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BMC Ecology and Evolution (2022) 22:19
https://doi.org/10.1186/s12862-022-01972-4

BMC Ecology and Evolution

RESEARCH ARTICLE

Open Access

Mid- and long-term responses of land snail communities to the intensification of mountain hay meadows management

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Abstract

Background: Species-rich semi-natural grasslands are impacted by the severe land-use changes that are affecting mountain regions, compromising their high biodiversity value. In particular, sprinkler irrigation and increased fertilisation stimulate vegetation growth, modifying and homogenising habitat conditions for ground-dwelling invertebrates. Among them, land snails have been largely understudied despite their commonness and vulnerability to small-scale habitat alteration. This study investigated the mid- and long-term responses of land snail communities to management intensification of montane and subalpine hay meadows. Mid-term effects were studied using a randomised block design experiment, mimicking an intensification gradient with different levels of irrigation and fertilisation applied during 5 years. Long-term effects were examined relying on an observational approach that consisted in comparing snail communities in meadows managed intensively for > 20 years with those from the 5-year experimental module.

Results: We show that management intensification initially boosts snail densities, but erodes species richness by − 35% in intensively-managed meadows in the long term. Contrary to our expectations, drought-tolerant (xerophilous) snails benefitted from grassland intensification, whereas mesophilous species accounted for most species losses due to intensification in the long run, indicating that the latter may be especially sensitive to the hostile microclimate conditions abruptly prevailing in a meadow after mowing. Soil pH was also a principal determinant of land snail occurrence, with almost no specimen recorded in acidic meadows (pH < 5.5), while plant diversity favoured overall snail abundance.

Conclusions: Despite the fact that xerophilous snails appear tolerant to management intensification, we found that several drought-sensitive species are lost in the long term. We conclude that the preservation of species-rich land snail communities in mountain hay meadows requires the conservation and restoration of low-input grasslands on basic soils for preventing further species losses of gastropod fauna.

Keywords: Alps, Conservation, Fertilisation, Gastropod, Grassland

Background

Semi-natural grasslands are among the most specious habitats of temperate biomes, harbouring at site scale many more plant and arthropod taxa than the native habitat that would naturally develop at their place in the absence of human management [1–4]. Nevertheless, rising socio-economic pressures to increase yield (forage

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production) and to optimize agricultural labour are triggering widespread land-use changes that cause a collapse of traditionally-managed biodiversity-rich grasslands [5, 6]. Farmland intensification aims to obtain higher yields mainly through the addition of fertilisers [7], favouring fast-growing plants and generating a more homogeneous and shaded understory [8]. Intensification in mountain regions is mostly restricted to sites where access to agricultural machinery is possible, while land abandonment follows in principle the cessation of farming in difficult terrain and naturally less productive areas [9]. Because of the constraints imposed by their complex topography, mountain meadows are generally smaller, and less frequently fertilised and mown than lowland grasslands [2, 3, 10], meaning that the impact of intensification in these areas is potentially milder than at low elevation.

Despite being key components of grassland ecosystem functioning (e.g. [11]), invertebrates, contrary to plants, have been little investigated for assessing the impact of mountain grassland intensification [12]. Invertebrate taxa show different responses to management intensification, mostly according to their life-history traits: ectothermic heat-demanding taxa are ecologically especially vulnerable, i.e. sensitive to intensification (e.g. orthopterans; [13]), whereas taxa relying on an abundant phytomass can thrive under a more intensive management regime (e.g. carabids, leafhoppers and spiders; [14–16]). Yet, responses remain hard to predict for some taxa whose various life-history traits tend to react in opposite directions under the action of a given driver. Land snails are a good example. They are both abundant and functionally important grass-dwelling invertebrates, this owing to their role as detritivores [17] and prey for the upper trophic levels of the food chain [18, 19]. Their general extremely low active mobility and the high specialization of many species [20–22] might render them particularly sensitive to grassland intensification, although their small body size and activity taking place mainly at ground level [23] could confer them an enhanced tolerance to vegetation disturbances (e.g. mowing) compared to other invertebrates [24, 25]. Understanding the response of land snails to farming intensification would represent an asset to better inform conservation strategies aiming at conciliating the preservation of open-land biodiversity and nature-friendly agricultural production.

The study was carried out in Valais (SW Swiss Alps), a region characterized by warm and dry summers where the management of montane and subalpine hay meadows was traditionally achieved via irrigation by open water channels (gravitation) and fertilisation with solid organic manure, while modern farming mostly involves irrigation with sprinklers and slurry inputs. Since snail activity is highly dependent on moisture conditions [26–28], we hypothesised that farming intensification would promote higher snail densities due to greater water and fertiliser inputs that entail a denser sward and induce cooler and wetter conditions at ground level [13, 29]. We also predicted that open-land, drought-tolerant (i.e. xerophilous) snail species would be well represented in low-input grasslands, but would gradually become less frequent with increasing management intensity and a long exposure to new management modes [30]. In effect, it has been suggested that sensitive species may show a delayed response to newly generated unsuitable environmental conditions, becoming less abundant over time and eventually disappearing locally [31].

In order to unravel the impact of grassland management intensification on land snail communities over time, we relied on two approaches. The mid-term effects of intensification (after 5 years) were investigated in a first module, with a randomised block design experiment, by applying different levels of irrigation and fertilisation that mimic an increasing gradient of farming intensity. To our knowledge, this is the first genuine experiment (random allocation of treatments to plots) that has tested the effects of grassland management intensification on land snails. In a second module, the long-term effects of intensification were investigated within an observational framework, by comparing snail communities collected from intensively-managed meadows (> 20 years of intensive management) with those stemming from the above mid-term experimental module. The combination of both modules offers a comprehensive analysis of the effects of grassland intensification on land snails, thus providing solid support for the conservation and restoration of hay meadow biodiversity. Finally, several environmental variables were recorded in the intensively-managed meadows of the observational module so as to (1) identify the key environmental factors driving the variation among meadow snail assemblages; and (2) disentangle the contribution of natural and anthropogenic factors in shaping their composition.

Methods

Study area and experimental design

Study sites were located in the canton of Valais, in the inner Swiss Alps, between 880 and 1768 m a.s.l. (Additional file 1: Appendix S1). Land snails from the experimental module were sampled in 2015 at eleven meadows scattered across the study area. These had to be managed extensively for at least 10 years before the onset of the experiment in 2010, with no or very low levels of fertilisation and irrigation and only a single cut per year. Within each meadow, three management treatments and a control were randomly allocated to 20 m diameter plots, with at least 5 m buffer between adjacent plots. The control plot received no input while the other three plots received low, medium or high inputs of fertiliser and water, with respectively 1/3, 2/3 or 3/3 of a quantity that had been estimated necessary to achieve maximum hay yield at a given locality (for further details on the experimental design see Appendix A in [14]). Snail abundance and species richness did not differ among plots before the different management treatments were applied [32]. All plots were mown twice a year, except control plots that were mown only once to mimic local standards for extensively-managed meadows. Weekly irrigation amounted to 10, 20 and 30 mm in, respectively, low, medium and high input plots. These plots were irrigated from mid-May until early September, except under heavy rainfall (> 20 mm water during the previous week). Fertiliser consisted of dried organic manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium sulphate (K_2SO_4) dissolved into water so as to reach the nutrient content and viscosity of standard farm slurry.

Snails from the observational module were collected in the year 2019 from 39 meadows at thirteen different sites. These meadows had a minimum area of 0.2 ha and had to be managed intensively (i.e. frequently fertilised with solid or liquid manure, mown at least twice a year, and often used as pasture in autumn) for at least 20 years. Different types of fertiliser (manure or slurry) were usually alternated haphazardly between years depending on local farming mode and constrains so that it was not possible to incorporate this factor in the analyses. Other management practices (e.g. autumn grazing, number of grass cuts, technique of mowing, historical management, etc.) were similar between study sites and were thus not accounted for in our models.

Data collection

Snails present in the soil and the litter layer were collected from soil cores. Following the Swiss Biodiversity Monitoring (BDM) protocol for terrestrial molluscs [33], eight soil samples of 125 cm^2 area and 5 cm depth each were extracted after the first hay cut and pooled afterwards into a 5 dm^3 sample. These samples were then 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 Boschi [34] and Hausser [35]. The same sampling method was adopted in both modules, allowing for quantitative comparison of community composition.

The moisture preferences of different species of snails were extracted from an extensive trait database [23]. Species were categorised into xerophilous, mesophilous or hygrophilous depending on whether they showed highest affinity for dry, moist or wet soils, respectively. Besides, a community weighted mean (CWM) of moisture was calculated by weighing the moisture value of each species by its relative abundance in a given meadow, and then summing these weighed values. These species-specific moisture values were calculated following the methodology of Astor et al. [36]. Information on the regional Red-List status for every species was extracted from Rüetschi et al. [37].

In both modules, eight soil subsamples of 10 cm depth were obtained from each plot 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.

In the observational module, vegetation-related variables were extracted from surveys conducted in two randomly allocated subplots of 2×4 m distant by 8 m, as in van Klink et al. [38]. In addition, several variables related to topography, soil, local landscape and agricultural management were collected. All measured variables and their description are presented in Additional file 2: Appendix S2.

Statistical analyses

Land snail communities from the experimental and observational modules were compared to investigate the long-term effects of grassland management practices, using agricultural management intensity of each meadow (i.e. extensive, mid-term intensified, long-term intensified) as a fixed effect in the analyses. The extensive and mid-term intensified treatments were taken from the control and high management intensity plots of the experimental module, respectively, while the long-term intensified treatment included the meadows of the observational module. Generalised linear mixed models (GLMM) with Poisson error distribution were used with snail density and species richness (total, and for each moisture preference group), as well as the number of red-listed species as response variables. Linear mixed models (LMM) were adopted to analyse the response of the CWM of soil moisture optima and Pielou's evenness index ($J = H/\ln(S)$, where $H =$ the Shannon–Wiener index and $S =$ number of species in the sample). In the models fitting a Gaussian error distribution, p-values were obtained using the *lmerTest* package [39]. Study site was set as a random factor in all models. An observation-level random effect was added in case overdispersion had to be handled [40]. Model-based community analyses were carried out with the function *manyglm* in the package *mvabund* (v. 4.1.3; [41]). This function fits a generalised linear model to a matrix of species abundances by performing univariate models to each taxon and then summing the test statistics [42]. Given the high amount of species occurring at few sites, we conducted the analyses only with those species present in at least nine samples from both the experimental and observational modules. Statistical significance was assessed with likelihood-ratio test statistics resampled 999 times with the PIT-trap method (function *anova.manyglm*). All the aforementioned analyses were done on a subset of samples delimited by a cut-off value of soil pH > 6, as this factor was strongly limiting snail communities in the study area (see 'Results'). After accounting for this limitation of soil pH, 23 replicates from long-term intensified meadows, 10 replicates from mid-term intensified plots and 9 replicates from extensive plots were analysed.

In the experimental module, management treatments were converted into a continuous management intensity gradient variable (0, 1, 2, 3, respectively) ranging from no input to high-input, and then treated as a fixed effect. Besides snails-related response variables, the impact of management intensification on soil pH was also analysed with LMM. Community analyses for this module alone were done with the species present in at least nine samples.

