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Land-use in Europe affects land snail assemblages directly and indirectly by modulating abiotic and biotic drivers

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Abstract. Type and intensity of land-use vary in space and time and strongly contribute to changes in richness and composition of species communities. In this study, we examined land snail communities in forests and grasslands in three regions of Germany. We aimed to quantify the extent to which snail density, diversity, and community composition in forests and grasslands are determined by (1) land-use intensity, (2) abiotic drivers and (3) biotic substrates, and (4) whether these effects are consistent across regions. In total, we collected 15,607 snail individuals belonging to 71 species and analyzed both direct and indirect effects using structural equation modeling. Snail densities and their local diversity varied across regions and between forest and grassland habitats within a region albeit with contrasting trends. Community composition also differed among regions—more strongly in forests than in grasslands—and each habitat had unique species (18 in forests, 21 in grasslands). In general, the direct impact of land-use on snail density, diversity, and community structure was on average nine (forests) and seven (grasslands) times lower than the impact of abiotic drivers and biotic substrates which both affected snail assemblages about equally. However, land-use factors had indirect effects on snail responses through abiotic variables such as soil moisture and soil pH. Furthermore, land-use factors also had indirect effects via changing biotic substrates, such as plant cover in grasslands and deadwood cover in forests. Our results show that land snails strongly respond to environmental gradients and add an important indicator taxon to the current evidence of land-use impacts, highlighting the complexity of direct and indirect effects via biotic and abiotic drivers across regions in Central Europe.

Key words: abiotic; environmental parameters; forests; grasslands; land-use factors; land-use intensity; snail community composition; snail densities; snail diversity; structural equation modeling; vegetation cover.

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INTRODUCTION

Habitat conversion, degradation, and habitat fragmentation by intensive land-use can reduce biodiversity on small- and large-scale levels affecting different groups of organisms at different trophic levels (Newbold et al. 2015). Land-use by humans provides natural resources for immediate human needs, and its quality and quantity differ greatly among regions worldwide

(Foley et al. 2005). Local land-use practices often change regional natural environments and conditions (Stohlgren et al. 1998, Socher et al. 2012). For instance, intensive mowing in grasslands or wood harvesting in forests affects vegetation characteristics and—intentionally or unintentionally—influences plant composition and abiotic factors like soil moisture, humidity, or temperature (Stohlgren et al. 1998, Poschlod et al. 2005, Socher et al. 2012). These changes in abiotic and biotic factors in turn have an impact on different local animal communities. Therefore, the impact of land-use practices on the biodiversity of a certain biological taxon can be indirect via changing abiotic conditions and species interactions or direct, for example, by the destructive impact of wood harvesting in forests and mowing in grasslands.

While the impact of land-use intensity on local and global diversity has already been studied (Sala et al. 2000, Chisté et al. 2016, Frank et al. 2017), studies on mollusks are rare and mainly focus on tropical regions (Schilthuizen et al. 2005, Nurinsiyah et al. 2016). Here, we examined the effects of land-use intensity in forests and grasslands on land snail densities, diversity, and community composition in Central Europe. About 24,000 species of land snails (Mollusca) are globally described, but potentially up to 65,000 may exist (Lydeard et al. 2004). This diversity arose at least since Jurassic times (about 180 million years) and enabled this group to adapt to a variety of different habitats not only in temperate forests and in the tropics but also in deserts and mountain regions (Morris and Taylor 2000). In their habitats, land snails are important for nutrient cycling by promoting fungal and microbial growth in processed leaf litter (Mason 1970) and as food source for a variety of different predators; especially, the calcium-rich shell is used by, for example, beetles, carnivorous snails, salamanders, or frogs, and it is a main source of calcium for birds while forming eggshells (Caldwell 1993, Perrins 1996, Dourson 2010).

Land snail species are characterized by a limited mobility which makes them vulnerable to habitat changes (Goodfried 1986, Baur and Baur 1988, Hylander et al. 2005). So far, much research has been done on the impact of abiotic factors on snail communities such as soil moisture, pH, calcium content, and leaf litter depth and on vegetation (Wäreborn 1992, Martin and Sommer 2004*a*, *b*, Hylander et al. 2005, Horsák 2006), yet less is known about the impact of land-use factors on snail communities. A study of Denmead et al. (2013) found a decrease in density and diversity of snails with increasing trampling intensity of grazing livestock. However, besides the direct trampling effects, land-use acted indirectly on snail communities, by changing litter depth and quality as well as the moisture level that influenced the availability of nutrients (Denmead et al. 2013). Therefore, some land-use practices may represent direct impacts on snails, but more importantly they may alter the abiotic and biotic environment and thus indirectly affect snail community composition.

