is thus necessary to support their conservation (Cuttelod, Seddon, & Neubert, 2011).

The main hypotheses were that (1) environmental factors are of major importance, particularly those related to topography (e.g. elevation, exposition) and soil conditions (Baur, Meier, Baur, & Schmera, 2014; Schmera & Baur, 2014; Wehner et al., 2019); (2) management factors are determinant, both the historical and current practices (Boschi & Baur, 2008; Dani, 2017); (3) the presence of structural elements (Boschi & Baur, 2007a) and other less intensive land use types in the local landscape promote richer communities (Knop et al., 2011), especially considering that the matrix is highly heterogeneous in such a montane landscape; finally, (4) as land snails are generalist feeders and are not constrained by plant species richness (Boschi & Baur, 2007b; Knop et al., 2011) or phytomass availability (Braschler et al., 2004), vegetation-related factors are likely to play a minor role in structuring land snail communities in this study system.

Materials and methods

Study area

The study was carried out in in 13 different sites located in canton of Valais, inner Swiss Alps. Elevations ranged between 893 and 1665 m (Table A1). The climate in the region is dry continental, with a mean annual precipitation of 603 mm and monthly average temperatures that range from -0.1 °C in January, to 20.1 °C in July, recorded at the valley bottom in Sion (482 m a.s.l.) between 1981 and 2010 (MeteoSwiss, 2019). Three meadows were sampled at each site, giving a total of 39 meadows. The meadows had a minimum area of 0.2 ha and had to be managed intensively (i.e. fertilised with solid or liquid manure, mown at least twice a year, and often used as pasture in autumn). Farmers were interviewed to obtain information about other current and historical management practices. However, only the occurrence of irrigation was variable enough across the sites to use it as an explanatory variable in this study. The use of different types of fertiliser (manure or slurry) was usually alternated in a yearly basis according to the farmers' preferences, so it was not possible to incorporate this factor in the analyses. Other management practices (e.g. autumn grazing, hay cuts, historical management) were almost identical in all study sites. All meadows had to be managed intensively for a minimum five years (on average, farmers had been managing the meadows intensively for at least 18 years).

This study was part of the mountain module of the grassland restoration project run by the Division of Conservation Biology of the University of Bern. A research project aimed to evaluate the response of grassland biodiversity to a relaxation of fertiliser input. Three experimental treatments were implemented in spring 2019, one at each meadow: intensive (usual fertiliser input), mid-intensive (1/3 of the usual fertiliser input), and extensive (no fertilisation). These treatments were not expected to have an effect on the baseline data collected in 2019, but rather in the next 3-6 years after the onset of the experiment.

Land snail sampling

Snails present in the soil and the litter layer were collected from soil cores. Following the Swiss Biodiversity Monitoring (BDM) protocol for terrestrial mollusc monitoring (Mandataire du Monitoring de la Biodiversité en Suisse, 2017), eight soil samples of 125 cm^2 area and 5 cm depth were extracted after the first hay cut and pooled afterwards into a 5 dm^3 sample. Later, samples were processed to separate the shells from the soil fraction, using a set of sieves (mesh sizes of 10, 2 and 0.7 mm) and then examined visually. Fresh shells were identified under the binocular microscope, according to Turner et al., 1998. All the individuals were identified to species level, except the immature shells of *Cochlicopa*, *Vallonia* and *Vertigo* when different species belonging to the same genus could be found in a meadow. In this case, it was not possible to allocate non-fully developed shells to a particular species with confidence. Old shells (i.e. those whose periostracum completely eroded) were not considered further because they can lead to distorted estimates of densities when comparing sites with different soil chemistry, strongly influencing their decay rate (Cernohorsky, Horsák, & Cameron, 2010). The regional Red-List status was extracted for every species (Rüetschi et al., 2012).

Functional traits were not considered in this study given that limited sound information is available for every snail species. Only rough categories for some life-history traits and ecological preferences have been defined so far (Falkner, Obrdlík, Castella, & Speight, 2001; Kerney & Cameron, 2006). For instance, Dani (2017) grouped snail species according to their habitat moisture preferences, but she found that even the so-called xerophilous species were more abundant after an increase of fertiliser input and irrigation. Her result suggests that such classification does not entirely represent the optimal range of humidity of the species. Instead, morphological traits may yield more trustworthy insights as they only rely on measurements of individuals. Adults shell size is a suitable surrogate of other life-history traits (e.g. clutch size, longevity) and could potentially be used in this study. However, the factors influencing this trait have already been properly identified in alpine grasslands: elevation (negatively) and heat load (positively) (Baur et al., 2014; Schmera & Baur, 2014). More detailed data on other functional traits (e.g. feeding habits, breeding requirements, phenology), if available, would have been enormously useful to explain potential patterns of community composition linked to environmental variables.

Environmental variables

At each meadow, the following environmental variables were measured: elevation, GPS coordinates, aspect (degrees from south) and slope (using a compass with clinometer) (Table A1). As soil temperature potentially influences land snail communities (Baur & Baur, 1993; Baur et al., 2014), an index of heat load was calculated based on the latitude, slope and aspect of the sites. Higher values of this index indicate that more heat by incident radiation is received throughout the year (McCune & Dylan, 2002)

Soil sampling and analyses

Eight soil subsamples of 10 cm depth were obtained after the first cut and pooled into a 1 kg sample. Soil samples were then dried at 50 °C and sieved with a 2 mm mesh size. Soil pH was measured with a pH meter, after diluting 20 g per sample into 50 mL H_2O. For the soil texture, 1 g per sample was first treated with peroxide and incubated to oxidise the organic matter. After dispersion, each sample was split into eight subsamples with a centrifuge before measuring the grain size distribution in the Mastersizer 2000 (Royston, UK) with Hydro 2000S wet sample dispersion unit. The subsamples were further diluted if their measurement fell beyond the optimum obscuration range. A minimum of three subsamples were analysed, and then averaged into a single value per meadow. The grain size distribution was described as the proportion of clay (0.02 μm-

2.00 µm), silt (2.00 – 63.00 µm) and sand (63.00 – 2000.00 µm), to account the potential water retention in the upper soil layer. Inorganic carbon, total carbon (C) and nitrogen content (N) were measured with a CNS elemental analyser (Vario EL cube, Elementar). The ratio of C to N was later calculated, as a measure of the nitrogen available for plant uptake (Hodge, Robinson, & Fitter, 2000).

Vegetation sampling

Vegetation relevés were conducted in two randomly allocated subplots of 2 × 4 m distant by 8 m, before the first cut in 2019. A 10-m buffer zone around the meadow was excluded to avoid edge effects. Herbaceous plants were identified to species level and their cover was estimated visually. After pooling the data of the two subplots, the plant species richness and Shannon index were calculated for each meadow. The percentages of bare ground, litter and mosses were also considered, but the latter variable was not included in the analyses because its occurrence in the study sites was negligible. The methodology was adapted from van Klink et al., 2017. The average conditions of moisture in the meadows were indirectly estimated by calculating the Community Weighted Mean (CWM) of the Landolt values of humidity. A different value is assigned to each plant species according to their soil humidity requirements, from 1 (very dry) to 5 (aquatic), and then weighted by their relative cover in the plot (Landolt et al., 2010). The vegetation height was measured for every contact point with a plant in 10 positions along two diagonal transects crossing the entire meadow. This was done twice, once after each cut; and the mean vegetation height of each meadow across the two sessions was calculated afterwards.

Local landscape attributes

The different land cover types were mapped in the field in a 50-m buffer from the edge of the meadows, and next digitised. The following categories were considered to be relevant for snail communities and therefore included in the analyses: grasslands, forest, extensive semi-natural structures (i.e. extensive grass strips, steppe-like vegetation) and artificial structures (i.e. paved roads, buildings). All the preparation of GIS data was carried out in QGIS 3.10 (QGIS Development Team, 2020).

Statistical analysis

Correlations between covariates were assessed as follows: if two explanatory variables had a Spearman correlation coefficient > 0.7, a variable representative of multiple collinear variables or the variable with more biological meaning was retained (Zuur et al. 2010, Harrison et al 2018). In order to improve model convergence (Bolker et al., 2009), continuous explanatory variables were standardised (mean = 0, standard deviation = 1). Generalised Linear Mixed Effect models (GLMM) with Poisson error distribution were performed to investigate the effect of the explanatory variables on overall snail density, species richness, and the occurrence of Red-Listed species. Site (n = 13) was set as a random factor in all models.

Model selection was performed in two steps. In a first step, a pre-selection of explanatory variables was done from the full initial set. For this purpose, univariate GLMMs were fitted for each standardised explanatory variable, and those statistically significant with $P < 0.05$ were retained. As low pH values could potentially be limiting for snail density and richness in the study system (based on several studies; e.g. Dani, 2017; Martin & Sommer, 2006; Ondina, Hermida, Outeiro, & Mato, 2004), interactions of soil pH with any of the other pre-selected variables were tested and then included in the next step providing statistical significance. The same approach was used to assess the addition of polynomial terms. In a second step, model selection was conducted with the function *dredge* in the package *MuMIn* (version 1.43.6; Bartón, 2019). In case several models had similar support, a subset of the top models within Δ AICc < 6 (Harrison et al., 2018) was selected for full model averaging with the function *model.avg* of the same package. The whole aforementioned procedure was repeated on a subset of meadows where we believed that soil pH could be less limiting for snail density. Based on the results of the analysis using the whole set of meadows, two cut-off thresholds, at pH > 5.5 or > 6, were investigated. This was done to corroborate the robustness of the variables identified in the analysis, regardless the limitation that pH may pose. Due to the scarcity of red-listed species (in terms of frequency and number of species), model selection was not implemented on this response variable. Instead, we only fitted univariate models to detect the variables having a significant influence ($P < 0.05$) on the number of red-listed species. These variables were ranked according to their absolute estimates, as shown in Table C4.