In the observational module, a model selection approach was used to identify the most influential environmental variables for snail communities in the study system. Before model selection, correlations between covariates were assessed; in case two explanatory variables correlated (Spearman correlation coefficient > 0.7), the variable of more direct biological significance was kept [43, 44]. 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 (mean = 0, standard deviation = 1), and only those statistically significant with $P < 0.05$ were retained. In a second step, all possible models (i.e. combinations of explanatory variables) were fitted and ranked using Akaike's Information Criterion corrected for small sample sizes (AICc, Additional file 6: Appendix S6) with the function *dredge* in the package MuMIn (version 1.43.6; [45]). In case several models had similar support, a subset of top models within Δ AICc < 6 (following the recent suggestion by [43]) was selected for full model averaging with the function *model.avg* of the same package. The variables influencing the number of red-listed species were assessed with univariate GLMMs, as these species were too scarce at the study sites to be able to perform model selection. Models always satisfied the underlying assumptions of normal distribution of residuals and homoscedasticity. All the analyses were performed with the software R (v. 4.0.0; [46]).

Results

Across all study sites, 8983 fresh shells were collected, belonging to 38 different species of land snails. 9 species were classified as xerophilous (23.7%), 22 as mesophilous (57.9%) and 6 as hygrophilous (15.8%; see Additional file 3: Appendix S3 for the complete species list).

Long-term effects of grassland management intensification on land snail communities (both modules)

Snail densities in long-term intensively-managed meadows (mean ± standard error = 43.2 ± 18.2 per 0.1 m^2) lied between those in extensive (37.6 ± 17.5) and mid-term intensified plots (93.8 ± 42.3; Fig. 1a). Species richness in long-term intensively-managed meadows was about 35% lower (5.4 ± 0.8) than in extensive (8.1 ± 1.3) and mid-term intensified plots (8.3 ± 1.3, Fig. 1b). Similarly, evenness was significantly lower in long-term intensively-managed (0.75 ± 0.02) than in extensively-managed plots (0.88 ± 0.03), and similar compared to mid-term intensified plots (0.82 ± 0.03, $P = 0.088$; Additional file 4: Appendix S4).

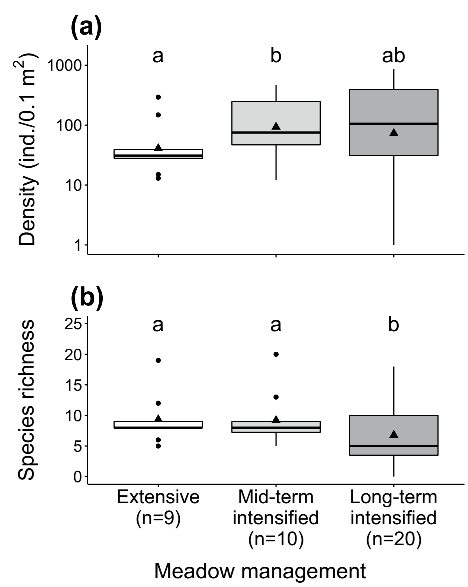

Fig. 1 Effects of meadow management intensification on **a** snail density and **b** species richness. Data for the extensive (no water and fertiliser inputs, i.e. control plots) and mid-term intensive (plots having received high inputs of water and fertiliser during 5 years) management types stemmed from the experimental module, whereas data from the long-term intensive management (> 20 years) are drawn from the observational module. Bold lines represent box-plot medians, solid triangles means, boxes the first and third quantiles, whiskers the inter-quartile distance multiplied by 1.5, and solid dots the outliers. Note the log-scale on the *y*-axis in graph (**a**). Different letters indicate significant differences between treatments at $P < 0.05$

Analyses of snail density and richness according to their soil moisture preferences showed that the richness of xerophilous species was similar in all management types (Fig. 2a), but their density was significantly lower in extensively-managed plots (14.4 ± 6.9) than in the other management types (mid-term intensified: 37.3 ± 17.2; long-term intensified: 32.7 ± 13.8; Fig. 3a, Additional file 4: Appendix S4). Moreover, the CWM of moisture preferences was lowest (i.e. greater contribution of drought-tolerant species) in long-term intensively-managed meadows (Additional file 4: Appendix S4). Long-term intensive management affected mesophilous snail species, with ~ 60% fewer species (1.6 ± 0.4) than in mid-term intensified (3.8 ± 0.8) and in extensively-managed plots (4.1 ± 0.9, Fig. 2b). Likewise, densities of mesophilous snails in long-term intensively-managed meadows (3.5 ± 1.5) were lower than in mid-term intensified (37.3 ± 16.9) and extensively-managed plots (15.5 ± 7.38; Fig. 3b). Hygrophilous species were similarly scarce in all treatments (Fig. 2c). No significant differences were found for the density of hygrophilous snails nor for the number of red-listed species (Fig. 3c; Additional file 4: Appendix S4).

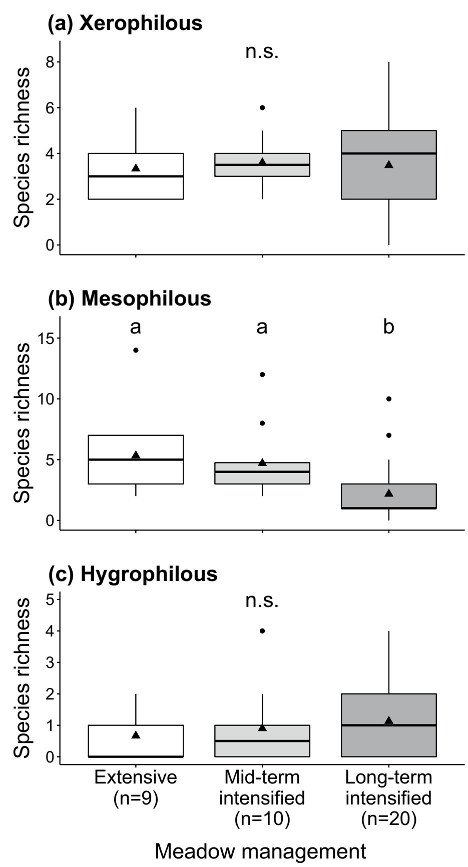

Fig. 2 Effect of meadow management intensification on species richness of land snails split according to their moisture preference: **a** xerophilous; **b** mesophilous; **c** hygrophilous. For management descriptions and box-plot features, see legend of Fig. 1

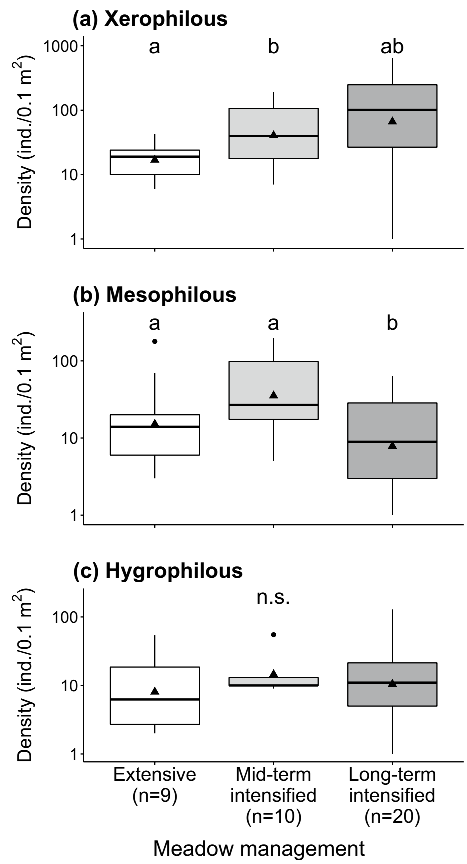

Fig. 3 Effect of meadow management intensification on densities of land snails split according to their moisture preference: **a** xerophilous, **b** mesophilous, **c** hygrophilous. Note the log-scale on the *y*-axis of the graphs. For management descriptions and box-plot features, see legend of Fig. 1

Community analysis was performed with 13 species (*Candidula unifasciata*, *Ceciliodes acicula*, *Cochlicopa lubrica*, *C. lubricella*, *Punctum pygmaeum*, *Pupilla muscorum*, *Trochulus* sp., *Truncatellina cylindrica*, *Vallonia costata*, *V. excentrica*, *V. pulchella*, *Vertigo pygmaea* and *Xerolenta obvia*) occurring in at least nine samples across both modules. This analysis revealed that community composition differed with time exposure to grassland intensification (Additional file 4: Appendix S4). The species that contributed most to these differences were *Pupilla muscorum* (more abundant in mid-term intensified plots and long-term intensively-managed meadows, $P = 0.056$), *Cochlicopa lubricella* and *Punctum pygmaeum* (both more abundant in extensively-managed and mid-term intensified plots, $P = 0.029$ and $P = 0.026$, respectively). Community composition differed as well between study sites. For detailed model outputs and graphs, see Additional file 4: Appendix S4.

Mid-term effects of grassland management intensification on land snail communities (experimental module)

Snail densities (Fig. 4) and soil pH increased along the management intensification gradient, whereas evenness declined slightly (Additional file 5: Appendix S5). Furthermore, densities of both xerophilous and mesophilous snails were positively influenced by mid-term management intensification. Significant effects were found neither for overall species richness nor for moisture preference groups (Additional file 5: Appendix S5). Hygrophilous species were scarce at all study sites, so that it was not possible to use this group in the analysis.

Community analysis was performed with 14 species (*Ceciliodes acicula*, *Cochlicopa lubricella*, *Nesovitrea hammonis*, *Punctum pygmaeum*, *Pupilla muscorum*, *Succinella oblonga*, *Trochulus* sp., *Truncatellina cylindrica*, *Vallonia costata*, *V. excentrica*, *V. pulchella*, *Vertigo pygmaea* and *Vitrina pellucida*) occurring in at least nine plots of the experimental module. Most species contributed to a differentiation of the community composition with the intensification gradient, but only *Vallonia costata* showed a marginally significant univariate positive response ($P = 0.058$; Additional file 5: Appendix S5). Community composition differed as well between study sites. For detailed model outputs and graphs, see Additional file 5: Appendix S5.

Environmental variables influencing land snail community composition in long-term intensively-managed meadows (observational module)

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 manner (Fig. 5a, b and Additional file 6: Appendix S6). Elevation had a quadratic effect with an optimum at around 1100 m a.s.l. (Fig. 5c, d), but its influence on snail density and species richness was generally negative. Finally, plant diversity (Shannon index) significantly enhanced snail density (Fig. 5e). For detailed model outputs and graphs, see Additional file 6: Appendix S6.

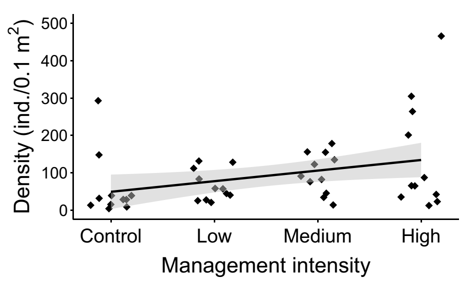

Fig. 4 Snail density in response to the management intensity gradient in the experimental module, consisting of control (no inputs), low-, medium- and high-input levels of water and fertiliser. The black line represents the fitted model, along with a 95% confidence band in grey

Discussion

Mountain grassland management intensification, through inputs of fertiliser in the form of slurry and irrigation with sprinklers, imposes novel microhabitat conditions that compromise both plant and invertebrate biodiversity (e.g. [13]). However, the impact of such practices on land snails remained poorly-understood until the present study. Given their low mobility and affinity for moisture, it was suspected that mid- and long-term exposure of land snail communities to agricultural intensification would show a progressive impoverishment of species assemblages but not necessarily a decrease in abundance. Our study confirms that community composition changed over time. Although snail densities were promoted in the mid-term following management intensification (within 5 years), they ended up with lower densities and ~35% fewer species in the long-term (>20 years). Contrary to our expectations, however, drought-tolerant (i.e. xerophilous) species were predominant and even more abundant in intensively-managed meadows in the long term, while mesophilous species seemed to lose ground. We shall next discuss more in detail the effects of management intensification on land snails during the course of time, focus on the mid-term responses observed in the experimental module and finally examine the key environmental variables shaping snail communities in long-term intensively-managed mountain meadows (observational module), before concluding with management recommendations.

