

RESEARCH ARTICLE

Open Access



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

Gerard Martínez-De León^{*†} , Lauriane Dani[†], Aline Hayoz-Andrey, Ségolène Humann-Guilleminot , Raphaël Arlettaz and Jean-Yves Humbert

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 speciose 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

*Correspondence: gerard.martinezdeleon@iee.unibe.ch; martinezdeleongerard@gmail.com

[†]Gerard Martínez-De León and Lauriane Dani are co-first authors
Division of Conservation Biology, Institute of Ecology and Evolution,
University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland



© The Author(s) 2022. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>. The Creative Commons Public Domain Dedication waiver (<http://creativecommons.org/publicdomain/zero/1.0/>) applies to the data made available in this article, unless otherwise stated in a credit line to the data.

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 constraints 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 cm² area and 5 cm depth each were extracted after the first hay cut and pooled afterwards into a 5 dm³ 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 H₂O.

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 $\Delta AICc < 6$ (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 \pm 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).

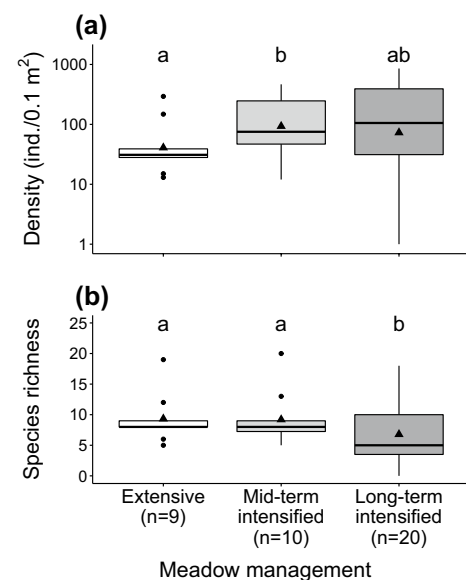


Fig. 1 Effects of meadow management intensification on **a** snail density and **b** species richness. Data for the extensive (no water and fertiliser inputs, i.e. control plots) and mid-term intensive (plots having received high inputs of water and fertiliser during 5 years) management types stemmed 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 quartiles, 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

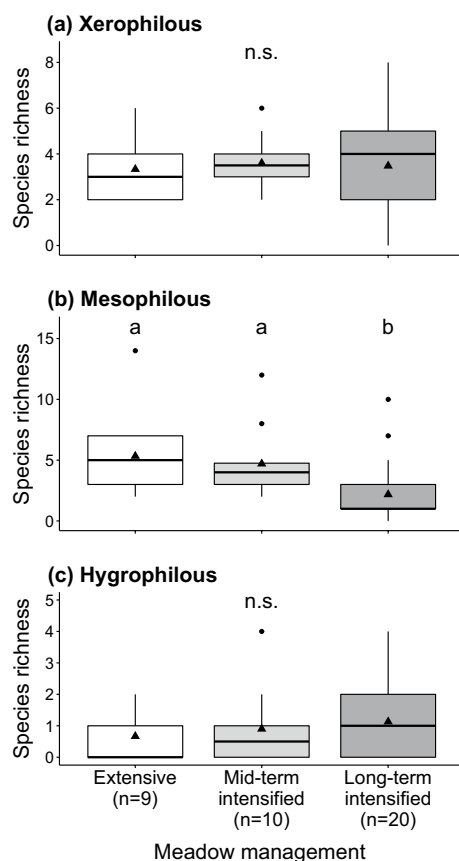


Fig. 2 Effect of meadow management intensification on species richness of land snails split according to their moisture preference: **a** xerophilous; **b** mesophilous; **c** hygrophilous. For management descriptions and box-plot features, see legend of Fig. 1