In the present study, we examined land snail densities, diversity, and community composition in three regions of Germany which comprise forest and grassland plots characterized by different land-use intensities (Fischer et al. 2010, Blüthgen et al. 2012). We address the questions (1) to what extent different land-use parameters, abiotic factors, and biotic substrates affect snail densities, diversity, and community composition in forests and agricultural grasslands, (2) whether land-use acts directly on snail communities or indirectly by changing the plant community, and (3) whether these effects differ among the three regions. Since we expected land-use intensity and abiotic and biotic environmental factors to influence land snail assemblages and to interact with each other, we used structural equation modeling (SEM) to disentangle direct and indirect effects.

MATERIALS AND METHODS

Study area

The study was conducted within the framework of the Biodiversity Exploratories Project in Germany (http://www.biodiversity-exploratories.de, Fischer et al. 2010). It addresses effects of land-use on biodiversity and biodiversity-related ecosystem processes, and different plots represent gradients of plant biodiversity and land-use intensity of the regions. The regions are the Swabian Alb, a low-mountain range in southwest Germany (460–860 m a.s.l., 09°10′49″–09°35′54″ E, 48°20′28″–48°32′02″ N); the Hainich-Dün, a hilly region in central Germany (285–550 m a.s.l., 10°10′24″–10°46′45″ E, 50°56′14″–51°22′43″ N); and the Schorfheide-Chorin, a glacially formed landscape in northeast Germany (3–140 m a.s.l., 13°23′27″–14°08′53″ E, 52°47′25″–53°13′26″ N). The Schorfheide is characterized by the lowest annual precipitation (520–580 mm), with a mean annual temperature of 6–7°C. It is followed by the Hainich (630–800 mm, 6.5–8°C) and the Swabian Alb (800–930 mm, 8–8.5°C).

In each region (see Appendix S1 for maps), 100 experimental plots (EPs; 50 in forests and 50 in grasslands) were set up along a land-use gradient covering different management types and intensities. Forest plots have a size of 100 × 100 m, and grassland plots are 50 × 50 m. More details on the Biodiversity Exploratories, plot site selection, and quantification of land-use intensity can be found in Fischer et al. (2010).

Sampling procedure

In June 2017, surface samples were taken from all 50 forest and 50 grassland EPs in the Swabian Alb and the Hainich, and from 49 forest and 34 grassland plots in the Schorfheide. For each EP, surface samples (20 × 20 cm in grasslands and 15 × 15 cm in forests, about 2 cm deep) were collected using a sharp knife, along with the herbaceous vegetation, mosses, litter, and the upper soil layer. Samples were taken at the southeast, southwest, and northwest corners of the plot and in the middle of the edges between (five replicates per plot). Samples were collected in plastic bags, transferred to the laboratory, and dried for 48 h at 40°C. Afterward, snail shells were collected by hand using a stereomicroscope (Cameron and Pokryszko 2005). However, slugs were not sampled in our study since our sampling method is inappropriate to give a quantitative and qualitative survey.

Shelled snails were subsequently determined to species level using Welter-Schultes (2012), Wiese (2016), and Glöer (2017). Although it has been frequently suggested (Pearce 2008), we did not distinguish between dead and living snail individuals. However, including empty shells holds the risk of overestimating species diversity (and abundance) since species may no longer live in the plot or be accidental immigrants (Cernohorsky et al. 2010). Furthermore, empty shells decay at different rates among species and sites, triggered by the present soil pH (Claassen 1998, Pearce 2008). We took the risk of probably slightly overestimating current snail diversity at our plots by the inclusion of empty shells since we aimed to display long-term effects of land-use intensity and therefore shells of past years needed to be included. Raw data are available at https://www.bexis.uni-jena.de/PublicData/PublicDataSet.aspx?DatasetId=24986.