Land snail communities are particularly affected by intensification in the long run

By comparing snail assemblages of mountain hay meadows that were either extensively-managed, intensified for 5 years (extensively-managed beforehand) or intensively-managed for at least 20 years, we could demonstrate that snail communities get impoverished under a long-term intensification regime. Mesophilous species, which typically occur in either dry or moist environments, were particularly impacted: they were underrepresented (minus ~60% species richness) in long-term intensively-managed meadows compared to the other management types. We had predicted that mesophilous species would benefit from the more shaded and wetter conditions prevailing at ground level

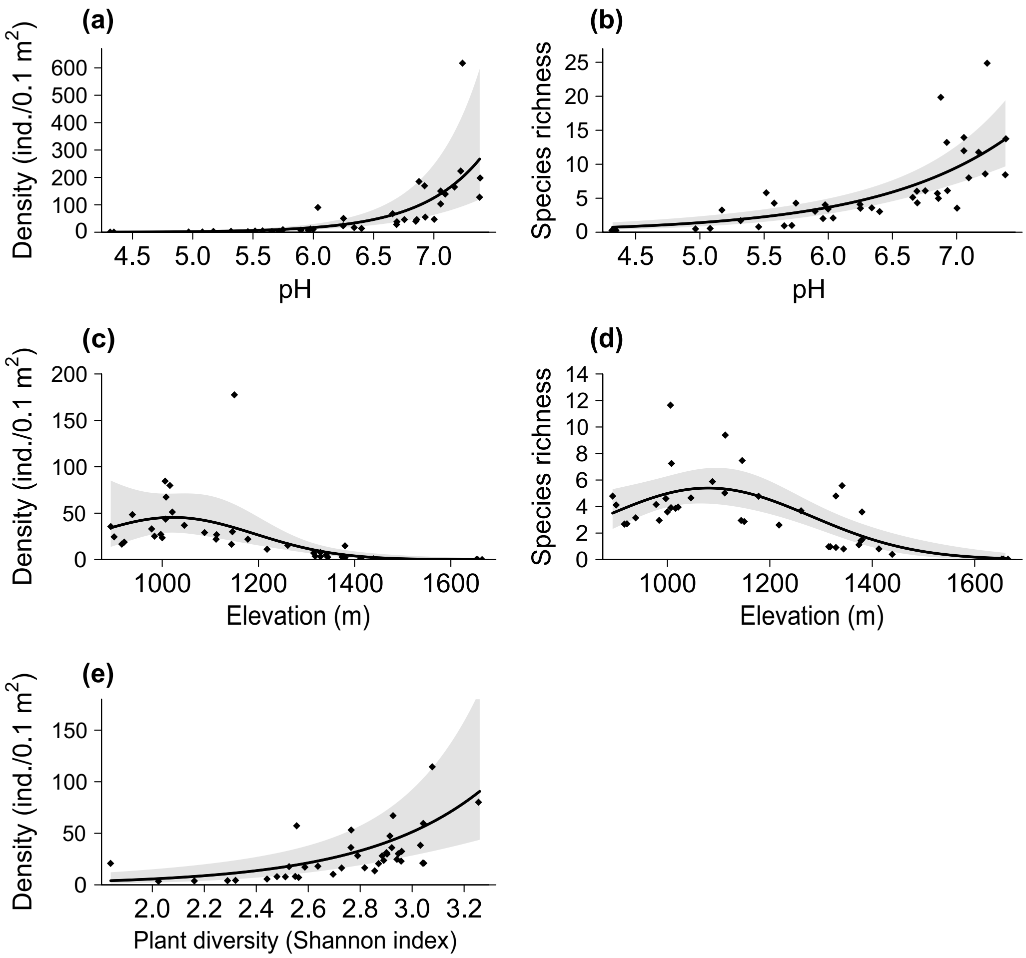

Fig. 5 Effect plots with partial residuals (i.e. the residuals left after subtracting the influence of the other variables in the model) for each of the predictors influencing snail density and snail species richness: **a**, **b** soil pH; **c**, **d** elevation; and **e** plant diversity (observational module). The black line in each plot represents the fitted model with a 95% confidence band (grey area)

due to a denser vegetation sward generated by intensification [13, 23, 47], but found a different pattern. A posteriori, we interpret these unexpected results, first, by an increased mowing frequency in intensively-managed meadows, which impacts mesophilous species more severely than xerophilous species [22, 48]. In effect, under these circumstances, the former species, generally more sensitive to desiccation, had to endure more frequent periods with no vegetation cover, i.e. longer exposure to direct solar radiation, with detrimental effects on their populations [49]. In contrast, xerophilous species have a greater natural ability to cope with xeric circumstances [50, 51] and were thus particularly well represented in intensively-managed meadows. This is well illustrated by the species *Pupilla muscorum*, that was most abundant in long-term intensively-managed meadows. Interestingly, this species characteristic of open-land habitat was established to vanish from Alpine hay meadows after agricultural abandonment [47], which corroborates our interpretation. Second, direct mortality caused by mowing machinery might also account for community impoverishment in long-term intensively-managed meadows [37, 52, 53]. However, a majority of the species recorded are ground-dwellers [23] so that this mortality source must be considerably lower than the mortality elicited by habitat alterations [52–54]. Third, a mere sampling year effect may in theory explain some of the differences observed between snail communities in the mid- and long-term [22, 32]. Yet, the fact that snail abundance was not affected while species richness was, argues against this interpretation. Finally, the decline in plant diversity driven by management intensification in the long-term [55, 56] could contribute to level off the mid-term positive response of snail density that follows intensification, probably due to overall ecological niche space reduction (see subsection 'Key environmental factors shaping snail communities in mountain hay meadows').

Our results for hay meadows differ markedly from findings obtained in pastures where intensive management via fertilizer application and grazing seems to negatively impact both snail density and species richness, especially of xerophilous species [57]. This difference is probably due to the negative effects of cattle trampling on soil fauna that increase with increased grazing pressure [58]. Furthermore, our meadows were not harbouring the very specialised xerophilous species of conservation concern that typically inhabit the dry steppic slopes of Valais [37], which is probably due to an absence of key structural elements such as rocks and wide patches of bare ground [37, 57].

Mid-term benefits of intensification for land snail communities

In our controlled experiment, the intensification of grassland management through site-adapted irrigation and fertilisation had boosted land snail densities after 5 years, this without compromising species richness. The highest snail densities (2.7 greater than in the extensively-managed, control plots) were reached when irrigation and fertilisation were combined at the levels needed to achieve maximum local hay yield (see 'Methods'). Since similar results had been reported for sward-dwelling snails in the same study meadows [32], we can generalise these effects to the entire meadow snail community [59]. Again, it is likely that the wetter and cooler microclimate generated by a denser vegetation favoured snails [13, 27, 60], providing them with better conditions for oviposition and egg survival, thus boosting their population sizes [61]. This interpretation of a primary effect of microclimate, instead of overall increased phytomass, is further supported by the recognition that food supply is generally not a limiting factor for snail populations [62, 63]. Increased nitrogen availability following fertilisation [64] can also not be inferred in the present case: the plants in our fertilised plots did not have higher nitrogen content than in control plots [65].

Remarkably, mesophilous snails were unaffected by mid-term intensification. On the contrary, they had even augmented in numbers after 5 years of experimental intensification, but this state was only transient as they showed a marked decline in the long run (see 'Land snail communities are particularly affected by intensification in the long run').

Our results also show that grassland farming intensification causes an increment of soil pH, most likely due to the buffering action of the organic compounds contained in organic fertilisers such as slurry [66]. A resulting lower acidity among intensively-managed meadows apparently benefit snail communities, particularly those adapted to moderately acid to neutral soils (see also 'Key environmental factors shaping snail communities in mountain hay meadows').

Key environmental factors shaping snail communities in mountain hay meadows

Soil pH, plant diversity and elevation were all identified as key environmental factors shaping the communities of land snails inhabiting those of our mountain meadows that had been intensively managed for at least the previous 20 years. Almost no snails were found in meadows with soil pH < 5.5, corroborating former findings in various habitats (e.g. [30, 54, 67]). The mechanism at play is evident: snails need access to sources of calcium, in particular for building their shells [61, 68], but this mineral is common only in soils on a limestone substrate, and rare in soils on silicate substrates (granite, gneiss).

The positive effect of plant diversity on land snails, essentially on their density, was remarkable but not novel [62, 69]. Albeit the underlying mechanism remains ill-understood, it is likely that a diverse plant community enhances the microhabitat structural complexity [69] that is necessary at different stages of a snail's life cycle (oviposition site, shelter, etc.) [27].

Lastly, the negative effect of elevation on our grassland snail communities is in line with the findings by Schmera and Baur [70] who reported a decrease of gastropod abundance along an elevational gradient. This is explained by the fact that the activity period of land snails depends on the length of the growing season, which shortens towards higher elevations. Note that the modest peak of abundance and richness we observed at ca 1′100 m a.s.l. reflects a spatial clustering of our most specious meadows at that elevation. This hump-shaped vertical distribution may be due to even more intensive farming practices in grasslands next to the plain (400–550 m a.s.l.) have led to extremely impoverished snail communities in the long run.

Conclusions

A major, and unexpected finding of this study is that drought-tolerant snail species remain fairly unharmed and even proliferate with grassland intensification in mountain hay meadows, this despite the fact that snail communities get altogether impoverished under the pressure of intensification in the long run. Certainly, the present results and management recommendations do not readily apply to lowland meadows where levels of intensification are of another order of magnitude, creating conditions way more hostile for biodiversity. If intensification of mountain hay meadows provides short-term benefits for snail communities via enhanced moisture and shade at ground level, it eliminates in the long run the most sensitive species to the very dry environmental conditions that characterise the post-mowing period. This phenomenon is exacerbated by the limited active mobility of snails [22, 71, 72] that represents a natural impediment to any recolonization process from nearby species reservoirs [30, 73, 74]. This calls for conserving in priority meadows with a high land snail diversity, as well as promoting uncut refuge strips to preserve areas without disturbances related to mowing [24]. Finally, if land snails are certainly not the best candidates to serve as bioindicators of integral meadowland invertebrate communities, we think they deserve more attention from conservation and restoration programmes aiming to preserve the whole set of interactions and functions that characterise biodiversity-rich montane and subalpine grassland ecosystems.

Abbreviation
CWM: Community weighted mean.

Supplementary Information
The online version contains supplementary material available at https://doi.org/10.1186/s12862-022-01972-4.

Additional file 1: Appendix S1. Description the study sites.

Additional file 2: Appendix S2. Explanatory variables of the observational module.

Additional file 3: Appendix S3. Snail species list.

Additional file 4: Appendix S4. Results of the response of snail communities to long-term management intensification (both modules).

Additional file 5: Appendix S5. Results of the experimental module.

Additional file 6: Appendix S6. Results of the observational module.

Acknowledgements
We are grateful to M. Lessard-Therrien, A. Serres-Hänni, S. Mettaz, E. Peris i Morente, S. Marti, C. Waber, D. Unternährer, C. Sonnay and D. Fischer for their help and support, J. Fournier and J. Rüetschi for the snails' verification and expert advice, our colleagues at the Division of Conservation Biology, University of Bern, the members of the project accompanying group, and all the farmers involved for their collaboration.

Authors' contributions
RA and JYH designed the study and raised the necessary funds. GMDL, LD and AHA collected and identified the snails. SHG collected the environmental data from the observational module. GMDL and LD analysed the data. GMDL wrote the manuscript with inputs from LD, JYH and RA. All authors read and approved the final manuscript.