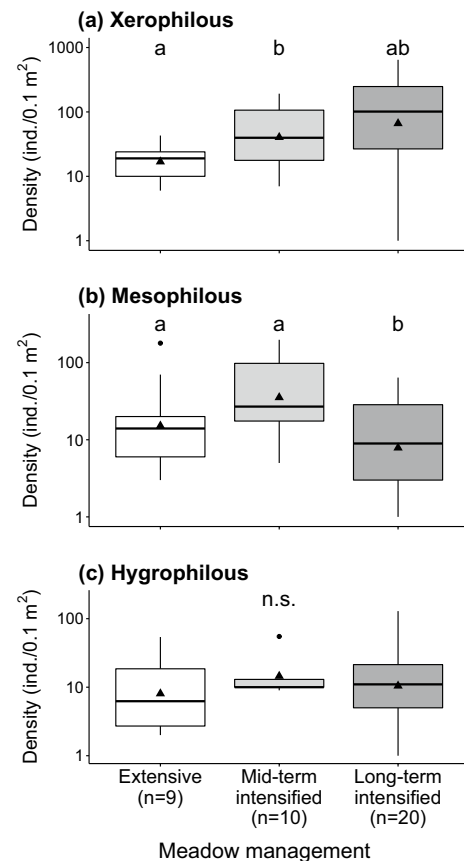


Fig. 3 Effect of meadow management intensification on densities of land snails split according to their moisture preference: **a** xerophilous, **b** mesophilous, **c** hygrophilous. Note the log-scale on the y-axis of the graphs. For management descriptions and box-plot features, see legend of Fig.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

differences were found for the density of hygrophilous snails nor for the number of red-listed species (Fig. 3c; Additional file 4: Appendix S4).

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:

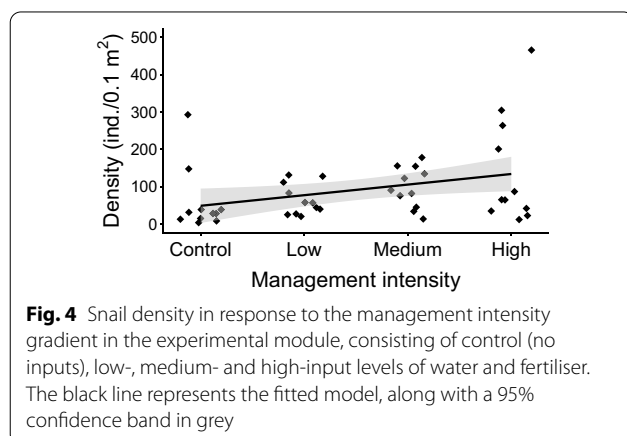
Appendix S6). Elevation had a quadratic effect with an optimum at around 1100 m a.s.l. (Fig. 5c, d), but its influence on snail density and species richness was generally negative. Finally, plant diversity (Shannon index) significantly enhanced snail density (Fig. 5e). For detailed model outputs and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