Simulations to check for overdispersion and zero inflation were carried out with the script provided in Harrison et al., 2018. In case overdispersion had to be handled, an observation-level random factor was added to the model (Harrison, 2014). In all cases, linear model assumptions were verified with QQ plots and Tukey-Ascombe plots, using Pearson residuals (Harrison et al., 2018; Zuur, Ieno, & Elphick, 2010).

For the community analyses, multivariate generalised linear models were used to investigate the effect of the explanatory variables on species abundance and community composition. The function *manyglm* in the package *mvabund* (v. 4.1.3; Wang, Naumann, Eddelbuettel, Wilshire, & Warton, 2020) fits a generalized linear model to a matrix of species abundances, by fitting univariate models to each species and then summing the test statistics (Warton, Wright, & Wang, 2012). Compared to the traditional pairwise distance-based methods (summarised in Anderson et al., 2011), model-based community analyses better account for the typical properties of multivariate abundance data (Wang, Naumann, Wright, & Warton, 2012; Warton et al., 2012). In addition, they have more power to detect patterns and are more flexible to apply in different settings (Jupke & Schäfer, 2020; Warton et al., 2012). It is not yet possible to handle spatial correlation in multivariate linear models (Niku, Hui, Taskinen, & Warton, 2019), so we acknowledge that the assumption of independence may be violated in meadows located in close contact (Wang et al., 2012), which is the case for some of the study sites. Nonetheless, we are confident that the information yielded with this method will still provide evidence about the factors influencing species abundance and therefore community composition, otherwise overlooked when analysing snail density overall. Given the high amount of species occurring in few plots, we performed these analyses only with the species present in more than 10 meadows (hence at least 4 different study sites). All explanatory variables were standardised (mean = 0, standard deviation = 1) as required to perform such analysis. After fitting a global model with the explanatory variables, model selection was done using AIC-based backward selection with the function *drop1*. A variable was dropped from the model when the resulting AIC was lower. None of the landscape or management factors were relevant in previous analyses ($P > 0.05$), so they were not considered for model selection. The negative binomial error distribution was adopted in the models, as it provided a better fit than the Poisson distribution. The statistical significance of each multivariate term was assessed with likelihood-ratio test statistics (LR) resampled 999 times with the PIT-trap method (function *summary.manyglm*). Significant effects on each species were inspected from the p-values (adjusted for multiple testing) of the univariate statistics. Coefficients of the covariates with confidence intervals for every species were plotted with *coefplot.manyglm*. Linear assumptions were checked by plotting the Dunn-Smyth residuals against the fitted values.

In order to get more insight into the long-term effects of grassland intensive management practices (~ 20 years) versus mid-term (after 5 years of intensification), we used the data collected in 2015 in the management intensification experiment carried out in the same region (see Dani 2017), to compare the snail communities with those of the present study. Snail density and richness from Dani (2017) in extensive (C) and recently intensified plots (I+F 3/3) were tested with the data in intensively managed meadows from this study, using generalised linear mixed models with Poisson distribution. All the analyses were performed with the software R (v. 4.0.0; R Team Core, 2020).

Results

Overall, we found 6'712 snail shells, of which 4'946 were fresh shells (73.7%). 27 species (4 Red-Listed) were identified, belonging to 20 different genera. 985 shells (19.9%) could be determined only to the genus level, as they belonged to immature individuals. Together with the unidentified individuals (114 shells, 2.3%), these were only included in the analysis of snail density (Appendix B). Correlations between raw variables and the description of the explanatory variables included in the analyses are presented in Appendix A. The following continuous variables were highly correlated ($\rho > 0.7$) with at least one of the other variables, and hence were removed from the analyses (their surrogate variables are shown in brackets): inorganic carbon (C/N ratio), slope (heat load), silt and sand (clay), plant richness (plant diversity), and N content (C content). Heat load was chosen as a surrogate of both slope and folded aspect (ρ = 0.66 with heat load) because it summarizes the effect of these two variables (McCune & Dylan, 2002).

Snail density, species richness and occurrence of red-listed species

All results of snail density, species richness and occurrence of red-listed species are detailed in Appendix C. Soil pH stood out as the most important variable in the study system, having the highest influence on snail density, richness and the number of red-listed species in a positive way (Figs. 1a and 2a; Table C6). No interaction of soil pH with any other variable was retained after full model averaging. Elevation had a quadratic effect with an optimum at around 1100 m (Figs. 1b and 2b), but its influence on snail density and species richness was generally negative. Plant diversity (Shannon index) significantly promoted snail density (Fig. 1c), as well as the number of snail species (Fig. 2c) in a marginally significant manner ($P = 0.07$ in full model averaging, Table C5). The analyses using a subset of meadows where pH may be less limiting for snail density did not reveal any additional variables of importance. Using a cut-off of pH 5.5 (n = 32), the significant variables were the same as in the models with the whole set of meadows (pH, plant diversity and elevation with quadratic effect), whereas only plant diversity was retained with a cut-off of pH 6 (n = 23; Table C3 and C4). The univariate models investigating the occurrence of RL species suggest a positive effect of C/N ratio (Estimate ± SE = 0.57 ± 0.28; $P = 0.04$) and bare ground (Estimate ± SE = 0.26 ± 0.12; $P = 0.03$; Table C6).

Community analysis

The output of the multivariate model and each of their univariate responses are shown in Appendix D. Soil C could not be used as an explanatory variable, as it affected the outcome of the whole model in a flawed manner. Seven species (*Cochlicopa lubrica*, *Cochlicopa lubricella, Pupilla muscorum*, *Vallonia costata*, *Vallonia excentrica*, *Vallonia pulchella* and *Vertigo pygmaea*) occurred in more than ten meadows and their absolute abundance was thus treated as the response variable in the community analysis. Soil pH, plant diversity and elevation had a significant effect on the community composition (Table D1), influencing the abundance of all species in a positive manner for pH and plant diversity, and negatively for elevation (Figs. 3). In addition, community composition was marginally affected by clay content and bare ground. This was mainly due to the addition of weak effects on the abundance of every species, as clay content was significant only for the species *Vallonia costata* (Tables D1 and D2). Clay content was generally detrimental for species abundance, whereas bare ground had a species-dependent effect (Fig. 3).

Comparison of snail communities differing in time exposure to intensification

The output of the generalized linear mixed models used in this analysis is described in Appendix E. Short-term intensively managed plots (I+F 3/3) had significantly higher snail densities than extensively managed plots (C) and intensively managed meadows (Fig. 4). In terms of species richness, intensive meadows had ~45% fewer snail species than both extensive (C) and short-term intensive plots (I+F 3/3) (Fig. 5).

Discussion

Soil pH, plant diversity and elevation were identified as key factors shaping land snail communities in intensively managed mountain meadows. Almost no individuals were found in meadows with soil pH < 5.5, indicating that this could be a strong limiting factor for land snails in the present study system. Our results suggest that long-term intensive grassland management is not detrimental to snail density but erodes snail species richness by 45%, compared to extensive and short-term intensive managements.

Key variables shaping land snail communities

Soil pH was the most influential variable for land snails in the study system, promoting abundant and species-rich snail communities. The importance of soil pH on snails is well-known, especially in sites with different soil chemistry (Martin & Sommer, 2006; Ondina et al., 2004; Wehner et al., 2019). Snails need calcium for their own shell growth, as well as for provisioning of the eggs during breeding (Baur, 1994). Calcium is diluted when pH is acid, and is therefore inaccessible for snails in these conditions (Growell, 1973). In our study system, snail communities were almost denudated in soils below pH 5.5 despite other factors being favourable, suggesting that soil pH can be a strong limiting factor. Basic calcareous grasslands therefore hold significant snail populations, even under an intensive management regime (but see Boschi & Baur, 2007a). In fact, inputs of organic manure can increase soil pH due to the buffering action of the organic compounds (Dani, 2017; Whalen, Chang, Clayton, & Carefoot, 2000), being particularly beneficial for snails in moderately acid to neutral soils. Calcium supply from irrigation with hard water could have also played a role, but there is no evidence proving this pathway in our study system. In the opposite direction, the application of products aiming to acidify the soil and reduce nitrate losses from leaching (Kemmitt, Wright, & Jones, 2005) is a farming practice related to intensification that can be extremely harmful for snails (Wäreborn, 1992), as supported by our results.