Funding
This project was financially supported by the Cantons of Valais and Graubünden, by the Swiss National Foundation (Grant Number 31003A_149656/1 and 31003A_172953, allocated to Prof. Raphaël Arlettaz) and the Swiss Federal Offices for Agriculture and the Environment. None of the funding sources were involved in the study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Availability of data and materials
The R script and complete dataset supporting the conclusions of this article are available in the Figshare repository: https://doi.org/10.6084/m9.figshare.12957776.v4. Complementary results and figures as well as model outputs are provided as Additional files 1, 2, 3, 4, 5, and 6.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
There are no conflicts or competing interests to declare that are relevant to the content of the article.

Received: 18 August 2021 Accepted: 3 February 2022
Published online: 15 February 2022

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Publisher's Note

Mid- and long-term responses of land snail communities to the intensification of mountain hay meadows management

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Appendix S1 – Description of the study sites

This appendix provides the location and soil pH of the study sites in both experimental and observational modules, along with a description of the management treatments of the experimental module.

Table of content

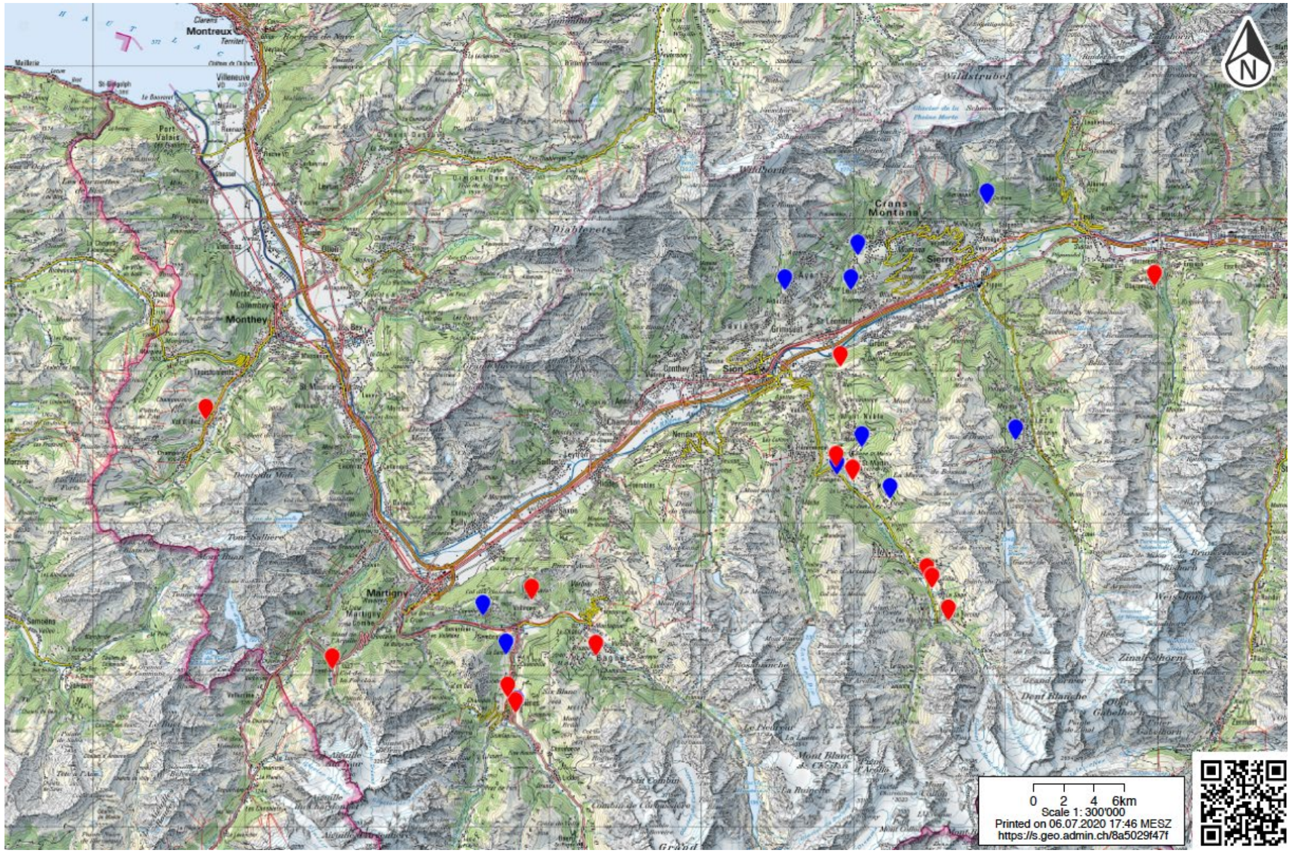

Fig. S1.1. Topographical map (1:300000) displaying the locations of the study sites in the canton of Valais, Inner Swiss Alps. The climate in the region is continental, with a mean annual precipitation of 603 mm and monthly average temperatures ranging from -0.1 °C in January, to 20.1 °C in July, recorded at the valley bottom in Sion (482 m.a.s.l.) between 1981 and 2010 (MeteoSwiss, 2019). Blue markers represent the locations of the extensively managed meadows of the experimental module. Red markers show the locations of the thirteen regions of the observational module, with three long-term intensively managed meadows selected per region (39 meadows in total). Source: Federal Office of Topograhpy swisstopo.

Table S1.1. Description of each meadow of the experimental module, including the name of the study site, elevation, and coordinates (WGS 84). Soil pH is used to define the subset of samples above a threshold of pH 6 in the analyses on the response of land snails to long-term grassland intensification. Therefore. the values of soil pH are provided for the extensive and recently intensified plots, and those included in the analyses are marked with an asterisk (*).

Study site	Elevation [m]	Soil pH		Coordinates	
		C-plots	I+F 3/3-plots	Latitude	Longitude
Icogne 1	1200	6.0	7.0*	46°17′56″N	7°26′31″E
Icogne 2	880	7.4*	7.6*	46°16′42″N	7°26′10″E
La Garde	880	7.4*	7.6*	46°16′42″N	7°26′10″E
Vens	1373	6.4*	7.3*	46°5′7″N	7°7′24″E
Arbaz	980	6.4*	7.0*	46°3′45″N	7°8′35″E
Cordona	1153	6.9*	7.1*	46°19′45″N	7°33′8″E
Eison	1373	6.5*	6.8*	46°5′7″N	7°7′24″E
Saint-Martin	1589	6.1*	6.4*	46°11′8″N	7°26′43″E
Grimentz	1270	5.5	5.7	46°16′42″N	7°22′47″E
Orsières 1	1022	7.6*	7.7*	46°1′ 44″N	7° 9′ 8″E
Euseigne	1028	7.4*	7.4*	46° 10′ 9″N	7° 25′ 27″E

Table S1.2. Management treatments applied on each meadow of the experimental module. These treatments consisted of control (no input), low-, medium- and high-input levels of fertilizer and irrigation, mimicking a management intensification gradient. Note that all meadows were managed extensively (i.e. any or minor application of fertiliser and irrigation) before the onset of the experiment. For each treatment indications are provided for: quantity of nitrogen (N), phosphorus (P) and potassium (K) fertiliser applied per hectare and year; amount of irrigation applied per week via sprinkler; and number of grass cuts per year. The fertiliser consisted of organic NPK pellets and mineral K_2O dissolved in water to reach the equivalent of standard-farm liquid manure. The amount of NPK depended on the potential productivity of each meadow, within the given range of values (for further details on the experimental design see Appendix A in Andrey, Humbert, & Arlettaz, 2016).

Management treatments	Number of cuts per year	Fertiliser applied [kg·ha^{-1}·year^{-1}]			Water irrigation [mm·week^{-1}]
		N	P	K	
Control	1	0	0	0	0
Low	2	13.3 – 26.7	4.8 – 9.7	36.9 – 73.8	10
Medium	2	26.7 – 53.3	9.6 – 19.4	73.8 – 147.5	20
High	2	40 - 80	14.5 – 29.1	110.6 – 221.4	30

Table S1.3. Description of each meadow of the observational module, including the name of the study site, elevation, soil pH, and coordinates (WGS 84). Note that each study site contained three long-term intensively managed meadows in close proximity. The sites above a threshold of pH 6 are marked with an asterisk (*), as they were included in the analyses on the response of land snails to long-term grassland intensification.

Study site	Elevation [m]	Soil pH	Coordinates	
			Latitude	Longitude
	1112	5.9	46° 3′ 43″N	7° 13′ 10″E
Bruson	1113	5.6	46° 3′ 43″N	7° 13′ 8″E
	1088	6.0	46° 3′ 35″N	7° 13′ 23″E
	1008	6.9*	46° 1′ 41″N	7° 9′ 5″E
Orsières 1	1006	6.9*	46° 1′ 37″N	7° 9′ 5″E
	1007	7.1*	46° 1′ 39″N	7° 9′ 5″E
	938	7.2*	46° 2′ 12″N	7° 8′ 35″E
Orsières 2	900	7.1*	46° 2′ 14″N	7° 8′ 41″E
	893	7.1*	46° 2′ 9″N	7° 8′ 42″E
	1000	5.3	46° 12′ 1″N	6° 53′ 11″E
Val d'Illiez	978	6.3*	46° 11′ 59″N	6° 53′ 13″E
	997	6.0	46° 12′ 2″N	6° 53′ 13″E
	1178	7.4*	46° 5′ 42″N	7° 10′ 6″E
Le Levron	1218	7.4*	46° 5′ 42″N	7° 9′ 53″E
	1261	7.2*	46° 5′ 49″N	7° 9′ 53″E
	1150	6.0	46° 13′ 59″N	7° 25′ 43″E
Nax	1144	6.0	46° 13′ 59″N	7° 25′ 38″E
	1146	5.8	46° 13′ 59″N	7° 25′ 40″E
	1021	6.6*	46° 9′ 56″N	7° 26′ 16″E
La Luette	1016	6.3*	46° 9′ 57″N	7° 26′ 15″E
	984	6.7*	46° 9′ 58″N	7° 26′ 11″E
	1046	6.3*	46° 10′ 16″N	7° 25′ 6″E
Euseigne	916	6.9*	46° 10′ 26″N	7° 25′ 25″E
	921	6.9*	46° 10′ 25″N	7° 25′ 30″E
	1374	6.9*	46° 6′ 26″N	7° 30′ 2″E
Evolène	1378	6.8*	46° 6′ 27″N	7° 30′ 2″E
	1380	7.2*	46° 6′ 36″N	7° 29′ 31″E
	1380	6.4*	46° 6′ 9″N	7° 30′ 5″E
La Tour	1413	6.7*	46° 6′ 7″N	7° 30′ 18″E
	1439	7*	46° 6′ 11″N	7° 30′ 23″E
	1656	5.7	46° 4′ 59″ N	7° 31′ 8″E
La Forclaz	1665	5.5	46° 5′ 24″N	7° 30′ 54″E
	1653	5.7	46° 5′ 27″N	7° 30′ 54″E
	1318	4.4	46° 3′ 10″N	6° 59′ 44″E
Trient	1315	4.3	46° 3′ 12″N	6° 59′ 44″E
	1329	5.0	46° 3′ 6″N	6° 59′ 46″E
	1341	5.5	46° 16′ 58″N	7° 41′ 11″E
Oberems	1344	5.1	46° 16′ 50″N	7° 41′ 42″E
	1329	5.2	46° 16′ 59″N	7° 41′ 9″E

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Mid- and long-term responses of land snail communities to the intensification of mountain hay meadows management

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Appendix S2 - **Explanatory variables of the observational module**

Table S2.1. Description of all explanatory variables collected in the observational module. According to their properties, variables were grouped into topographical, soil, vegetation and landscape related type of variables.