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



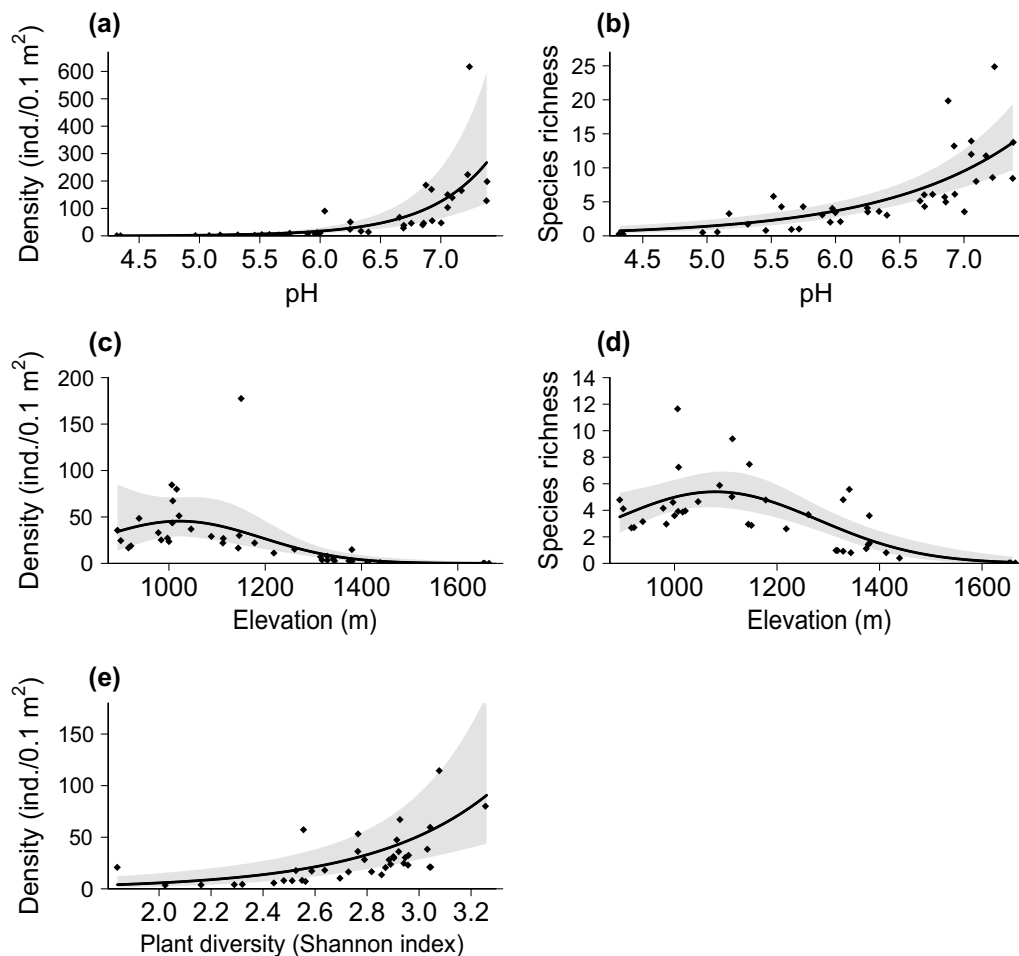


Fig. 5 Effect plots with partial residuals (i.e. the residuals left after subtracting the influence of the other variables in the model) for each of the predictors influencing snail density and snail species richness: **a, b** soil pH; **c, d** elevation; and **e** plant diversity (observational module). 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 speciose 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

References

- Grime JP. Competitive exclusion in herbaceous vegetation. *Nature*. 1973;242(1):344–7.
- Marini L, Fontana P, Battisti A, Gaston KJ. Response of orthopteran diversity to abandonment of semi-natural meadows. *Agric Ecosyst Environ*. 2009;132:232–6. <https://doi.org/10.1016/j.agee.2009.04.003>.
- Marini L, Fontana P, Klimek S, Battisti A, Gaston KJ. Impact of farm size and topography on plant and insect diversity of managed grasslands in the Alps. *Biol Conserv*. 2009;142(2):394–403. <https://doi.org/10.1016/j.biocon.2008.10.034>.
- Wilson JB, Peet RK, Dengler J, Pärtel M. Plant species richness: the world records. *J Veg Sci*. 2012;23:796–802. <https://doi.org/10.1111/j.1654-1103.2012.01400.x>.
- MacDonald D, Crabtree JR, Wiesinger G, Dax T, Stamou N, Fleury P, Lazpita JG, Gibon A. Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *J Environ Manag*. 2000;59(1):47–69. <https://doi.org/10.1006/jema.1999.0335>.
- Srijker D. Marginal lands in Europe—causes of decline. *Basic Appl Ecol*. 2005;6:99–106. <https://doi.org/10.1016/j.baae.2005.01.001>.