Statistical analyses

All statistical analyses were performed with R 3.5.1 (R Core Team 2012). Numbers of collected individuals, irrespective whether alive or represented as empty shells, were standardized to densities per square meter (Ind/m^2), and the number of species was used for calculating Shannon diversity. To avoid overestimation of species numbers, juvenile individuals that could only be determined to genus level were added to the most abundant species of the genus in the respective plot.

To compare land snail assemblages among regions and habitats, density and Shannon diversity were statistically analyzed as response variables, while Exploratory (region: Swabian Alb, Hainich, Schorfheide) and Habitat (forest, grassland) were fixed as explanatory variables using ANOVA type III. Abundances were square-rooted before analyses to obtain normal distribution of variances. Habitat differences among regions were analyzed using one-way ANOVA.

To compare land snail communities among regions and habitats, multivariate statistical analysis of the community composition was based on the standardized densities (Ind/m^2) of the snails. Non-linear multidimensional scaling (NMDS) analyses and ordination plots of either the whole communities from all regions and habitats or every region separately were performed upon Bray-Curtis similarity matrices (Bray and Curtis 1957) after square-root and Wisconsin standardization (Legendre and Gallagher 2001) using meta-MDS in vegan (Oksanen et al. 2018). Vectors in the ordination space, which represent species that significantly contribute to plot separation, were fitted onto the NMDS plot of the individual regions as arrows, using the envfit() function in vegan (Oksanen et al. 2018). Significance of fitted vectors was assessed using permutations (n = 10,000) and goodness-of-fit statistics (Oksanen et al. 2018). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) and affiliated permutational analysis of multivariate dispersions (PERMDISP; Anderson 2006) were performed using all regions' and habitats' similarity matrix to test for region-dependent differences in habitat community composition and community variability (multivariate beta diversity), respectively. The grassland EP SEG48 was excluded from the NMDS plots, because it was mainly dominated by one species (*Pupilla pratensis*; according to Nekola et al. (2015), *P. pratensis* should be treated as *P. alpicola*) and would have hampered a clear 2D representation of the ordination of the other plots, yet we did not exclude the data from the statistical analyses.

For further statistical analyses, land-use factors for forests (proportion of wood harvested, proportion of deadwood cuts, and proportion of non-native trees) and those for grasslands (mowing frequency [cuts/year], grazing [livestock unit/ha × day], and fertilization [kg $N \cdot ha^{-1} \cdot yr^{-1}$]) were used (see Blüthgen et al. 2012, Kahl and Bauhus 2014). In addition to land-use factors, we used the factors soil pH, precipitation, and soil moisture as abiotic factors, as well as cover or number of grasses, cover or number of herbs (without legumes), cover or number of legumes, cover of litter, and cover of deadwood as biotic substrate variables. Details on datasets are given in Appendix S2.

To test for the proportional influence of abiotic factors, biotic substrate, and land-use intensity on snail density, diversity, and community structure in forests and grasslands, we used a structural equation model on a combined dataset of all three regions. The three main pathways of influence were represented by composite variables: (1) Abiotic comprised soil pH, soil moisture, and precipitation; (2) management comprised the land-use factors for forests and grasslands; and (3) biotic substrate comprised the cover of litter, deadwood, and herbs in forests and the cover of grasses, herbs, and legumes in grasslands. Within the model for snail diversity, cover of plant groups was replaced by their diversity (number). Since we assume abiotic factors to influence biotic substrates, we included an additional pathway between those two composites.

In order to understand the underlying mechanisms behind the effects of three composite variables, we also analyzed a structural equation model including all possible interactions between the individual abiotic factors, land-use factors, and biotic substrates. After testing the full model, we used a stepwise deletion of paths when the model structure did not fit the data, indicated by low regression weights and χ^2 statistics (Grace 2006). We successively excluded correlations with path coefficients lower than 0.1 until no further significant improvement was achieved.

To test for geographical differences, additional structural equation models were analyzed for the three regions separately. The latent (=unmeasured) variable land-use was added to describe the combined land-use effects of either forests or grasslands and to account for correlations between different land-use modes in different regions (Simons et al. 2014). Structural equation modeling was performed in lavaan (Rosseel 2012). All included parameters were *z*-transformed prior to analyses to obtain homogeneity of variances, and predictor values for the community composition analyses were calculated based on the factor loading of one-dimensional principal component analyses (PCAs) of the plot's environmental parameters (each region and habitat separately) using vegan (Oksanen et al. 2018). Prior to PCAs, all parameters were min–max-normalized to transform them to the same scale (between 0 and 1). The model fits of SEMs were estimated as overall model *P*-value which indicates whether the covariance matrix defined by the model is significantly different from the covariance matrix of the original data ($P < 0.05$ = poor model fit) or not ($P > 0.05$ = good model fit; Grace 2006).