Type of variable	Variable	Definition
Topographical	Elevation	Meters above sea level
	Slope	Steepness of the meadow [°], measured using a compass with clinometer
	Folded aspect	Exposition of the meadow [°], measured using a compass with clinometer. The values were later rescaled into 0-180° following McCune & Dylan (2002), resulting into a proxy of potential direct incident radiation
	Heat load	Index based on latitude, slope and aspect of the sites. Higher values of this index indicate more heat received in the meadow by incident radiation (McCune & Dylan, 2002)
Soil	pH	Acidity of the soil (acid: [1-6], neutral: [7] and basic: [8-14])
	Grain size distribution	Proportion of clay (0.02 µm - 2.00 µm), silt (2.00 – 63.00 µm) and sand (63.00 – 2000.00 µm)
	Inorganic and total carbon	Carbon concentration in the soil [% of weight]. Inorganic carbon was measured as the difference between total carbon and organic carbon after reaction with HCl
	Nitrogen	Nitrogen concentration in the soil [% of weight]
	C:N ratio	Ratio of carbon and nitrogen in the soil, as a measure of nitrogen available for plant uptake (Hodge, Robinson, & Fitter, 2000)
Vegetation	Plant species richness	Total number of species recorded in the two vegetation plots
	Shannon index of plant diversity	Plant species richness weighted with the percentage cover
	Landolt humidity - Community Weighted Mean	Value of each plant species according to their soil humidity requirements, from 1 (very dry) to 5 (aquatic), weighted by their cover in the plot (Landolt et al., 2010)
	Cover of plant functional groups (forbs, grasses, legumes)	Groups were defined according to the family to which each plant species belonged: legumes (Fabaceae), grasses (Poaceae, Juncaceae, Cyperaceae) and forbs (other families).

Type of variable	Variable	Definition
Vegetation	Bare ground	Visual estimation of the cover of bare ground [%]
	Litter	Visual estimation of the cover of litter [%]
	Mean vegetation height	Mean height [cm] of every contact point with a plant in measuring location. This was done in 10 locations along two diagonal transects crossing the entire meadow, once before each hay cut.
Management	Irrigation	Presence or absence of irrigation with sprinklers
Landscape	Grassland	Relative cover of semi-natural grasslands (i.e. meadows and pastures) in a 50 m buffer around the study meadows [%]
	Forest	Relative cover of forests (i.e. coniferous, mixed, broadleaved) in a 50 m buffer around the study meadows [%]
	Extensive semi-natural structures	Relative cover of extensively managed structures (i.e. grasslands with low productivity, steppe-like vegetation) in a 50 m buffer around the study meadows [%]
	Artificial structures	Relative cover of artificial structures (i.e. buildings, paved roads) in a 50 m buffer around the study meadows [%]

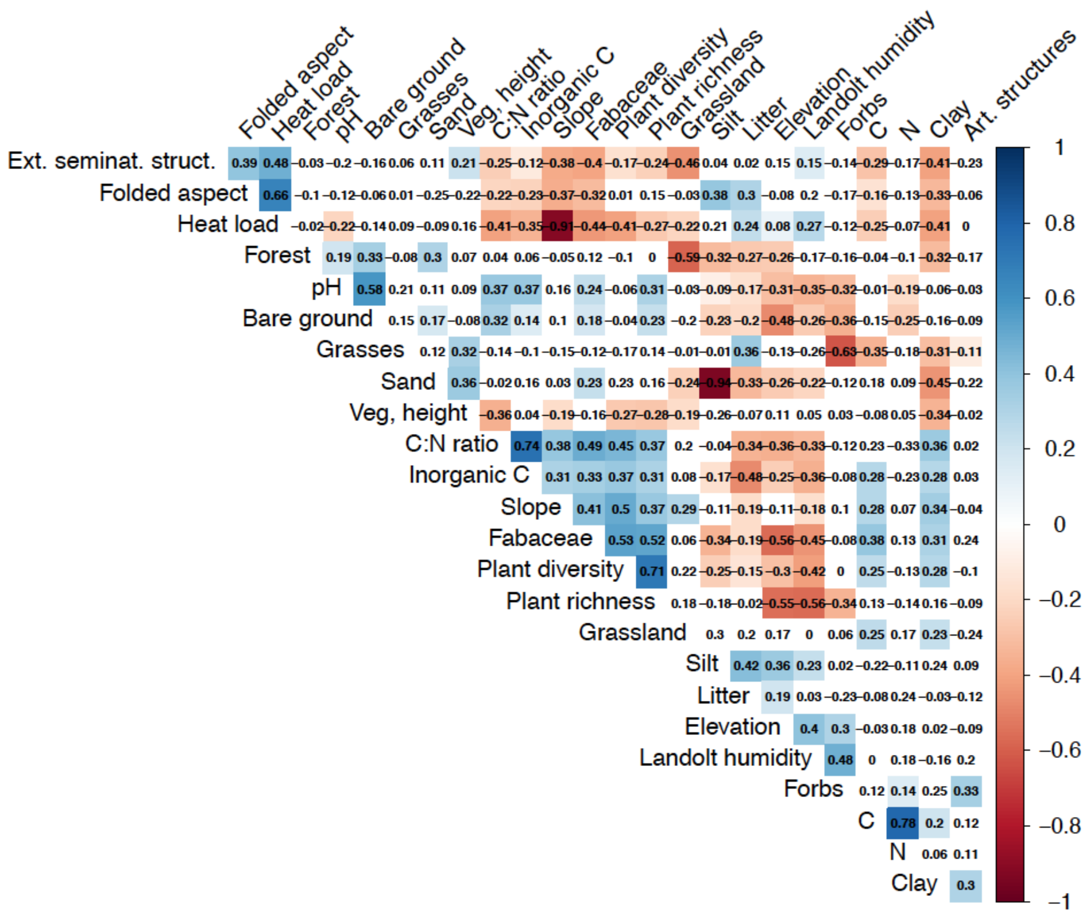

Figure S2.1. Correlation plot of all continuous variables with Spearman correlation values. Significant correlations (P < 0.05) have a coloured background in blue (positive correlation) or red (negative correlation). After assessing the variables having a pairwise correlation coefficient > 0.7, the following 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 (ρ = 0.66).

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Appendix S3 – Snail species list

Table S3.1. List of snail species and absolute abundance of fresh shells across all study sites. Nomenclature followed Hausser (2005), with consideration for later taxonomical updates (Horsáková, Nekola, & Horsák, 2020). 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 sample. In this case, it was not possible to allocate non-fully developed shells to a particular species with confidence. Furthermore, individuals of the genus *Trochulus* could not be identified to species level, as the two species to which they belonged (*T. hispida* and *T. sericeus*) are hardly distinguishable. All two-toothed individuals of *Pupilla* were considered as *Pupilla muscorum*, given that identifications based on apertural features in *Pupilla* often lead to oversplitting (Balashov, Neiber, Bogon, & Hausdorf, 2019; Nekola, Coles, & Horsák, 2015). Old shells (i.e. those whose periostracum was 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). All uncertain identifications were verified by an expert. Snails from the experimental module (n = 44) were sampled in 2015, while those from the observational module (n = 39) were sampled in 2019. 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. Soil moisture preferences were established from the species affinity for each moisture category, extracted from Falkner, Obrdlík, Castella, & Speight (2001).

Species	Moisture preference	Red-List status	Abundance	
			Experimental module	Observational module
Aegopinella minor	Mesophilous	LC	41	2
Aegopinella pura	Mesophilous	LC	0	10
Candidula unifasciata [1]	Xerophilous	VU	5	84
Carychium minimum	Hygrophilous	LC	81	0
Carychium tridentatum	Mesophilous	LC	33	1
Cecilioides acicula [1,2]	Mesophilous	LC	92	10
Cepaea hortensis	Mesophilous	LC	0	2
Cepaea nemoralis cf	Mesophilous	LC	0	4

Species	Moisture preference	Red-List status	Abundance	
			Experimental module	Observational module
Cochlicopa lubrica [1]	Hygrophilous	LC	55	108
Cochlicopa lubricella [1,2]	Mesophilous	LC	364	56
Columella columella	Mesophilous	LC	0	1
Discus rotundatus	Mesophilous	LC	1	1
Ena montana	Mesophilous	LC	2	0
Euconulus fulvus	Mesophilous	LC	21	0
Euomphalia strigella	Mesophilous	NT	13	0
Fruticicola fruticum	Mesophilous	LC	3	0
Helicella itala	Xerophilous	NT	2	0
Jaminia quadridens	Xerophilous	VU	0	4
Merdigera obscura	Mesophilous	LC	1	0
Nesovitrea hammonis [2]	Mesophilous	LC	58	0
Nesovitrea petronella	Hygrophilous	LC	0	36
Oxyloma elegans	Hygrophilous	NT	2	0
Platyla polita	Mesophilous	LC	16	1
Punctum pygmaeum [1,2]	Mesophilous	LC	335	4
Pupilla muscorum [1,2]	Xerophilous	LC	228	623
Succinella oblonga [2]	Mesophilous	LC	74	19
Trochulus sp. [1,2]	Mesophilous	LC	245	105
Truncatellina cylindrica [1,2]	Xerophilous	LC	439	147
Vallonia costata [1,2]	Xerophilous	LC	722	1490
Vallonia excentrica [1,2]	Xerophilous	LC	293	842
Vallonia pulchella [1,2]	Hygrophilous	LC	105	242
Vertigo angustior	Mesophilous	EN	6	1
Vertigo antivertigo	Hygrophilous	VU	0	4
Vertigo pygmaea [1,2]	Mesophilous	LC	297	111
Vitrea contracta	Mesophilous	LC	16	0
Vitrina pellucida [2]	Mesophilous	LC	19	0
Xerolenta obvia [1]	Xerophilous	NT	73	51
Zebrina detrita	Xerophilous	VU	2	1
Not identified			62	67
Cochlicopa sp.			26	76
Vallonia sp.			294	836
Vertigo sp.			0	18

[1] Species included in the community analysis used to investigate the long-term effects of grassland management intensification (both modules).
[2] Species included in the community analysis used to investigate the mid-term effects of grassland management intensification (experimental module).

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Appendix S4 – Results of the response of snail communities to long-term management intensification (both modules)

This appendix provides the outputs of the generalised linear mixed-effects models (GLMM), linear mixed-effects models (LMM) and multivariate generalised linear models performed to analyse the response of snail communities to long-term grassland management intensification. Data from the extensive and mid-term intensified managements came from the experimental module, while data from the long-term intensified management are from the observational module. The response variables investigated were density and species richness (overall, and by moisture preference groups), evenness (Pielou's index), number of red-listed species, community weighted mean (CWM) of moisture preferences and community composition. For the latter, the results on the overall community and the univariate responses of each species are presented. In all the analyses, a subset of samples with soil pH > 6 was considered in order to control the limitation effect of pH on snail communities (see Table S1.1 and S1.3 for a description of soil pH in each meadow). In the GLMM and LMM, post hoc test for multiple comparison analysis were performed using the function *relevel* to set other treatments as intercept. The figures showing relevant results are displayed as well.