- Socher SA, Prati D, Boch S, Müller J, Klaus VH, Hölzel N, Fischer M. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *J Ecol*. 2012;100(6):1391–9. <https://doi.org/10.1111/j.1365-2745.2012.02020.x>.
- Hautier Y, Niklaus PA, Hector A. Competition for light causes plant biodiversity loss after eutrophication. *Science*. 2009;324(5927):636–8. <https://doi.org/10.1126/science.1169640>.
- Zimmermann P, Tasser E, Leitinger G, Tappeiner U. Effects of land-use and land-cover pattern on landscape-scale biodiversity in the European Alps. *Agric Ecosyst Environ*. 2010;139(1–2):13–22. <https://doi.org/10.1016/j.agee.2010.06.010>.
- Kampmann D, Herzog F, Jeanneret P, Konold W, Peter M, Walter T, Wildi O, Lüscher A. Mountain grassland biodiversity: impact of site conditions versus management type. *J Nat Conserv*. 2008;16(1):12–25. <https://doi.org/10.1016/j.jnc.2007.04.002>.
- De Deyn GB, Raaijmakers CE, Zoomer HR, Bezemer TM, Van Der Putten WH. Soil invertebrate fauna enhances grassland succession and diversity. *Nature*. 2003;422:711–3.
- Humbert J-Y, Dwyer JM, Andrey A, Arlettaz R. Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: a systematic review. *Glob Change Biol*. 2016;22(1):110–20. <https://doi.org/10.1111/gcb.12986>.
- Humbert J-Y, Delley S, Arlettaz R. Grassland intensification dramatically impacts grasshoppers: experimental evidence for direct and indirect effects of fertilisation and irrigation. *Agric Ecosyst Environ*. 2021;314:107412. <https://doi.org/10.1016/j.agee.2021.107412>.
- Andrey A, Humbert J-Y, Arlettaz R. Functional response of leaf- and planthoppers to modern fertilisation and irrigation of hay meadows.