RESULTS

Land snail communities

In total, we found 15,607 snail individuals (4243 individuals in the Swabian Alb, 3790 individuals in the Hainich, and 7574 individuals in the Schorfheide, respectively) of 71 species in 50 genera and 26 families (systematics follows Wiese 2016; Table 1). Generally, mean densities of snail individuals per square meter were highest in grassland plots (1028 ± 1611 m^2) and lowest in forest plots (75 ± 65 m^2) in the Schorfheide, whereas the other regions had intermediate abundances between 215 ± 380 and

Table 1. Species list of snails and their mean species abundances (Ind/m^2) in forests (F) and grasslands (G) in the Swabian Alb, the Hainich-Dün, and the Schorfheide-Chorin.

	Alb		Hainich		Schorfheide		Red list status for Germany
Species	F	G	F	G	F	G	
Aciculidae							
Platyla polita (Hartmann, 1840)	3.9	0.1	0.2	0	0	0	3
Carychiidae							
Carychium sp. (*minimum/tridentatum*)	33.6	1.6	8.1	0.1	0.3	22.3	*
Succineidae							
Succinella oblonga (Draparnaud, 1801)	0.4	4.1	0	1.2	0	0.4	*
Succinea putris (Linnaeus, 1758)	0	0	0	0	0	24.3	*
Cochlicopidae							
Cochlicopa sp.	1.2	0.2	0	0	0	7.5	
Cochlicopa lubrica (Müller, 1774)	7.4	14.9	1.6	6	0.7	41.8	*
Cochlicopa lubricella (Porro, 1838)	0	0.2	0	0	0	0	V
Vertiginidae							
Columella aspera Waldén, 1966	0.2	0	0	0	0	0	*
Truncatellina cylindrica (Férussac, 1807)	0	1.2	0	0.2	0	0	3
Vertigo sp.	0	1	0	0	0.4	2.4	
Vertigo angustior Jeffreys, 1830	0.2	0	0	0	0	5.4	3†
Vertigo antivertigo (Draparnaud, 1801)	0	0.1	0	0	0	14.3	V
Vertigo pygmaea (Draparnaud, 1801)	0	9.2	0.4	6.4	1.5	27.8	*
Vertigo substriata (Jeffreys, 1833)	0	0.2	0	0	0.5	0	3
Chondrinidae							
Abida secale (Draparnaud, 1801)	0	0.1	0	0	0	0	G
Granaria frumentum (Draparnaud, 1801)	0	1.8	0	0	0	0	2
Valloniidae							
Acanthinula aculeata (Müller, 1774)	6.4	0.1	2.7	0.1	1.8	0	*
Vallonia sp.	0	25.9	0	41.5	1.3	104.4	
Vallonia costata (Müller, 1774)	0.1	21.1	0	16.4	0.2	4.3	*
Vallonia enniensis (Gredler, 1856)	0	0.2	0	0	0	8.8	1
Vallonia excentrica Sterki, 1893	0.4	25.1	4.1	89.1	0	24.1	*
Vallonia pulchella (Müller, 1774)	1.1	24.7	2.1	18.4	2.5	332.4	*
Pupillidae							
Pupilla sp.	0	5.2	2	20.1	0	46.6	
Pupilla muscorum (Linnaeus, 1758)	0	14.2	0	12.1	0.2	64.1	V
Pupilla pratensis (Clessin, 1871)‡	0	0	0	0	0	51.9	R
Enidae							
Enidae	0.2	0	0.4	0	0	0	
Ena montana (Draparnaud, 1801)	0.7	0	0.9	0	0	0	V
Clausiliidae							
Clausiliidae	0.9	0	0.7	0	0.5	0	
Clausilia bidentata (Strøm, 1765)	0	0	2.1	0	0.4	0	*
Cochlodina laminata (Montagu, 1803)	1.1	0	3.7	0.1	0	0	*
Macrogastra plicatula (Draparnaud, 1801)	0.2	0	0	0	0	0	V
Macrogastra ventricosa (Draparnaud, 1801)	0.4	0.2	0.9	0	0	0	*
Ferrussaciidae							
Cecilioides acicula (Müller, 1974)	0	0.2	0	0.2	0	0.3	*
Punctidae							
Punctum pygmaeum (Draparnaud, 1801)	21.2	1.6	1.8	0.2	9.1	1.5	*
Patulidae							
Discus rotundatus (Müller, 1774)	36.5	1.9	21.5	0.7	6.3	0.3	*
Zonitidae							
Zonitoides nitidus (Müller, 1774)	0.2	0	0	0	0.2	0.1	*

(Table 1. Continued.)