The causal link in the relation between plant diversity and snail communities is difficult to establish, given that the effect of plant diversity may be multiple (Braschler et al., 2004; Labaune & Magnin, 2001). First, even though snails are generalist feeders overall, some species may have narrower feeding habits (Iglesias & Castillejo, 1999; Kiss, 2017). The presence of several abundant plant species may thus provide diverse feeding resources for snails (Richardson, 1975). However, this effect was not detected when investigating the response to plant functional groups (grasses, forbs, legumes), so we believe this may not be relevant for the overall snail community. Second, plant diversity may not have a direct effect on snails, but rather be a surrogate of both vertical and horizontal habitat structural complexity (Labaune & Magnin, 2001). Not only different species have particular small-scale habitat requirements, but each individual also needs several microhabitats along its life cycle, such as oviposition sites or shelter (Dedov et al., 2006). This could explain why plant diversity has a stronger effect on overall snail density than on species richness. Regardless of the mechanism, management intensity, in particular nitrogen addition, could ultimately account for much of the variation of plant diversity (Humbert et al., 2016), indirectly affecting snail communities. The meadows in our study sites were similarly managed in terms of the amount of fertiliser, number of cuts or the occurrence of grazing, but other practices that could not be well defined (e.g. historical fertiliser inputs or grazing intensity) could have a major influence on the vegetation, and consequently on snails (Boschi & Baur, 2008).

Elevation is directly related to the length of the snail activity period, becoming shorter with increasing altitude (Baur et al., 2014; Schmera & Baur, 2014). Snails living at high elevations must hibernate to avoid the harsh winter conditions, and they only have a few suitable months to grow and breed (Nicolai & Ansart, 2017). We believe that the modest peak of snail abundance and richness around 1100 m is mostly explained by the fact that the richest meadows are clustered around this elevation by chance. Our results are thus in line with Schmera & Baur (2014), reporting a decline in gastropod abundance with increasing altitude in alpine grasslands.

Community analyses revealed that the most well-represented species respond in the same direction to the key variables influencing snail density and species richness, whereas the magnitude of the response is particular for each species. In the case of pH, our results support that all snail species have minimum calcium demands, although their threshold is species-dependant (Martin & Sommer, 2006). The general negative effect of elevation was initially surprising as we expected a turnover of species with increasing altitude (Labaune & Magnin, 2001), but no typical alpine species were occurring in the study sites. Interestingly, some variables that had no influence on snail density and species richness seem to have an effect on species abundances, but weak overall. For instance, coarse-textured soils with low water retention are generally preferred, especially by the common species *Vallonia costata*. Soil texture is known to be relevant for grassland-dwelling snails (Ondina et al., 2004), but its role may be weaker in intensive meadows because the denser and more homogeneous vegetation canopy provides stable moisture conditions (Boschi & Baur, 2007a). Finally, bare ground was influential for the community composition despite the low availability of such feature in intensive meadows. This result suggests that even widespread mesic species may need vegetation-free patches along their life cycle (e.g. *Pupilla muscorum*).

Occurrence of red-listed species

Most snail species in the Swiss Red-List occurring in mountain meadows are drought-tolerant species adapted to heated and steep slopes, with vegetation-free patches (Rüetschi et al., 2012; Schmera & Baur, 2014). This explains why these species were hardly found in the mesic meadows of our study system. We found that besides soil pH, C/N ratio and bare ground promote the amount of red-listed species. Their effect was nonetheless weak, given the low number of red-listed species in our intensively managed meadows. In addition, the cover of bare ground was most likely underrepresented in the study system. The sites had 5.1% of bare ground cover on average, much lower than the 10-20% required to support endangered species (Rüetschi et al., 2012). The positive influence of high C/N ratios is in line with the hypothesis that a milder management could favour the conditions for many red-listed species.

Comparison of snail communities differing in time exposure to intensification

Snail communities in long-term intensively managed meadows have around 45% less species than those found in recently intensified and extensively managed grassland plots. Despite the noteworthy differences in study sites and the year effect (Dani, 2017), this comparison suggests that management intensification affects the composition of land snail communities in mountain meadows. Most endangered, drought-tolerant species thrive in vegetation-free patches that are scarce in fertilised meadows (Rüetschi et al., 2012). From the moment fertiliser application starts, it may take some years for the vegetation cover to increase (Lessard-Therrien, Humbert, & Arlettaz, 2017) and drive these species to local extinction. This would explain why snail species richness is not yet eroded after five years of intensification, but can potentially be in the long-term if intensification continues. On the other hand, the abundance of mesic species is promoted in the more moist and shaded conditions typical of intensively managed meadows (Dani, 2017; Wehner et al., 2019). The situation in meadows is contrasting with that in pastures, where intensive management is detrimental for both snail abundance and species richness because of the combined effect of heavy trampling, grazing and fertilisation (Boschi & Baur, 2007a). It is worth noting that our intensively managed meadows have a lower estimated snail density than recently intensified plots according to the results, even though this can be mostly attributed to a higher limitation of soil pH in the sites where these particular intensive meadows occur.

Conclusions and conservation relevance

A deep understanding of the factors that influence terrestrial gastropod community composition is key to better comprehend to which extent natural or anthropogenic sources of variation play a role in structuring the community. This gets even more importance in mountain areas, where a large range of environmental conditions is found over small spatial scales. Our results, highlighting the strong limitation of soil pH for snail communities and the positive role of plant diversity, are as well expected to be applicable to lowland grasslands.

The most relevant finding for the conservation of grassland biodiversity is that long-term management intensification is not detrimental for snail density, but causes snail communities to be more species-poor compared to a shorter time exposure or an extensive management. Based on these results, we recommend to maintain a certain proportion of extensively managed grasslands to ensure the persistence of more sensitive species at the regional scale, especially in sites with basic soils and high plant diversity. Due to the energetic costs of gastropod movement (Denny, 1980) and low dispersal ability of small species (Dahirel, Olivier, Guiller, Martin, & Madec, 2015; Stoll et al., 2009), degraded meadows would hardly receive individuals colonising from the surroundings (Knop et al., 2011), so it is essential to keep existing valuable sites for land snail diversity. This study aimed to raise awareness and better consider gastropod biodiversity, since this group is still underrepresented in the scientific literature and conservation policies (Cuttelod et al., 2011),

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Supporting information

Appendix A – Description of study sites and explanatory variables

Appendix B – Snail species list

Appendix C – Results of the analyses of snail density, species richness and occurrence of red-listed species

Appendix D - Results of the community analysis

Appendix E – Comparison of snail communities differing in time exposure to intensification

Figures

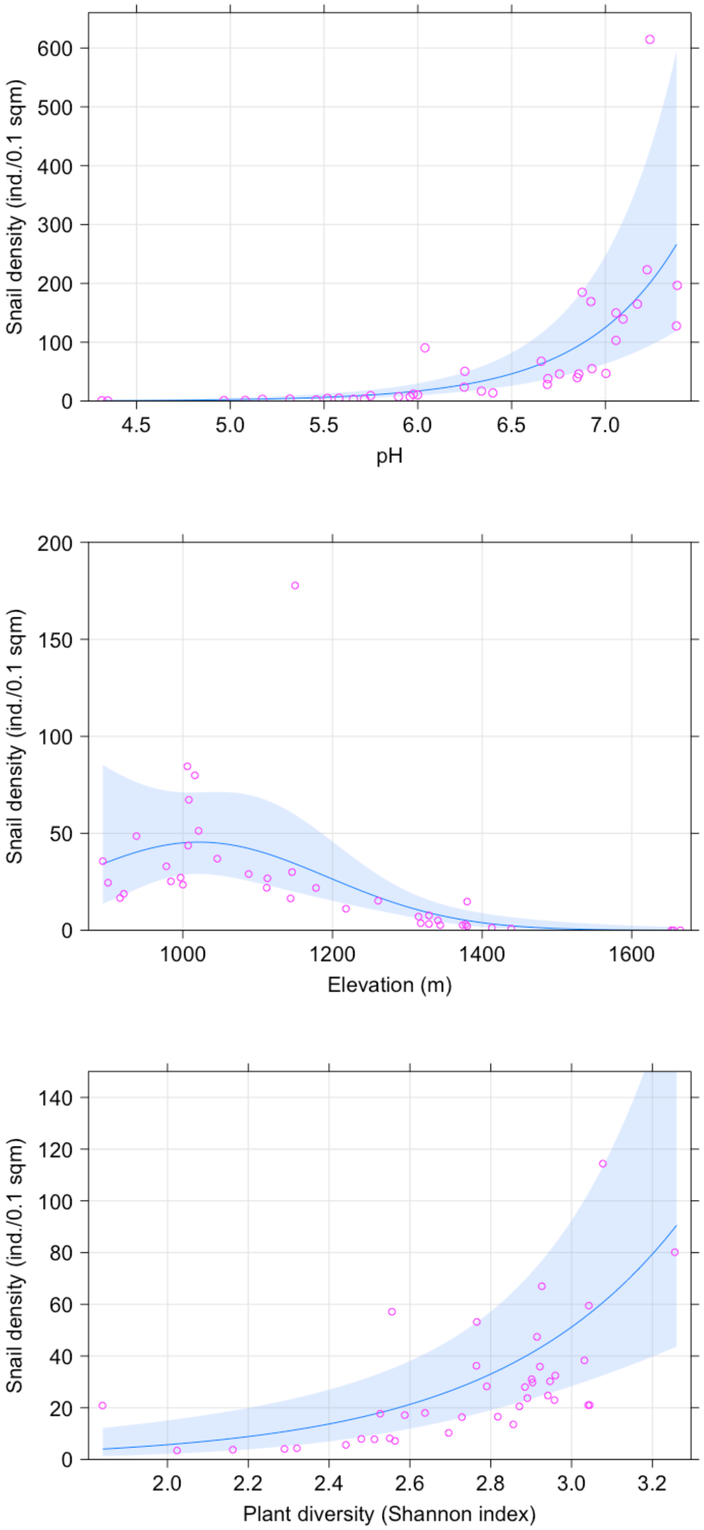

Figure 1. Effect plots with partial residuals for each of the predictors influencing snail density after full model averaging: a) soil pH; b) elevation; c) plant diversity. The blue line in each plot represents the fitted model with a 95% confidence band.