- Basic Appl Ecol. 2016;17(7):627–37. <https://doi.org/10.1016/j.baae.2016.07.002>.
15. Grandchamp AC, Bergamini A, Stofer S, Niemelä J, Duelli P, Scheidegger C. The influence of grassland management on ground beetles (Carabidae, Coleoptera) in Swiss montane meadows. *Agric Ecosyst Environ*. 2005;110(3–4):307–17. <https://doi.org/10.1016/j.agee.2005.04.018>.
 16. Lessard-Therrien M, Humbert J-Y, Hajdamowicz I, Stańska M, van Klink R, Lischer L, Arlettaz R. Impacts of management intensification on ground-dwelling beetles and spiders in semi-natural mountain grasslands. *Agric Ecosyst Environ*. 2018;251:59–66. <https://doi.org/10.1016/j.agee.2017.08.025>.
 17. Astor T, Lenoir L, Berg MP. Measuring feeding traits of a range of litter-consuming terrestrial snails: leaf litter consumption, faeces production and scaling with body size. *Oecologia*. 2015;178:833–45. <https://doi.org/10.1007/s00442-015-3257-y>.
 18. González-Solis J, Abella JC, Aymí R. Shell size relationships in the consumption of gastropods by migrant Song Thrushes *Turdus philomenos*. *Avocetta*. 1996;20:147–9.
 19. Graveland J, Van Der Wal R, Van Balen JH, Van Noordwijk AJ. Poor reproduction in forest passerines from decline of snail abundance on acidified soils. *Nature*. 1994;368(6470):446–8. <https://doi.org/10.1038/368446a0>.
 20. Baur B, Meier T, Baur A, Schmera D. Terrestrial gastropod diversity in an alpine region: disentangling effects of elevation, area, geometric constraints, habitat type and land-use intensity. *Ecography*. 2014;37(4):390–401. <https://doi.org/10.1111/j.1600-0587.2013.00312.x>.
 21. Nekola JC. Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. *Divers Distrib*. 2003;9:55–71. <https://doi.org/10.1046/j.1472-4642.2003.00165.x>.
 22. Stoll P, Oggier P, Baur B. Population dynamics of six land snail species in experimentally fragmented grassland. *J Anim Ecol*. 2009;78:236–46. <https://doi.org/10.1111/j.1365-2656.2008.01478.x>.
 23. Falkner G, Obrdlík P, Castella E, Speight MCD. Shelled Gastropoda of Western Europe. Munich: Friedrich-Held-Gesellschaft; 2001.
 24. van Klink R, Menz MHM, Baur H, Dosch O, Kühne I, Lischer L, Luka H, Meyer S, Szikora T, Unternährer D, Arlettaz R, Humbert J-Y. Larval and phenological traits predict insect community response to mowing regime manipulations. *Ecol Appl*. 2019;29(4):e01900. <https://doi.org/10.1002/eap.1900>.
 25. Wehner K, Renker C, Simons NK, Weisser WW, Blüthgen N. Narrow environmental niches predict land-use responses and vulnerability of land snail assemblages. *BMC Ecol Evol*. 2021;21(1):15. <https://doi.org/10.1186/s12862-020-01741-1>.
 26. Boycott AE. The habitats of land Mollusca in Britain. *J Ecol*. 1934;22(1):1–38.
 27. Cook A. Behavioural ecology: on doing the right thing, in the right place at the right time. In: Barker GM, editor. *The biology of terrestrial molluscs*. Wallingford: CABI Publishing; 2001. p. 447–88.
 28. Oggier P, Zschokke S, Baur B. A comparison of three methods for assessing the gastropod community in dry grasslands. *Pedobiologia*. 1998;42:348–57.
 29. Boch S, Kurtogullari Y, Allan E, Lessard-therrien M, Simone N, Fischer M, De León GM, Arlettaz R, Humbert J. Effects of fertilization and irrigation on vascular plant species richness, functional composition and yield in mountain grasslands. *J Environ Manag*. 2021;279:111629. <https://doi.org/10.1016/j.jenvman.2020.111629>.
 30. Boschi C, Baur B. Past pasture management affects the land snail diversity in nutrient-poor calcareous grasslands. *Basic Appl Ecol*. 2008;9(6):752–61. <https://doi.org/10.1016/j.baae.2007.09.006>.
 31. Hylander K, Ehrlén J. The mechanisms causing extinction debts. *Trends Ecol Evol*. 2013;28(6):341–6. <https://doi.org/10.1016/j.tree.2013.01.010>.
 32. Dani L. Positive effects of management intensification on land snail communities in Swiss traditionally managed montane and subalpine meadows. Master thesis. University of Bern, Bern. 2017.
 33. Mandataire du Monitoring de la Biodiversité en Suisse. Instruction pour le travail sur le terrain de l'indicateur «Z9-Mollusques». 2017. https://www.biodiversitymonitoring.ch/images/dokumente/daten/anleitungen/1750%20Anleitung%20Z9-Moll%20Feld%20v17_fr.pdf.
 34. Boschi C. Die Schneckenfauna der Schweiz. Ein umfassendes Bild- und Bestimmungsbuch. Bern/Stuttgart/Wien: Haupt; 2011.