Table of content

Table S4.1. Output of the GLMM with Poisson distribution used to investigate the effect of long-term management intensification on overall snail density. An observation-level random factor was added to the models to account for overdispersion. Study site was also set as a random factor. Estimates, standard errors (SE) and p-values (*P*) are provided**.**

	Snail density (log-scale)		
Meadow management	Estimate	SE	*P*
Intercept (Extensive)	3.628	0.464	**< 0.001**
Mid-term intensified vs Extensive	0.913	0.401	**0.023**
Long-term intensified vs Extensive	0.138	0.492	0.779
Intercept (Mid-term intensified)	4.541	0.451	**< 0.001**
Long-term intensified vs Mid-term intensified	-0.775	0.487	0.112
Random effects			
Observation-level	0.707		
Site	1.724		

Table S4.2. Output of the GLMM with Poisson distribution used to investigate the effect of long-term management intensification on overall snail species richness. Study site was set as a random factor. Estimates, standard errors (SE) and p-values (*P*) are provided**.**

	Snail species richness (log-scale)		
Meadow management	Estimate	SE	*P*
Intercept (Extensive)	2.096	0.162	**< 0.001**
Mid-term intensified vs Extensive	0.017	0.151	0.911
Long-term intensified vs Extensive	-0.417	0.174	**0.016**
Intercept (Mid-term intensified)	2.113	0.157	**< 0.001**
Long-term intensified vs Mid-term intensified	-0.434	0.171	**0.011**
Random effects			
Site	0.174		

Table S4.3. Output of the LMM used to investigate the effect of long-term management intensification on evenness (Pielou's index). Study site was set as a random factor. Estimates, standard errors (SE) and p-values (*P*) are provided**.**

	Evenness (Pielou's index)		
Meadow management	Estimate	SE	*P*
Intercept (Extensive)	0.881	0.032	**< 0.001**
Mid-term intensified vs Extensive	-0.064	0.042	0.143
Long-term intensified vs Extensive	-0.129	0.038	**0.002**
Intercept (Mid-term intensified)	0.817	0.030	**< 0.001**
Long-term intensified vs Mid-term intensified	-0.065	0.037	0.088
Random effects			
Site	0.001		
Residual	0.008		

Table S4.4. Output of the GLMM with Poisson distribution used to investigate the effect of long-term management intensification on the number of red-listed species. Study site was set as a random factor. Estimates, standard errors (SE) and p-values (*P*) are provided**.**

	Number of red-listed species (log-scale)		
Meadow management	Estimate	SE	*P*
Intercept (Extensive)	-1.865	0.927	**0.044**
Mid-term intensified vs Extensive	-1.176	1.159	0.310
Long-term intensified vs Extensive	0.324	0.770	0.674
Intercept (Mid-term intensified)	-3.040	1.222	**0.013**
Long-term intensified vs Mid-term intensified	1.500	1.122	0.181
Random effects			
Site	1.487		

Table S4.5. Output of the GLMM with Poisson distribution used to investigate the effect of long-term management intensification on snail density for each of the moisture preference groups: xerophilous, mesophilous and hygrophilous. An observation-level random factor was added to the models to account for overdispersion. Study site was also set as a random factor. Estimates, standard errors (SE) and p-values (*P*) are provided**.**

	Meadow management	Estimate	SE	*P*
Density of xerophilous (log-scale)	Intercept (Extensive)	2.668	0.477	**< 0.001**
	Mid-term intensified vs Extensive	0.951	0.434	**0.028**
	Long-term intensified vs Extensive	0.821	0.516	0.112
		2.668	0.477	
	Intercept (Mid-term intensified)	3.619	0.460	**< 0.001**
	Long-term intensified vs Mid-term intensified	-0.130	0.506	0.797
	Random effects			
	Observation-level	0.711		
	Site	1.618		
Density of mesophilous (log-scale)	Intercept (Extensive)	2.740	0.477	**< 0.001**
	Mid-term intensified vs Extensive	0.879	0.535	0.101
	Long-term intensified vs Extensive	-1.487	0.594	**0.012**
	Intercept (Mid-term intensified)	3.618	0.452	**< 0.001**
	Long-term intensified vs Mid-term intensified	-2.366	0.583	**< 0.001**
	Random effects			
	Observation-level	1.256		
	Site	0.811		
Density of hygrophilous (log-scale)	Intercept (Extensive)	-0.456	0.946	0.629
	Mid-term intensified vs Extensive	0.903	0.947	0.340
	Long-term intensified vs Extensive	0.740	1.045	0.479
	Intercept (Mid-term intensified)	0.446	0.870	0.608
	Long-term intensified vs Mid-term intensified	-0.162	1.032	0.875
	Random effects			
	Observation-level	2.538		
	Site	3.435		

Table S4.6. Output of the GLMM with Poisson distribution used investigate the effect of long-term management intensification on snail species richness for each of the moisture preference groups: xerophilous, mesophilous and hygrophilous. Study site was set as a random factor. Estimates, standard errors (SE) and p-values (*P*) are provided**.**

	Meadow management	Estimate	SE	*P*
Richness of xerophilous (log-scale)	Intercept (Extensive)	1.144	0.208	**< 0.001**
	Mid-term intensified vs Extensive	0.083	0.247	0.737
	Long-term intensified vs Extensive	0.057	0.241	0.812
	Intercept (Mid-term intensified)	1.227	0.192	**< 0.001**
	Long-term intensified vs Mid-term intensified	-0.025	0.229	0.911
	Random effects			
	Site	0.083		
Richness of mesophilous (log-scale)	Intercept (Extensive)	1.420	0.219	**< 0.001**
	Mid-term intensified vs Extensive	-0.088	0.205	0.667
	Long-term intensified vs Extensive	-0.964	0.243	**0.007**
	Intercept (Mid-term intensified)	1.332	0.216	**< 0.001**
	Long-term intensified vs Mid-term intensified	-0.876	0.244	**< 0.001**
	Random effects			
	Site	0.283		
Richness of hygrophilous (log-scale)	Intercept (Extensive)	-0.584	0.457	0.201
	Mid-term intensified vs Extensive	0.324	0.529	0.540
	Long-term intensified vs Extensive	0.390	0.497	0.433
	Intercept (Mid-term intensified)	-0.260	0.385	0.500
	Long-term intensified vs Mid-term intensified	0.066	0.441	0.881
	Random effects			
	Site	0.301		

Table S4.7. Output of the LMM used to investigate the effect of long-term management intensification on the community weighted mean (CWM) of moisture preference. Values range from 1 (preference for dry habitats) to 3 (preference for wet habitats). Study site was set as a random factor. Estimates, standard errors (SE) and p-values (*P*) are provided**.**

	CWM of moisture preference		
Meadow management	Estimate	SE	*P*
Intercept (Extensive)	1.618	0.098	**< 0.001**
Mid-term intensified vs Extensive	-0.018	0.101	0.857
Long-term intensified vs Extensive	-0.262	0.113	**0.026**
Intercept (Mid-term intensified)	1.599	0.094	**< 0.001**
Long-term intensified vs Mid-term intensified	-0.243	0.110	**0.034**
Random effects			
Site	0.051		
Residual	0.047		

Table S4.8. Output of the multivariate generalised linear model with negative binomial distribution performed to investigate the effect of long-term management intensification on community composition, based on species abundances. Study site was also added as a fixed factor in the model. Species included in the analysis are listed in Table S2.1 and Table S4.9. The function *anova.manyglm* in the package *mvabund* (Wang, Naumann, Eddelbuettel, Wilshire, & Warton, 2020) was used to compute the analysis of deviance table for the model fit. Likelihood-ratio values were summed across all species to get a statistic for the whole community. P-values were calculated using 999 iterations via PIT-trap resampling. Values with $P < 0.05$ are marked in bold.

	Deviance	Df of residuals	*P*
(Intercept)		41	
Meadow management	75.8	39	**0.003**
Site	574.9	23	**0.001**

Table S4.9. Univariate test statistics from the multivariate generalised linear models with negative binomial distribution performed to investigate the effect of long-term management intensification on community composition, based on snail species abundances. The function *anova.manyglm* in the package *mvabund* (Wang, Naumann, Eddelbuettel, Wilshire, & Warton, 2020) was used to compute the analysis of deviance table for the model fit. P-values were calculated using 999 iterations via PIT-trap resampling and adjusted for multiple testing. Values with $P < 0.05$ are marked in bold.

Species		Meadow management	Site
Candidula unifasciata	Deviance	5.127	51.852
	P	0.542	**0.045**
Cecilioides acicula	Deviance	3.443	43.330
	P	0.763	0.115
Cochlicopa lubrica	Deviance	1.724	25.178
	P	0.835	0.370
Cochlicopa lubricella	Deviance	13.842	47.419
	P	**0.029**	**0.071**
Punctum pygmaeum	Deviance	14.213	39.220
	P	**0.026**	0.158
Pupilla muscorum	Deviance	11.683	48.472
	P	0.056	**0.071**
Trochulus sp.	Deviance	2.316	49.299
	P	0.835	**0.071**
Truncatellina cylindrica	Deviance	2.123	32.710
	P	0.835	0.274
Vallonia costata	Deviance	8.840	60.615
	P	0.164	**0.008**
Vallonia excentrica	Deviance	7.671	47.459
	P	0.210	**0.071**
Vallonia pulchella	Deviance	3.297	47.626
	P	0.763	**0.071**
Vertigo pygmaea	Deviance	1.306	40.968
	P	0.835	0.158
Xerolenta obvia	Deviance	0.217	40.726
	P	0.835	0.158

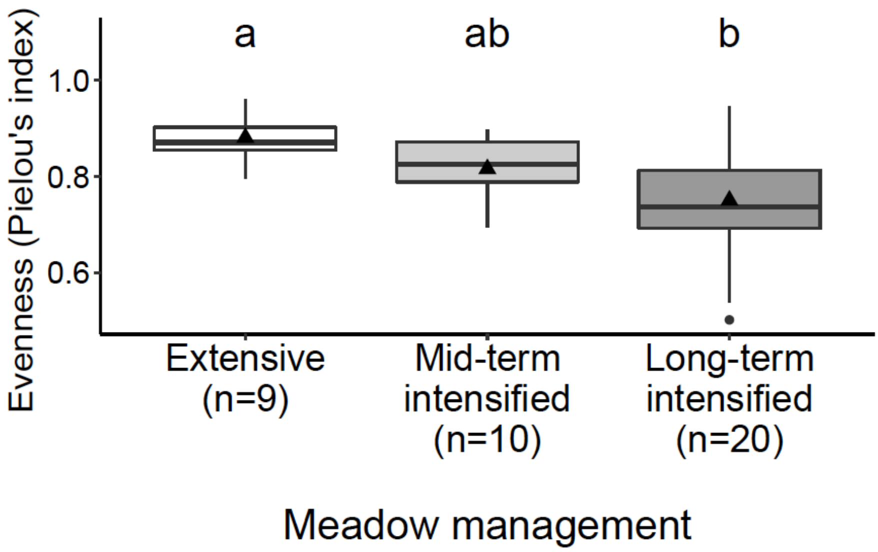

Fig. S4.1. Effect of meadow management intensification on snail evenness (Pielou's index). Data for the extensive (no water and fertiliser inputs, i.e. control plots) and mid-term intensive (plots having received high inputs of water and fertiliser during five years) management types stemmed from the experimental module, whereas data from the long-term intensive management (> 20 years) are drawn from the observational module. Bold lines represent box-plot medians, solid triangles means, boxes the first and third quantiles, whiskers the inter-quartile distance multiplied by 1.5, and solid dots the outliers. Different letters indicate significant differences between treatments at $P < 0.05$.