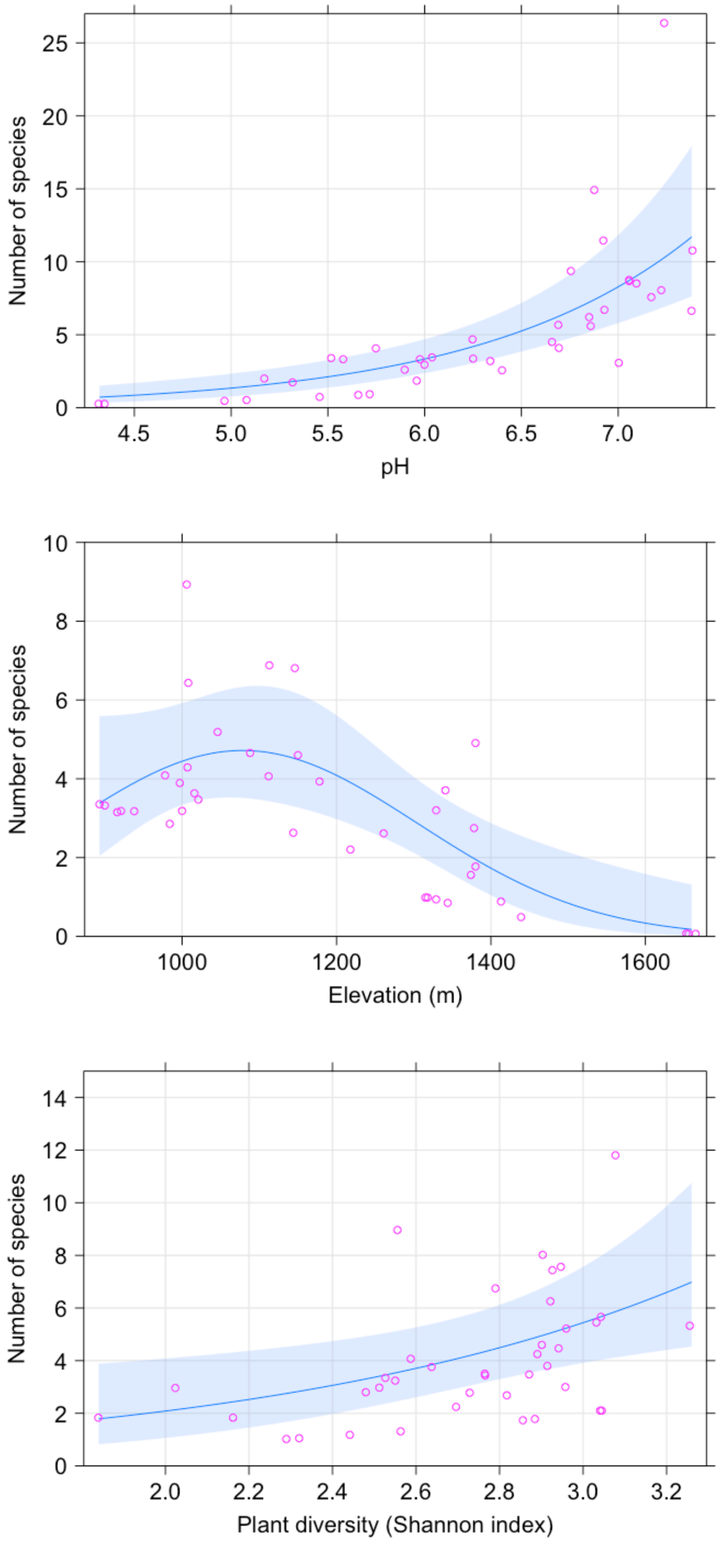

Figure 2. Effect plots with partial residuals for each of the predictors influencing snail species richness after full model averaging: a) soil pH; b) elevation; c) plant diversity. Plant diversity was marginally significant (*P* = 0.09). The blue line in each plot represents the fitted model with a 95% confidence band.

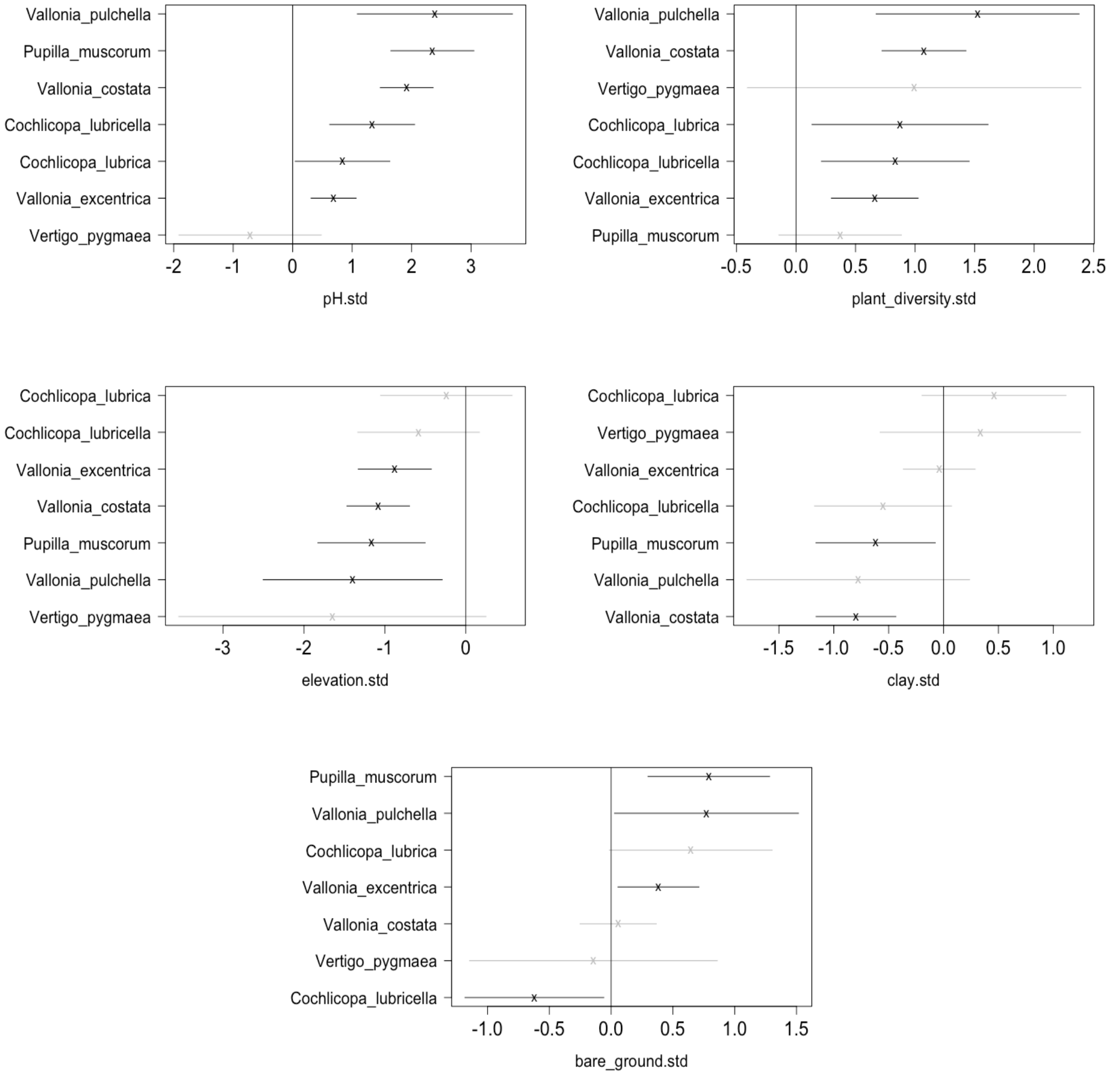

Figure 3. Plots of the point estimates for the coefficients of explanatory variables influencing species abundance. The bars show 95% confidence intervals, with those coloured in black indicating intervals not containing zero. Only the variables of the best model having an influence ($P < 0.1$) on the overall community composition (Table D1) are displayed: a) pH, b) Plant diversity, c) Elevation, d) Clay content, e) Bare ground. Values of significance of the effect of the each predictor on single species abundance are shown in Table D2. Explanatory variables were standardised (mean = 0, SD = 1).