 35. Hausser J. Fauna helvetica: mollusca identification. Neuchâtel: Centre suisse de cartographie de faune (CSCF/SZKF) & Schweizerisches Entomologische Gesellschaft (SEG/SES); 2005.
 36. Astor T, von Proschwitz T, Strengbom J, Berg MP, Bengtsson J. Importance of environmental and spatial components for species and trait composition in terrestrial snail communities. *J Biogeogr*. 2017;44:1362–72. <https://doi.org/10.1111/jbi.12946>.
 37. Rüetschi J, Stucki P, Müller P, Vicentini H, Claude F. Liste rouge Mollusques (gastéropodes et bivalves). Espèces menacées en Suisse, état 2010. L'environnement pratique, n° 1216. Office fédéral de l'environnement, Bern, & Centre suisse de cartographie de la faune, Neuchâtel; 2012.
 38. van Klink R, Boch S, Buri P, Rieder NS, Humbert J-Y, Arlettaz R. No detrimental effects of delayed mowing or uncut grass refuges on plant and bryophyte community structure and phytomass production in low-intensity hay meadows. *Basic Appl Ecol*. 2017;20:1–9. <https://doi.org/10.1016/j.baae.2017.02.003>.
 39. Kuznetsova A, Brockhoff PB, Christensen RHB. lmerTest package: tests in linear mixed effects models. *J Stat Softw*. 2017;82(13):1–26. <https://doi.org/10.18637/jss.v082.i13>.
 40. Harrison XA. Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*. 2014. <https://doi.org/10.7717/peerj.616>.
 41. Wang Y, Naumann U, Edelbuettel D, Wilshire J, Warton D. mvabund: statistical methods for analysing multivariate abundance data. R package version 4.1.3. 2020. <https://cran.r-project.org/package=mvabund>.
 42. Warton DI, Wright ST, Wang Y. Distance-based multivariate analyses confound location and dispersion effects. *Methods Ecol Evol*. 2012;3:89–101. <https://doi.org/10.1111/j.2041-210X.2011.00127.x>.
 43. Harrison XA, Donaldson L, Correa-Cano ME, Evans J, Fisher DN, Goodwin CED, Robinson BS, Hodgson DJ, Inger R. A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*. 2018. <https://doi.org/10.7717/peerj.4794>.
 44. Zuur AF, Ieno EN, Elphick CS. A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol*. 2010;1:3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.
 45. Barton K. MuMIn: multi-model inference. R package version 1.43.6. 2020. <https://cran.r-project.org/package=MuMIn>.
 46. R Team Core. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing; 2020. <https://doi.org/10.1108/eb003648>.
 47. Riedener E, Rusterholz HP, Baur B. Land-use abandonment owing to irrigation cessation affects the biodiversity of hay meadows in an arid mountain region. *Agr Ecosyst Environ*. 2014;185:144–52. <https://doi.org/10.1016/j.agee.2013.12.023>.
 48. Pech P, Dolanský J, Hrdlička R, Lepš J. Differential response of communities of plants, snails, ants and spiders to long-term mowing in a small-scale experiment. *Community Ecol*. 2015;16(1):115–24. <https://doi.org/10.1556/168.2015.16.1.13>.
 49. Hylander K, Nilsson C, Göthner T. Effects of buffer-strip retention and clearcutting on land snails in boreal riparian forests. *Conserv Biol*. 2004;18(4):1052–62.
 50. Nicolai A, Ansart A. Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. *Conserv Physiol*. 2017;5(1):1–17. <https://doi.org/10.1093/conphys/cox007>.
 51. Schweizer M, Triebkorn R, Köhler HR. Snails in the sun: strategies of terrestrial gastropods to cope with hot and dry conditions. *Ecol Evol*. 2019;9(22):12940–60. <https://doi.org/10.1002/ece3.5607>.
 52. Humbert J-Y, Ghazoul J, Richner N, Walter T. Hay harvesting causes high orthopteran mortality. *Agric Ecosyst Environ*. 2010;139:522–7. <https://doi.org/10.1016/j.agee.2010.09.012>.
 53. Humbert J-Y, Ghazoul J, Sauter GJ, Walter T. Impact of different meadow mowing techniques on field invertebrates. *J Appl Entomol*. 2010;134:592–9. <https://doi.org/10.1111/j.1439-0418.2009.01503.x>.
 54. Wehner K, Renker C, Brückner A, Simons NK, Weisser WW, Blüthgen N. Land-use in Europe affects land snail assemblages directly and indirectly by modulating abiotic and biotic drivers. *Ecosphere*. 2019. <https://doi.org/10.1002/ecs2.2726>.
 55. Dietschi S, Holderegger R, Schmidt SG, Linder P. Agri-environment incentive payments and plant species richness under different management intensities in mountain meadows of Switzerland. *Acta Oecol*. 2007;31:216–22. <https://doi.org/10.1016/j.actao.2006.10.006>.