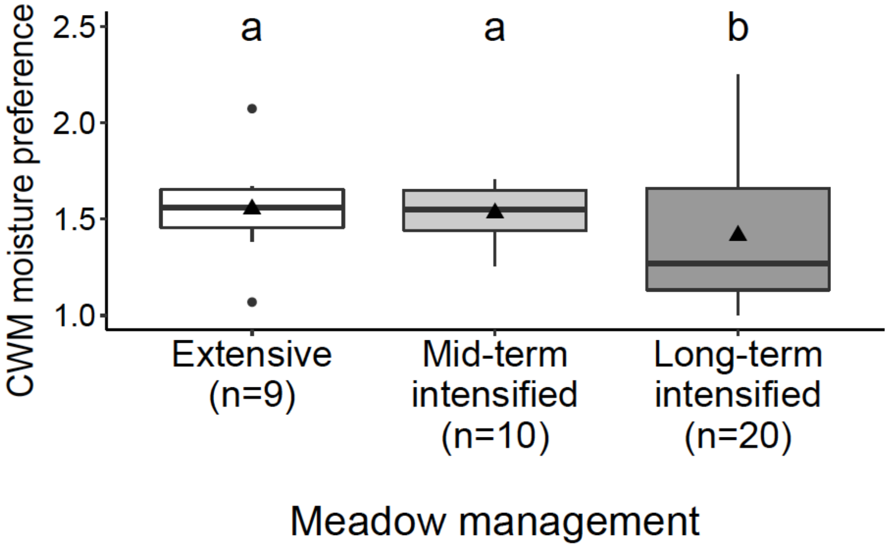

Fig. S4.2. Effect of meadow management intensification on the community weighted mean (CWM) of moisture preferences, on a scale ranging from 1 (xerophilous community) to 3 (hygrophilous community). For management descriptions and box-plot features, see legend of Fig. S4.1.

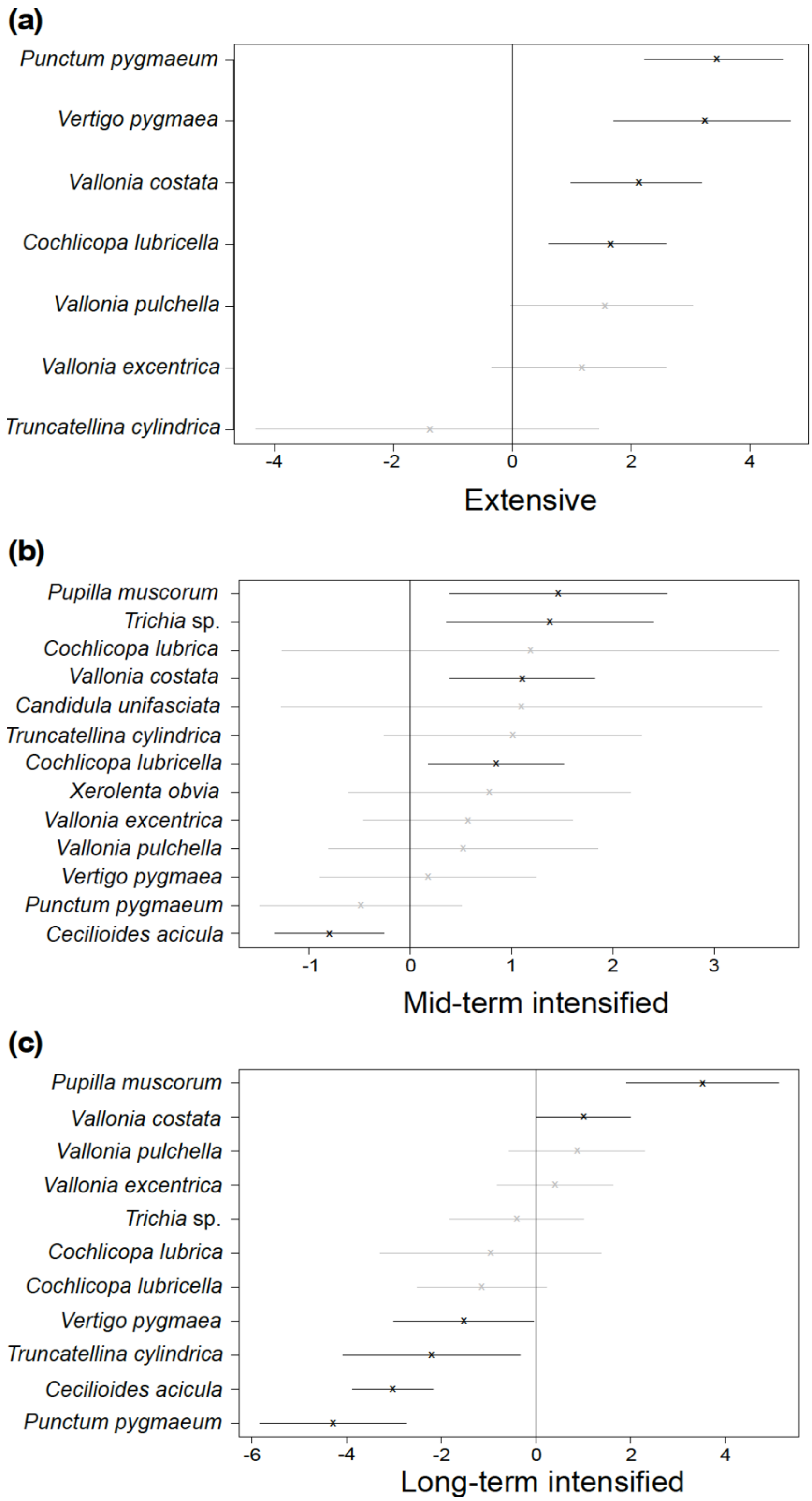

Fig. S4.3. Plots of the point estimates for the coefficients of the model-based community analysis: a) extensive meadow management; b) mid-term intensified; c) long-term intensified. Bars show 95% confidence intervals, with those coloured in black indicating intervals not containing zero. Species showing significant responses are shown in Table S4.9 (p-values calculated with permutational methods and corrected for multiple testing). Species with very large confidence intervals are not displayed for visualisation purposes.

References

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Mid- and long-term responses of land snail communities to the intensification of mountain hay meadows management

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Appendix S5 – Results of the experimental module

This appendix provides the outputs of the generalised linear mixed-effects models (GLMM), linear mixed-effects models (LMM) and multivariate generalised linear models used to investigate the mid-term effect (after five years) of management intensification (4-levels management intensity gradient consisting of control (no input), low-, medium- and high-input levels) on snail communities and soil pH. The variables used to measure the effect on snail communities were density and species richness (overall, as well as on xerophilous and mesophilous snails), evenness and community composition. For the latter, the results on the overall community and the univariate responses of each species are presented. The figures showing relevant results are displayed as well.

Table of content

Table S5.1. Output of the GLMM with Poisson distribution to measure the impact of mid-term management intensification on snail density and snail species richness. Estimates, standard errors (SE) and p-values (*P*) are provided. Significant p-values are highlighted in bold. "Intercept" represents the intercept of the regression; "Management intensity" represents the slope of the regression. An observation-level random factor was added to the models to account for overdispersion. Study site was also set as a random factor.

		Estimate	SE	*P*
Snail density (log-scale)	Intercept	3.537	0.270	**< 0.001**
	Management intensity	0.328	0.082	**< 0.001**
	Random effects			
	Observation-level	0.337		
	Site	0.538		
Snail species richness (log-scale)	Intercept	2.086	0.112	**< 0.001**
	Management intensity	0.031	0.046	0.491
	Random effects			
	Site	0.052		

Table S5.2. Output of the LMM used to measure the impact of mid-term management intensification on evenness (Pielou's index). Estimates, standard errors (SE) and p-values (*P*) are provided. Significant p-values are highlighted in bold. "Intercept" represents the intercept of the regression; "Management intensity" represents the slope of the regression. Study site was set as a random factor.

	Evenness		
	Estimate	SE	*P*
Intercept	0.854	0.020	**< 0.001**
Management intensity	-0.017	0.008	**0.039**
Random effects			
Site	0.002		
Residual	0.004		

Table S5.3. Outputs of the GLMM with Poisson distribution used to measure the impact of mid-term management intensification on the density of xerophilous and mesophilous snails. Estimates, standard errors (SE) and p-values (*P*) are provided**.** Significant p-values are highlighted in bold. "Intercept" represents the intercept of the regression; "Management intensity" represents the slope of the regression. An observation-level random factor was added to the models to account for overdispersion. Study site was also set as a random factor.

		Estimate	SE	*P*
Density of xerophilous (log-scale)	Intercept	3.218	0.203	**< 0.001**
	Management intensity	0.250	0.074	**< 0.001**
	Random effects			
	Observation-level	0.264		
	Site	0.237		
Density of mesophilous (log-scale)	Intercept	2.386	0.318	**< 0.001**
	Management intensity	0.401	0.100	**< 0.001**
	Random effects			
	Observation-level	0.463		
	Site	0.703		

Table S5.4. Outputs of the GLMM with Poisson distribution used to measure the impact of mid-term management intensification on the richness of xerophilous and mesophilous snail species. Estimates, standard errors (SE) and p-values (*P*) are provided. Significant p-values are highlighted in bold. "Intercept" represents the intercept of the regression; "Management intensity" represents the slope of the regression Estimates, standard errors (SE) and p-values (*P*) are provided**.** Study site was set as a random factor.

		Estimate	SE	*P*
Richness of xerophilous (log-scale)	Intercept	1.464	0.127	**< 0.001**
	Management intensity	0.028	0.063	0.658
	Random effects			
	Site	0.018		
Richness of mesophilous (log-scale)	Intercept	1.407	0.169	**< 0.001**
	Management intensity	0.010	0.063	0.873
	Random effects			
	Site	0.069		

Table S5.5. Output of the LMM used to assess the relationship between mid-term management intensification and soil pH. Estimates, standard errors (SE) and p-values (*P*) are provided. Significant p-values are highlighted in bold. “Intercept” represents the intercept of the regression; “Management intensity” represents the slope of the regression. Study site was set as a random factor.

	pH		
	Estimate	SE	*P*
Intercept	6.673	0.193	**< 0.001**
Management intensity	0.109	0.042	**0.014**
Random effects			
Site	0.341		
Residual	0.096		

Table S5.6. Output of the multivariate generalised linear model with negative binomial distribution performed to investigate the effect of mid-term management intensification (continuous variable) on community composition, based on species abundances. Study site was also added as a fixed factor in the model. Species included in the analysis are listed in Table S3.1 and Table S5.7. The function *anova.manyglm* in the package *mvabund* (Wang, Naumann, Eddelbuettel, Wilshire, & Warton, 2020) was used to compute the analysis of deviance table for the model fit. Likelihood-Ratio values were summed across all species to get a statistic for the whole community. P-values were calculated using 999 iterations via PIT-trap resampling. Values with *P* < 0.05 are marked in bold.

	Deviance	Df of residuals	*P*
(Intercept)		43	
Management intensity	38.7	42	**0.026**
Site	606.6	32	**< 0.001**

Table S5.7. Univariate test statistics from the multivariate generalised linear model with negative binomial distribution performed to investigate the effect of mid-term management intensification (continuous variable) on community composition, based on species abundances. The function *anova.manyglm* in the package *mvabund* (Wang, Naumann, Eddelbuettel, Wilshire, & Warton, 2020) was used to compute the analysis of deviance table for the model fit. P-values were calculated using 999 iterations via PIT-trap resampling and adjusted for multiple testing. Values with $P < 0.05$ are marked in bold.