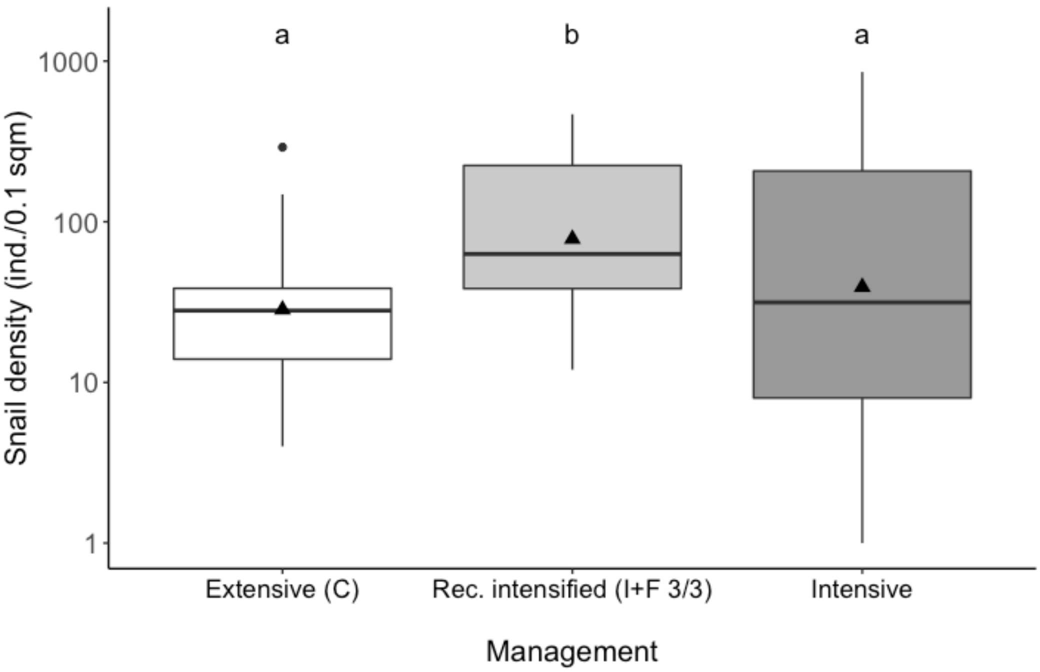

Figure 4. Boxplots showing the snail density in the intensively managed meadows in 2019 (n=39), and the extensive (C) and recently intensified (I+F 3/3 for 5 years) plots (n=11 each) from the management intensification experiment in 2015. Mean values are marked with solid triangles. Different letters represent significant differences at $P < 0.05$.

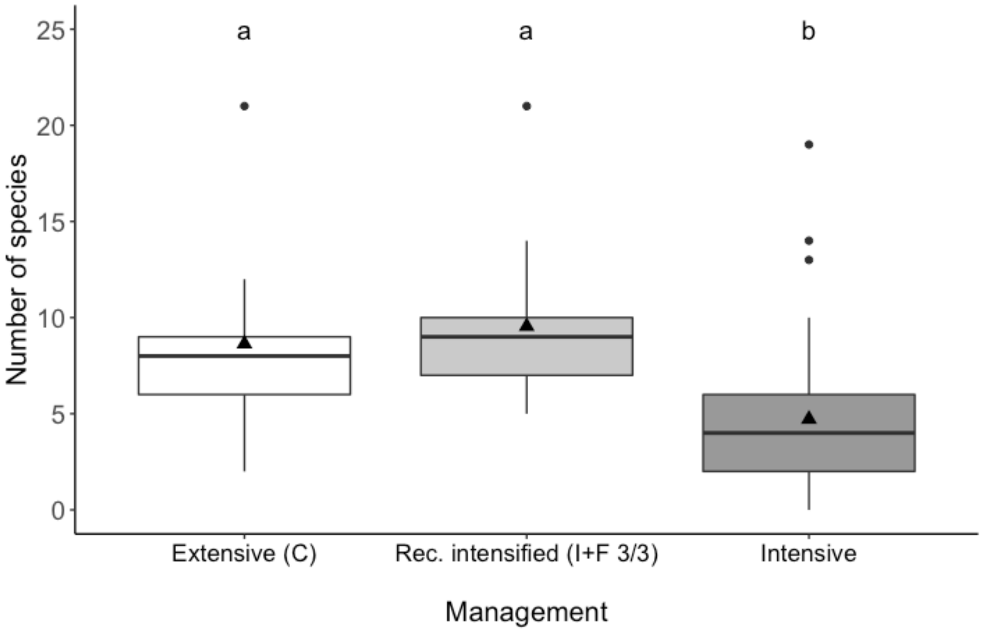

Figure 5. Boxplots showing the snail species richness in the intensively managed meadows in 2019 (n=39), and the extensive (C) and recently intensified (I+F 3/3 for 5 years) plots (n=11 each) from the management intensification experiment in 2015. Mean values are marked with a solid triangles. Different letters represent significant differences at $P < 0.05$.

Appendix A – Description the study sites and explanatory variables

Table A1. Location of each meadow, with its experimental treatment, elevation, slope, aspect and coordinates. Column “Treatment” refers to the quantity of organic fertiliser applied in the meadows since 2019: “Intensive” meadows received the current amount of fertiliser, “Mid-Intensive” received 1/3 of the fertiliser applied in the intensive meadows, and “Extensive” meadows had no application of fertiliser. As these treatments were not expected to have an effect in 2019, all meadows are referred as “intensively managed” throughout the thesis.

Study site	Treatment	Elevation [m]	Slope [°]	Aspect [°]	Coordinates	
					Latitude	Longitude
Val d’Illiez	Mid-Intensive	1000	16	49	46° 12’ 1”N	6° 53’ 11”E
	Intensive	978	17	52	46° 11’ 59”N	6° 53’ 13”E
	Extensive	997	13	50	46° 12’ 2”N	6° 53’ 13”E
Orsières 1	Mid-Intensive	1006	11	58	46° 1’ 41”N	7° 9’ 5”E
	Intensive	1008	16	45	46° 1’ 37”N	7° 9’ 5”E
	Extensive	1007	21	41	46° 1’ 39”N	7° 9’ 5”E
Orsières 2	Mid-Intensive	938	14	64	46° 2’ 12”N	7° 8’ 35”E
	Intensive	900	26	90	46° 2’ 14”N	7° 8’ 41”E
	Extensive	893	16	110	46° 2’ 9”N	7° 8’ 42”E
Bruson	Mid-Intensive	1112	17	91	46° 3’ 43”N	7° 13’ 10”E
	Intensive	1113	23	115	46° 3’ 43”N	7° 13’ 8”E
	Extensive	1088	16	95	46° 3’ 35”N	7° 13’ 23”E
Le Levron	Mid-Intensive	1178	16	101	46° 5’ 42”N	7° 10’ 6”E
	Intensive	1218	29	70	46° 5’ 42”N	7° 9’ 53”E
	Extensive	1261	23	69	46° 5’ 49”N	7° 9’ 53”E
Nax	Mid-Intensive	1150	2	106	46° 13’ 59”N	7° 25’ 43”E
	Intensive	1144	8	115	46° 13’ 59”N	7° 25’ 38”E
	Extensive	1146	1	118	46° 13’ 59”N	7° 25’ 40”E
La Luette	Mid-Intensive	1021	2.5	111	46° 9’ 56”N	7° 26’ 16”E
	Intensive	1016	7	108	46° 9’ 57”N	7° 26’ 15”E
	Extensive	984	2	98	46° 9’ 58”N	7° 26’ 11”E

Site	Treatment	Altitude [m]	Slope [º]	Aspect [º]	Coordinates	
					Latitude	Longitude
Euseigne	Mid-Intensive	1046	14	115	46º 10’ 16”N	7º 25’ 6”E
	Intensive	916	1	280	46º 10’ 26”N	7º 25’ 25”E
	Extensive	921	11	95	46º 10’ 25”N	7º 25’ 30”E
Evolène	Mid-Intensive	1374	1	95	46º 6’ 26”N	7º 30’ 2”E
	Intensive	1378	7	115	46º 6’ 27”N	7º 30’ 2”E
	Extensive	1380	25	84	46º 6’ 36”N	7º 29’ 31”E
La Tour	Mid-Intensive	1380	9	59	46º 6’ 9”N	7º 30’ 5”E
	Intensive	1413	11	65	46º 6’ 7”N	7º 30’ 18”E
	Extensive	1439	17	45	46º 6’ 11”N	7º 30’ 23”E
La Forclaz	Mid-Intensive	1656	1	87	46º 4’ 59” N	7º 31’ 8”E
	Intensive	1665	10	41	46º 5’ 24”N	7º 30’ 54”E
	Extensive	1653	13	39	46º 5’ 27”N	7º 30’ 54”E
Trient	Mid-Intensive	1318	28	59	46º 3’ 10”N	6º 59’ 44”E
	Intensive	1315	25	64	46º 3’ 12”N	6º 59’ 44”E
	Extensive	1329	10	68	46º 3’ 6”N	6º 59’ 46”E
Oberems	Mid-Intensive	1341	11	315	46º 16’ 58”N	7º 41’ 11”E
	Intensive	1344	45	295	46º 16’ 50”N	7º 41’ 42”E
	Extensive	1329	19	308	46º 16’ 59”N	7º 41’ 9”E

Table A2. Explanatory variables used in the analyses after checking for correlations (see Fig. A2).