56. Homburger H, Hofer G. Diversity change of mountain hay meadows in the Swiss Alps. *Basic Appl Ecol.* 2012;13(2):132–8. <https://doi.org/10.1016/j.baae.2011.12.004>.
57. Boschi C, Baur B. Effects of management intensity on land snails in Swiss nutrient-poor pastures. *Agric Ecosyst Environ.* 2007;120(2–4):243–9. <https://doi.org/10.1016/j.agee.2006.09.008>.
58. Boschi C, Baur B. The effect of horse, cattle and sheep grazing on the diversity and abundance of land snails in nutrient-poor calcareous grasslands. *Basic Appl Ecol.* 2007;8(1):55–65. <https://doi.org/10.1016/j.baae.2006.02.003>.
59. Cameron RAD, Pokryszko BM. Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. *J Conchol.* 2005;38(5):529–47.
60. Cameron RAD. The survival, weight-loss and behaviour of three species of land snail in conditions of low humidity. *J Zool.* 1970;160:143–57. <https://doi.org/10.1111/j.1469-7998.1970.tb02900.x>.
61. Baur B. Parental care in terrestrial gastropods. *Experientia.* 1994;50:5–14.
62. Braschler B, Zschokke S, Dolt C, Thommen GH, Oggier P, Baur B. Grain-dependent relationships between plant productivity and invertebrate species richness and biomass in calcareous grasslands. *Basic Appl Ecol.* 2004;24:15–24. <https://doi.org/10.1078/1439-1791-00184>.
63. Speiser B. Food and feeding behaviour. In: Barker GM, editor. *The biology of terrestrial molluscs.* Wallingford: CABI Publishing; 2001. p. 259–88.
64. Hudewenz A, Klein AM, Scherber C, Stanke L, Tschamtkke T, Vogel A, Weigelt A, Weisser WW, Ebeling A. Herbivore and pollinator responses to grassland management intensity along experimental changes in plant species richness. *Biol Conserv.* 2012;150(1):42–52. <https://doi.org/10.1016/j.biocon.2012.02.024>.
65. Lessard-Therrien M. A balance between productivity and biodiversity conservation in montane and subalpine semi-natural grasslands. Bern: University of Bern; 2017.
66. Whalen JK, Chang C, Clayton GW, Carefoot JP. Cattle manure amendments can increase the pH of acid soils. *Soil Sci Soc Am.* 2000;64:962–6. <https://doi.org/10.2136/sssaj2000.643962x>.
67. Martin K, Sommer M. Relationships between land snail assemblage patterns and soil properties in temperate-humid forest ecosystems. *J Biogeogr.* 2006;31(4):531–45.
68. Growell HH. Laboratory study of calcium requirements of the brown garden snail, *Helix aspersa* Müller. *J Molluscan Stud.* 1973;40(6):491–503.
69. Labaune C, Magnin F. Land snail communities in Mediterranean upland grasslands: the relative importance of four sets of environmental and spatial variables. *J Molluscan Stud.* 2001;67:463–74. <https://doi.org/10.1093/mollus/67.4.463>.
70. Schmera D, Baur B. Gastropod communities in alpine grasslands are characterized by high beta diversity. *Community Ecol.* 2014;15(2):246–55. <https://doi.org/10.1556/ComEc.15.2014.2.13>.
71. Dahirel M, Olivier E, Guiller A, Martin M, Madec L. Movement propensity and ability correlate with ecological specialization in European land snails: comparative analysis of a dispersal syndrome. *J Anim Ecol.* 2015;84:228–38. <https://doi.org/10.1111/1365-2656.12276>.
72. Denny M. Locomotion: the cost of gastropod crawling. *Science.* 1980;208:1288–90.
73. Knop E, Herzog F, Schmid B. Effect of connectivity between restoration meadows on invertebrates with contrasting dispersal abilities. *Restor Ecol.* 2011;19(201):151–9. <https://doi.org/10.1111/j.1526-100X.2010.00737.x>.
74. Santos X, Bros V, Miño À. Recolonization of a burned Mediterranean area by terrestrial gastropods. *Biodivers Conserv.* 2009;18(12):3153–65. <https://doi.org/10.1007/s10531-009-9634-2>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Ready to submit your research? Choose BMC and benefit from:

- fast, convenient online submission
- thorough peer review by experienced researchers in your field
- rapid publication on acceptance
- support for research data, including large and complex data types
- gold Open Access which fosters wider collaboration and increased citations
- maximum visibility for your research: over 100M website views per year

At BMC, research is always in progress.

Learn more biomedcentral.com/submissions