Species		Management	Site
Cecillioides acicula	Deviance	0.465	58.747
	P	0.915	**0.001**
Cochlicopa lubricella	Deviance	7.801	27.153
	P	0.100	0.070
Nesovitrea hammonis	Deviance	1.903	25.895
	P	0.702	0.070
Punctum pygmaeum	Deviance	0.336	58.982
	P	0.918	**0.001**
Pupilla muscorum	Deviance	4.536	31.905
	P	0.308	**0.027**
Succinella oblonga	Deviance	0.855	21.361
	P	0.848	0.199
Trochulus sp.	Deviance	3.545	58.460
	P	0.458	**0.001**
Truncatellina cylindrica	Deviance	3.052	38.058
	P	0.477	**0.006**
Vallonia costata	Deviance	9.556	45.358
	P	0.058	**0.002**
Vallonia excentrica	Deviance	1.997	55.622
	P	0.702	**0.001**
Vallonia pulchella	Deviance	0.962	45.725
	P	0.846	**0.002**
Vertigo pygmaea	Deviance	3.552	61.756
	P	0.458	**0.001**
Vitrina pellucida	Deviance	0.050	21.700
	P	0.968	0.199

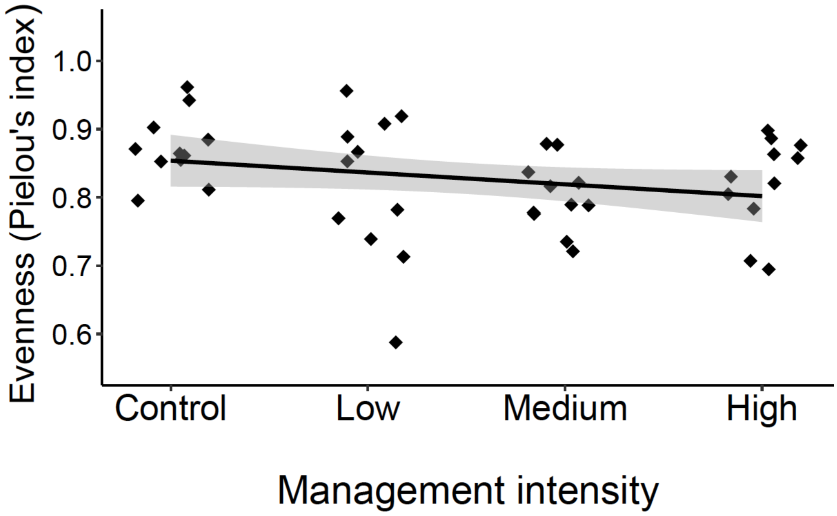

Fig. S5.1. Evenness (Pielou's index) in response to mid-term management intensification, represented by a 4-level intensity gradient consisting of control (no input), low-, medium- and high-input levels. The black line represents the fitted model, along with a 95% confidence band in grey. For further details of the model outputs, see Table S5.2.

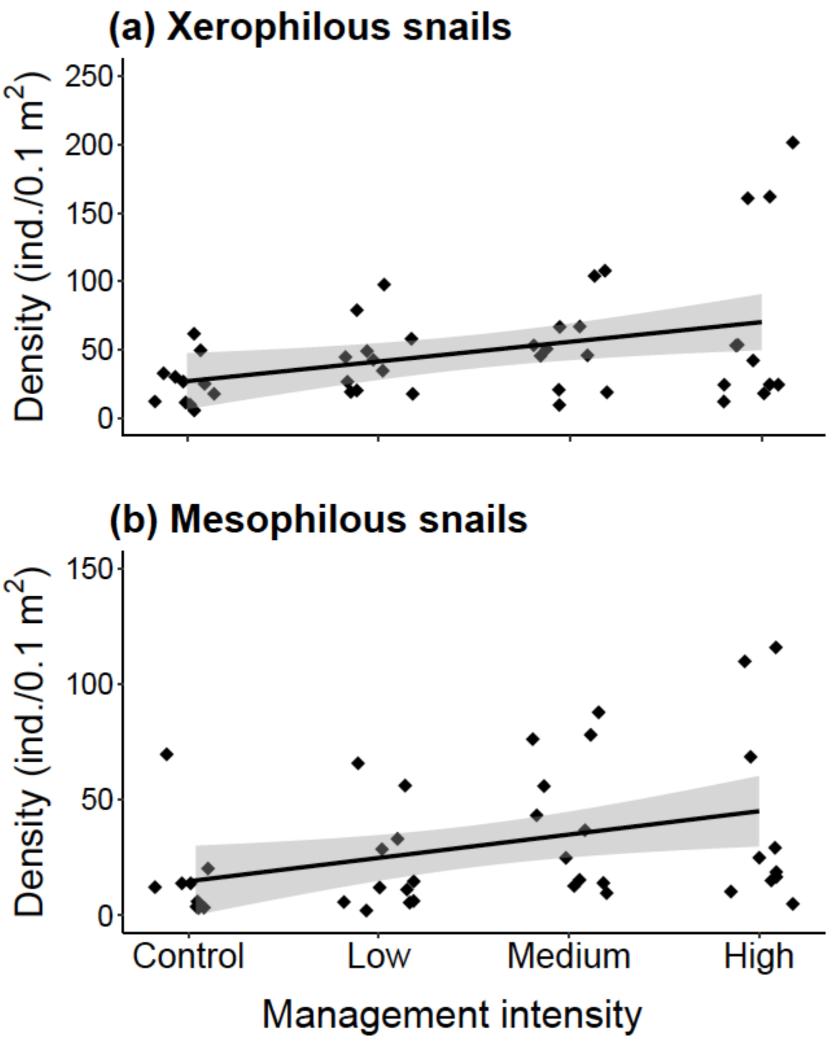

Fig. S5.2. Density of snails in response to mid-term management intensification, classified according to their moisture preferences: (a) xerophilous and (b) mesophilous snails. The 4-level management intensity gradient consisted of control (no input), low-, medium- and high-input levels. The black line represents the fitted model, along with a 95% confidence band in grey. For further details of the model outputs, see Table S5.3.

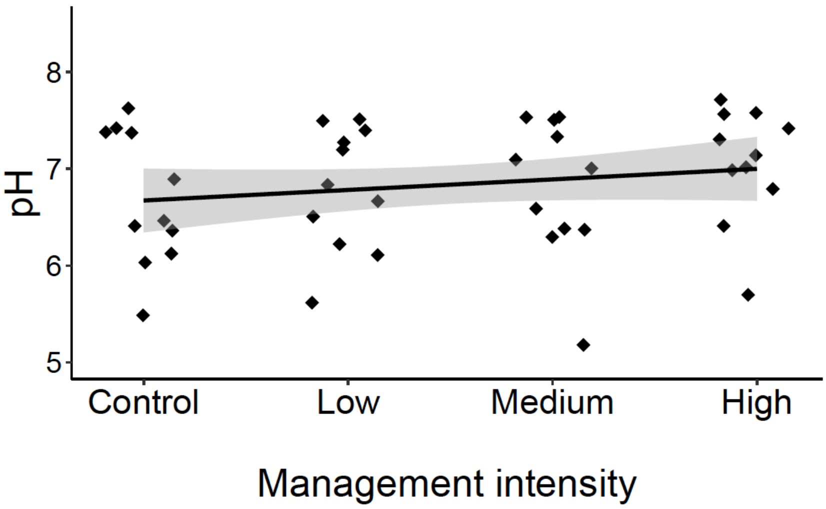

Fig. S5.3. Soil pH in response to response to mid-term management intensification, represented by a 4-level intensity gradient consisting of control (no input), low-, medium- and high-input levels. The black line represents the fitted model, along with a 95% confidence band in grey. For further details of the model outputs, see Table S5.5.

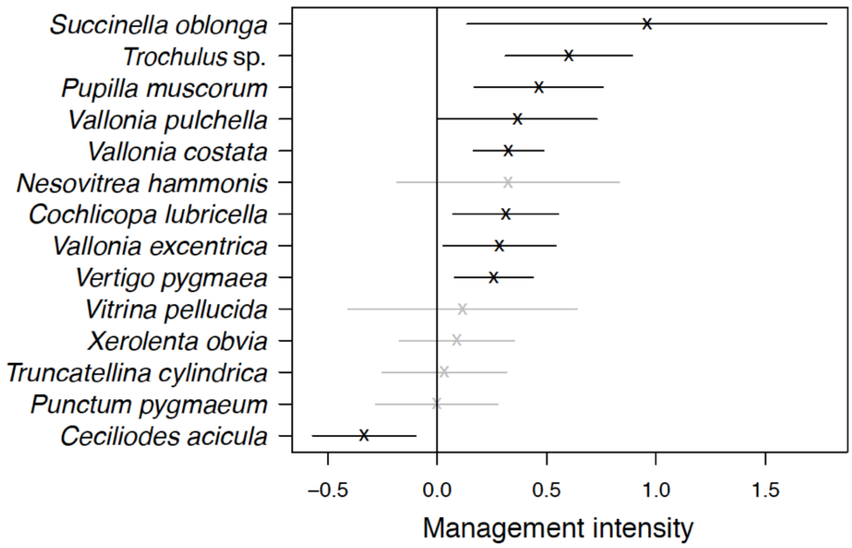

Fig. S5.4. Plots of the point estimates of the model-based community analysis, representing the response of species abundances to mid-term management intensification. The bars show 95% confidence intervals, with those coloured in black indicating intervals not containing zero. Species showing significant responses are shown in Table S5.7 (p-values calculated with permutational methods and corrected for multiple testing).

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Appendix S6 – Results of the observational module

The key variables shaping snail communities in the meadows of the observational module (long-term effects of intensive management) were identified using a model selection approach. This appendix provides the output of the best set of generalised linear mixed-effects models (GLMM) that were incorporated for model selection and averaging. Model selection could not be performed with the number of red-listed species as a response variable given that their scarce occurrence in the study sites impeded doing so. Instead, the variables having significant effects ($P < 0.05$) in univariate generalised linear mixed models are presented.

Table of content

Table S6.1. GLMM outputs performed to analyse the effect of explanatory variables on snail density and snail 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 with univariate GLMMs (see Table S2.1). 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.

Rank	Model	Df	logLik	AICc	Δ AICc	Model weight
	Snail density (with observation-level random effect)					
1	bare ground + pH: plant diversity + poly(elevation,2)	9	-155.75	335.70	0.00	0.39
2	pH : plant diversity + poly(elevation,2)	8	-157.81	336.40	0.72	0.27
3	bare ground + pH + plant diversity + poly(elevation,2)	8	-157.83	336.50	0.76	0.26
4	pH + plant diversity + poly(elevation,2)	7	-160.59	338.80	3.10	0.08
	Snail species richness					
1	bare ground + pH + plant diversity + poly(elevation,2)	7	-68.18	154.00	0.00	0.64
2	pH + plant diversity + poly(elevation,2)	6	-70.87	156.40	2.38	0.19
3	bare ground + pH + poly(elevation,2)	6	-71.14	156.90	2.93	0.15

Table S6.2. Output of the full model averaging performed on the best set of models (Δ AICc < 6) analysing the effect of explanatory variables on snail density (see Table S6.1). 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*	Rel. importance
(**Intercept**)	2.647	(2.109, 3.185)	**< 0.001**	
Bare ground	0.194	(-0.163, 0.551)	0.287	0.65
pH	1.454	(0.985, 1.923)	**< 0.001**	1.00
Plant diversity	0.581	(0.253, 0.910)	**< 0.001**	1.00
Elevation	-9.306	(-14.213, -4.400)	**< 0.001**	1.00
Elevation^2	-5.494	(-10.338, -0.649)	**0.026**	1.00
Plant diversity : pH	0.368	(-0.297, 1.032)	0.279	0.65

Table S6.3. 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 S6.1). 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*	Rel. importance
(**Intercept**)	0.957	(0.655, 1.260)	**< 0.001**	
Bare ground	0.186	(-0.067, 0.440)	0.150	0.85
pH	0.713	(0.463, 0.964)	**< 0.001**	1.00
Plant diversity	0.198	(-0.052, 0.448)	0.121	0.85
Elevation	-4.735	(-7.392, -2.078)	**< 0.001**	1.00
Elevation^2	-3.617	(-6.001, -1.233)	**0.003**	1.00

Table S6.4. Output of the univariate GLMM analysing the effect of explanatory variables on the number 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*
pH	3.472	1.549	**0.025**
Bare ground	0.270	0.117	**0.021**