Type of variable	Variable	Influence on snails	References
Topographical	Elevation	Activity period, breeding strategy, adult shell size	Baur, 1994; Baur et al., 2014; Nicolai & Ansart, 2017; Schmera & Baur, 2014
	Heat load	Moisture, winter survival	Baur & Baur, 1993; Nicolai & Ansart, 2017
Soil	pH	Calcium supply for shell formation	Baur, 1994; Dani, 2017; Schmera & Baur, 2014; Wehner et al., 2019
	Clay content (%)	Nesting, moisture	Baur, 1994; Ondina, Hermida, Outeiro, & Mato, 2004
	Total C and C:N ratio	General soil properties, calcium supply, indirect effects through plants	Hodge, Robinson, & Fitter, 2000; Martin & Sommer, 2004; Ondina et al., 2004
Vegetation	Shannon index of plant diversity	Feeding resources, habitat structure	Dedov et al., 2006; Wehner et al., 2019
	Landolt humidity - Community Weighted Mean	Moisture	Baur, 1994; Braschler et al., 2004; Horsák, Hájek, Tichy, & Jurickovà, 2007; Martin & Sommer, 2004
	Cover of plant functional groups (forbs, grasses, legumes)	Feeding resources	Allan & Crawley, 2011; Dedov et al., 2006; Wehner et al., 2019
	Bare ground (%)	Moisture, presence of xerophilous species	Dedov et al., 2006; Rüetschi et al., 2012
	Litter (%)	Feeding resources, nesting	Baur, 1994; Dedov et al., 2006
	Mean vegetation height	Vegetation structure, moisture	Dedov et al., 2006; Wehner et al., 2019
Management	Irrigation (presence/absence)	Moisture, calcium supply, indirect effects through plants	Andrey, Humbert, Pernollet, & Arlettaz, 2014; Dani, 2017; Riedener et al., 2013
Landscape	Meadows (%)	Habitat diversity, dispersal, fragmentation	Knop et al. 2011; Rüetschi et al 2012; Dahirel et al. 2015; Nicolai & Ansart 2017
	Forest (%)		
	Extensive seminatural structures (%)		
	Artificial structures (%)		

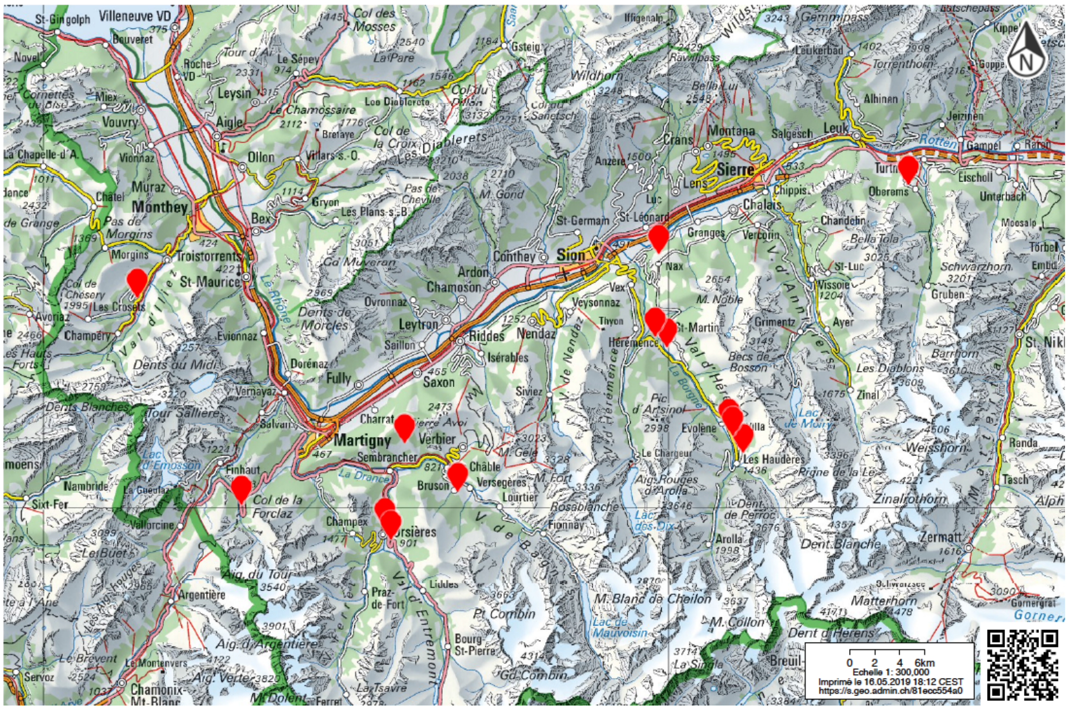

Figure A1. Location of the study sites in the region of Valais, inner Swiss Alps. Modified from Swisstopo.

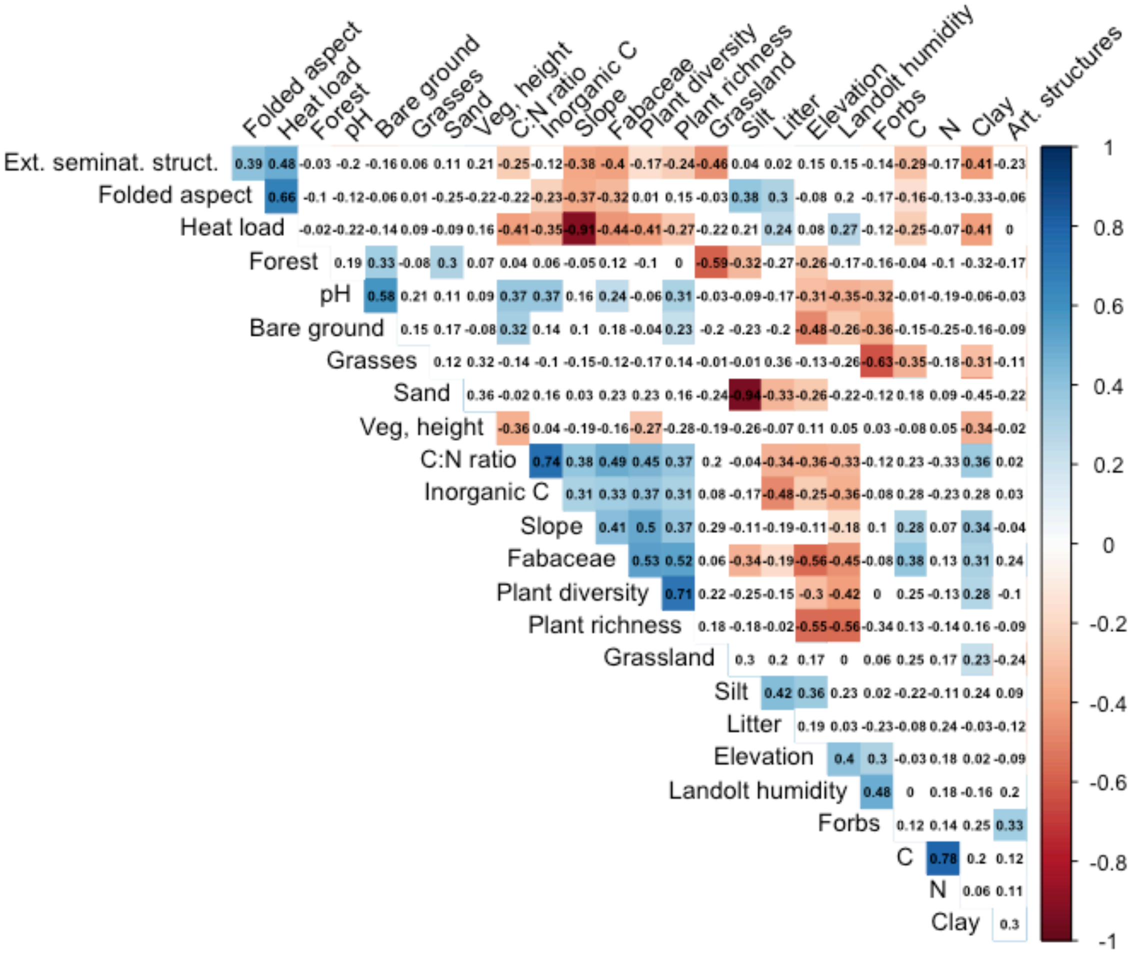

Figure A2. Correlation plot of all continuous variables with Spearman correlation values. Significant correlations ($P < 0.01$) have a coloured background in blue (positive correlation) or red (negative correlation). After assessing the variables having a pairwise correlation coefficient > 0.7, the following variables were removed from the analyses: *inorganic C*, *N content*, *plant richness, sand, silt* and *slope*. *Silt* and *sand* could be merged into a single variable, but instead we decided to use the variable *clay,* as it represents the complementary proportion. *Folded aspect* was also removed because it is involved in the calculation of *heat load* and it is considerably correlated with this variable ($\rho = 0.66$).

Appendix B – Snail species list

Table B1. List of snail species and absolute abundance of fresh shells across all study sites. Nomenclature follows Falkner, Obrdlík, Castella, & Speight, 2001. Regional Red-List status in Switzerland according to Rüetschi, Stucki, Müller, Vicentini, & Claude, 2012. LC stands for Least Concern, NT for Near Threatened, VU for Vulnerable, EN for Endangered. No Critically Endangered (CR) or Data Deficient (DD) species were found. Species in bold were included in the community analysis.

Species	Total abundance	Red-List status in Switzerland
Aegopinella minor	2	LC
Aegopinella pura	10	LC
Candidula unifasciata	83	VU
Carychium tridentatum	1	LC
Cecilioides acicula	10	LC
Cepaea cf. *nemoralis*	4	LC
Chilostoma zonatum	1	LC
Cochlicopa lubrica	96	LC
Cochlicopa lubricella	56	LC
Columella columella	1	LC
Discus rotundatus	1	LC
Jaminia quadridens	3	VU
Nesovitrea petronella	36	LC
Platyla polita	1	LC
Punctum pygmaeum	4	LC
Pupilla muscorum	618	LC
Succinella oblonga	18	LC
Trichia hispida	5	NT
Trichia sericea	58	LC
Truncatellina cylindrica	147	LC
Vallonia_costata	1490	LC
Vallonia_excentrica	803	LC
Vallonia_pulchella	232	LC
Vertigo angustior	1	EN
Vertigo antivertigo	4	VU
Vertigo pygmaea	111	LC
Xerolenta obvia	51	NT
No ID	114	
Cochlicopa sp.	88	
Vallonia sp.	879	
Vertigo sp.	18	
TOTAL	4946	

Table B2. Snail density, species richness and number of Red-Listed species per meadow.

Study site	Treatment	Snail density	Species richness	Number of Red-Listed species
Val d'Illiez	Mid-Intensive	8	2	0
	Intensive	36	4	0
	Extensive	30	4	0
Orsières 1	Mid-Intensive	438	14	1
	Intensive	676	19	3
	Extensive	159	8	1
Orsières 2	Mid-Intensive	553	8	1
	Intensive	518	10	1
	Extensive	856	10	1
Bruson	Mid-Intensive	16	4	0
	Intensive	14	5	0
	Extensive	31	5	0
Le Levron	Mid-Intensive	276	13	2
	Intensive	109	6	0
	Extensive	474	10	0
Nax	Mid-Intensive	9	2	0
	Intensive	8	2	0
	Extensive	17	5	0
La Luette	Mid-Intensive	206	6	0
	Intensive	102	4	0
	Extensive	62	4	0
Euseigne	Mid-Intensive	31	5	0
	Intensive	32	5	0
	Extensive	43	5	0
Evolène	Mid-Intensive	5	2	0
	Intensive	6	3	0
	Extensive	210	10	0
La Tour	Mid-Intensive	5	3	0
	Intensive	1	1	0
	Extensive	0	0	0
La Forclaz	Mid-Intensive	0	0	0
	Intensive	0	0	0
	Extensive	0	0	0
Trient	Mid-Intensive	0	0	0
	Intensive	1*	0	0
	Extensive	0	0	0
Oberems	Mid-Intensive	8	3	0
	Intensive	0	0	0
	Extensive	6	2	0

* The only individual found in this meadow was immature, so it could not be assigned to a certain species with confidence.

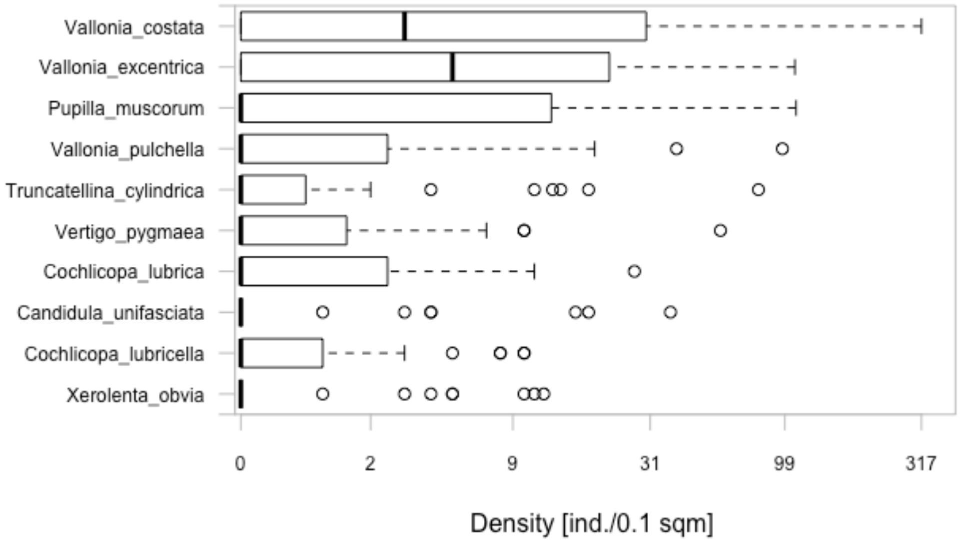

Figure B1. Snail densities for the subset of 11 species with the highest total abundance. Species are ranked according to their absolute abundance.

Appendix C – Results of the analyses of snail density, species richness and occurrence of red-listed species

Table C1. Generalised linear mixed model outputs performed to analyse the effect of explanatory variables on snail density and species richness. Models were run with Poisson error distribution. The table shows the best set of models (Δ AICc < 6) retained for model averaging. Explanatory variables were first pre-selected from the whole set of variables (see Table A2) with univariate GLMMs. Those with significant effects (*P* < 0.05) were used for model selection. Interactions with soil pH and any of the other pre-selected explanatory variables were tested and incorporated in the analysis, providing statistical significance. Likewise, polynomial relationships were only considered in case they had significant effects. The analysis using cut-off thresholds of soil pH (pH > 5.5 or > 6), was done for both snail density and species richness, but the results did not provide any additional important explanatory variable for either of the response variables. Therefore, only the output of the models of snail density is displayed in order to illustrate the process.

Rank	Model	Df	logLik	AICc	Δ AICc	Model weight
	Snail density (with observation-level random effect)					
1	bare ground + pH + plant diversity + pH: plant diversity + poly(elevation,2)	9	-155.73	335.70	0.00	0.39
2	pH : plant diversity + poly(elevation,2)	8	-157.79	336.40	0.71	0.27
3	bare ground + pH + plant diversity + poly(elevation,2)	8	-157.82	336.40	0.77	0.26
4	pH + plant diversity + poly(elevation,2)	7	-160.58	338.80	3.10	0.08
	Snail density, meadows with pH > 5.5 (with observation-level random effect)					
1	bare ground + pH + plant diversity + poly(elevation,2)	8	-147.12	316.50	0.00	0.48
2	pH + plant diversity + poly(elevation,2)	7	-149.60	317.90	1.36	0.24
3	C/N ratio + plant diversity + poly(elevation,2)	8	-148.38	319.00	2.51	0.14
4	bare ground + C/N ratio + pH + plant diversity + poly(elevation,2)	9	-146.45	319.10	2.58	0.13

Rank	Model	Df	logLik	AICc	Δ AICc	Model weight
	Snail density, meadows with pH > 6 (with observation-level random effect)					
1	plant diversity	4	-127.88	266.00	0.00	0.28
2	elevation + plant diversity	5	-126.29	266.10	0.12	0.27
3	bare ground + plant diversity	5	-126.32	266.20	0.20	0.26
4	bare ground + elevation + plant diversity	6	-124.72	266.70	0.71	0.20
	Species richness					
1	bare ground + pH + plant diversity + poly(elevation,2)	7	-68.68	155.00	0.00	0.66
2	pH + plant diversity + poly(elevation,2)	6	-71.35	157.30	2.35	0.20
3	bare ground + pH + poly(elevation,2)	6	-71.92	158.50	3.51	0.11

Table C2. Output of the full model averaging performed on the best set of models (ΔAIC < 6) analysing the effect of explanatory variables on snail density (see Table C1). Statistically significant variables (*P* < 0.05) are marked in bold. Relative importance (rel. importance) was calculated by summing up all Akaike weights of the models in the best set where the predictor variable occurs. Variables were standardised (mean = 0, SD = 1).

Fixed effects	Estimate	95% CI	P value	Rel. importance
(**Intercept**)	2.65	(2.11, 3.19)	< 0.001	
Bare ground	0.19	(-0.16, 0.55)	0.29	0.65
pH	1.45	(0.98, 1.92)	< 0.001	1.00
Plant diversity	0.58	(0.25, 0.91)	< 0.001	1.00
Elevation	-9.30	(-14.20, -4.39)	< 0.001	1.00
Elevation^2	-5.48	(-10.33, -0.64)	< 0.05	1.00
Plant diversity : pH	0.37	(-0.30, 1.03)	0.28	0.66

Table C3. Output of the full model averaging performed on the best set of models (ΔAIC < 6) analysing the effect of explanatory variables on snail density, in the subset of meadows with pH > 5.5 (n = 32; see Table C1). Statistically significant variables (*P* < 0.05) are marked in bold. Relative importance (rel. importance) was calculated by summing up all Akaike weights of the models in the best set where the predictor variable occurs. Variables were standardised (mean = 0, SD = 1).

Fixed effects	Estimate	95% CI	P value	Rel. importance
(**Intercept**)	2.78	(2.25, 3.31)	< 0.001	
Bare ground	0.21	(-0.19, 0.60)	0.31	0.62
pH	1.50	(0.89, 2.11)	< 0.001	1.00
Plant diversity	0.67	(0.33, 1.01)	< 0.001	1.00
Elevation	-8.12	(-12.23, -4.00)	< 0.001	1.00
Elevation^2	-4.72	(-8.98, -0.45)	< 0.05	1.00
C/N ratio	0.07	(-0.23, 0.37)	0.65	0.27

Table C4. Output of the full model averaging performed on the best set of models (ΔAIC < 6) analysing the effect of explanatory variables on snail density, in the subset of meadows with pH > 6 (n = 23; see Table C1). Statistically significant variables (*P* < 0.05) are marked in bold. Relative importance (rel. importance) was calculated by summing up all Akaike weights of the models in the best set where the predictor variable occurs. Variables were standardised (mean = 0, SD = 1).

Fixed effects	Estimate	95% CI	P value	Rel. importance
(**Intercept**)	4.12	(3.21, 5.02)	< 0.001	
Plant diversity	1.06	(0.59, 1.53)	< 0.001	1.00
Elevation	-0.36	(-1.33, 0.61)	0.46	0.46
Bare ground	0.16	(-0.28, 0.60)	0.47	0.45

Table C5. Output of the full model averaging performed on the best set of models (Δ AICc < 6) analysing the effect of explanatory variables on snail species richness (see Table C1). Statistically significant variables (*P* < 0.05) are marked in bold. Relative importance (rel. importance) was calculated by summing up all Akaike weights of the models in the best set where the predictor variable occurs. Variables were standardised (mean = 0, SD = 1).

Fixed effects	Estimate	95% CI	P value	Rel. importance
(**Intercept**)	0.96	(0.65, 1.27)	< 0.001	
Bare ground	0.19	(-0.07, 0.44)	0.16	0.79
pH	0.68	(0.42, 0.95)	< 0.001	1.00
Plant diversity	0.23	(-0.04, 0.49)	0.09	0.88
Elevation	-4.54	(-7.26, -1.82)	< 0.01	1.00
Elevation^2	-3.45	(-5.95, -0.96)	< 0.01	1.00

Table C6. Output of the univariate generalised linear mixed models analysing the effect of explanatory variables on the occurrence of Red-Listed species. Variables are ranked according to their absolute estimates (log scale). Statistically significant variables (*P* < 0.05) are marked in bold.

Fixed effects	Estimate	SE	P value
pH	3.17	1.55	0.04
C/N ratio	0.57	0.28	0.04
Bare ground	0.26	0.12	0.03

References

Falkner, G., Obrdlík, P., Castella, E., & Speight, M. C. D. (2001). *Shelled Gastropoda of Western Europe*. München: Friedrich-Held-Gesellschaft.

Rüetschi, J., Stucki, P., Müller, P., Vicentini, H., & Claude, F. (2012). Liste rouge Mollusques (gastéropodes et bivalves). Espèces menacées en Suisse, état 2010. *L'environnement Pratique*.

Appendix D - Results of the community analysis

Table D1. Output of the multivariate generalised linear models with negative binomial distribution used to analyse the effect of the explanatory variables on species abundance. Likelihood-Ratio (LR) values were summed across all species to get a statistic for the whole community. Variables influencing community composition (*P* < 0.1) are marked in bold. P-values calculated using 999 iterations via PIT-trap resampling. Explanatory variables were standardised (mean = 0, SD = 1).

Fixed effects	LR value	P value
(Intercept)	94.46	< 0.001
pH	99.91	< 0.001
Plant diversity	65.94	< 0.001
Elevation	51.56	< 0.001
Clay	24.73	0.08
Bare ground	23.50	0.09
Landolt humidity CWM	22.75	0.10
Forbs	17.18	0.22
Mean vegetation height	16.25	0.21

Table D2. Univariate test statistics from the multivariate generalised linear models with negative binomial distribution used to analyse the effect of the explanatory variables on species abundance. P-values calculated using 999 iterations via PIT-trap resampling and adjusted for multiple testing. Values with $P < 0.1$ are marked in bold. Variables were standardised (mean = 0, SD = 1).

		Cochlicopa lubrica	*Cochlicopa lubricella*	*Pupilla muscorum*	*Vallonia costata*	*Vallonia excentrica*	*Vallonia pulchella*	*Vertigo pygmaea*
(Intercept)	LR value	0.09	10.43	0.64	30.91	38.37	10.65	3.38
	P	0.89	0.29	0.89	**< 0.01**	**< 0.01**	0.29	0.61
pH	LR value	2.83	12.34	24.05	36.87	8.40	14.35	1.09
	P	0.32	**< 0.05**	**< 0.01**	**< 0.001**	**0.08**	**< 0.05**	0.42
Plant diversity	LR value	3.53	7.46	1.65	27.34	12.42	11.75	1.79
	P	0.41	0.21	0.53	**< 0.01**	0.12	0.13	0.53
Elevation	LR value	0.26	2.30	8.59	16.66	13.32	6.09	4.34
	P	0.65	0.41	0.18	**< 0.05**	**0.06**	0.27	0.28
Clay	LR value	1.69	2.98	4.24	12.86	0.05	2.58	0.34
	P	0.70	0.70	0.57	**0.08**	0.87	0.70	0.87
Bare ground	LR value	3.55	4.57	8.41	0.11	3.56	3.26	0.04
	P	0.57	0.50	0.22	0.96	0.57	0.57	0.96
Landolt humidity CWM	LR value	0.42	1.89	4.27	0.99	5.79	1.18	8.22
	P	0.77	0.73	0.47	0.77	0.35	0.77	0.23
Forbs	LR value	0.41	2.82	4.14	6.71	0.95	1.97	0.19
	P	0.85	0.66	0.54	0.34	0.81	0.70	0.85
Mean vegetation height	LR value	0.04	6.55	6.47	0.28	2.70	0.04	0.18
	P	0.99	0.31	0.31	0.99	0.65	0.99	0.99

Appendix E – Comparison of snail communities differing in time exposure to intensification.

Table E1. Output of the generalised linear mixed models with Poisson distribution and analysing the effect of time exposure to intensification on snail density. Observation-level and site were treated as random effects. Intensive meadows (i.e. ~20 years with fertiliser application) in the year 2019 (n=39) were tested against the plots from the management intensification experiment of Dani (2017). All plots were managed extensively before the start of the experiment (i.e. no irrigation or fertiliser application), and then received the experimental treatments “extensive” (C) and “recently intensified” (I+F 3/3) for five years (n=11 each). Abbreviations for the treatments: C = Control; I+F 3/3 = fertilised and irrigated at the dose that would be necessary to achieve the maximum theoretical local hay yield (for more information see Andrey, Humbert, & Arlettaz, 2016). The function *relevel* was used to set other levels as intercept and perform multiple comparison analysis. Statistically significant values ($P < 0.05$) are marked in bold.

	Abundance (log scale)		
	Estimate	SE	P value
Intercept (C)	3.00	0.52	**< 0.001**
I+F 3/3 vs C	1.02	0.35	**0.004**
Intensive vs C	-0.14	0.48	0.770
Random effect	3.44		

Intercept (I/F 3/3)	4.02	0.51	**< 0.001**
Intensive vs I+F 3/3	-1.16	0.48	**0.016**
Random effect	3.44		

Table E2. Output of the generalised linear mixed models with Poisson distribution) analysing the effect of time exposure to intensification on snail species richness. Site was set as a random effect. Intensive meadows (i.e. ~20 years with fertiliser with fertiliser application) in the year 2019 (n=39) were tested against the plots from the management intensification experiment of Dani (2017). All plots were managed extensively before the start of the experiment (i.e. no irrigation or fertiliser application), and then received the experimental treatments "extensive" (C) and "recently intensified" (I+F 3/3) for five years (n=11 each). Abbreviations for the treatments: C = Control; I+F 3/3 = fertilised and irrigated at the dose that would be necessary to achieve the maximum theoretical local hay yield (for more information see Andrey, Humbert, & Arlettaz, 2016). The function *relevel* was used to set other levels as intercept and perform multiple comparison analysis. Statistically significant values ($P < 0.05$) are marked in bold.

	Species richness (log scale)		
	Estimate	SE	P value
Intercept (C)	1.85	0.20	**< 0.001**
I+F 3/3 vs C	0.10	0.14	0.475
Intensive vs C	-0.54	0.18	**0.003**
Random effect	0.48		

Intercept (I/F 3/3)	1.94	0.20	**< 0.001**
Intensive vs I+F 3/3	-0.65	0.18	**< 0.001**
Random effect	0.48		

References

Andrey, A., Humbert, J. Y., & Arlettaz, R. (2016). Functional response of leaf- and planthoppers to modern fertilisation and irrigation of hay meadows. *Basic and Applied Ecology*, *17*(7), 627–637. doi:10.1016/j.baae.2016.07.002

Dani, L. (2017). *Positive effects of management intensification on land snail communities in Swiss traditionally managed montane and subalpine meadows. Master thesis.* University of Bern.

Declaration of consent

on the basis of Article 30 of the RSL Phil.-nat. 18

Name/First Name: Martínez De León, Gerard

Registration Number: 18-119-875

Study program: Ecology and Evolution

Bachelor ☐ Master ☑ Dissertation ☐

Title of the thesis: Soil pH and plant diversity shape land snail communities in intensively-managed montane and subalpine meadows

Supervisor: PD Dr. Jean-Yves Humbert and Prof. Dr. Raphäel Arlettaz

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