Species	Alb		Hainich		Schorfheide		Red list status for Germany
	F	G	F	G	F	G	
Euconulidae							
Euconulus fulvus (Müller, 1774)	4.4	0	5.3	0	5.6	0.1	*
Oxychilidae							
Aegopinella sp.	3.4	0.3	0.7	0	0	0	
Aegopinella pura (Alder, 1830)	46.6	2.8	23.6	0.9	0.2	0	*
Aegopinella nitens (Michaud, 1831)	16.3	0.9	3.2	0.1	1.3	0.4	*
Aegopinella nitidula (Draparnaud, 1805)	0.7	0	1.8	0.2	0	0	*
Nesovitrea sp.	0	0.1	0	0	1.5	0	
Nesovitrea hammonis (Ström, 1765)	5.7	1.8	2.8	0.3	21.2	2.1	*
Nesovitrea petronella (Pfeiffer, 1853)	0	0	0	0	0.7	0	2
Oxychilidae	12.2	2.8	2.5	0.1	7.6	1	
Oxychilus alliarius (Miller, 1822)	0.2	0	0.4	0	0	0	V
Oxychilus draparnaudi (Beck, 1837)	0	0.2	2.3	0	0	0	*
Oxychilus cellarius (Müller, 1774)	0	0	21.8	0	0	0	*
Pristilomatidae							
Vitrea sp.	1.9	0.1	1.8	0	0.2	0	
Vitrea contracta (Westerlund, 1871)	10.4	0.7	3.6	0.1	0.4	0	*
Vitrea crystallina (Müller, 1974)	2.7	0	2	0	0	0	*
Vitrea diaphana (Studer, 1820)	0	0	3.7	0.2	0	0	G
Vitrinidae							
Vitrinidae	0.9	0.7	0.7	1.5	0	2.6	
Eucobresia diaphana (Draparnaud, 1805)	0	0	0.2	0	0	0	*
Vitrina pellucida (Müller, 1774)	0	0.7	0	0.7	0.5	0.3	*
Vitrinobrachium breve (Férussac, 1821)	0.4	0	0	0	0	0	*
Bradybaenidae							
Fruticicola fruticum (Müller, 1774)	0	0	0	0.1	0	0	*
Helicodontidae							
Helicodonta obvoluta (Müller, 1774)	3.7	0.1	10	0	0	0	*
Hygromiidae							
Hygromiidae	3.9	1.6	0.2	0.3	0	0.7	
Candidula unifasciata (Poiret, 1801)	0	3.9	0	0.7	0	0	2
Euomphalia strigella (Draparnaud, 1801)	0.4	0	0	0	0	0	G
Helicella itala (Linnaeus, 1758)	0	0.8	0	2	0	0	3
Monacha cartusiana (Müller, 1774)	0	0	0.4	3.1	0	0.4	*
Monachoides incarnatus (Müller, 1774)	2.8	0.2	18.1	0.1	0	0	*
Pseudotrichia rubiginosa (Rossmässler, 1838)	0	0	0	0	0	36.9	2
Trochulus sp.	0.7	0.2	0.4	0	0	6.6	
Trochulus striolatus (Pfeiffer, 1828)	3.9	0.1	0	0	0	0	V
Trochulus hispidus (Linnaeus, 1758)	1.2	5.9	1.2	1.4	0	15	*
Trochulus sericeus (Draparnaud, 1801)	1.8	0.9	0.4	0.4	0	0	*
Urticicola umbrosus (Pfeiffer, 1828)	0	0	0.2	0	0	0	V
Helicidae							
Helicidae	0	0	0	0	0	0.3	
Arianta arbustorum (Linnaeus, 1758)	0.7	0	3.6	0	0	0	*
Cepaea sp.	1.2	0	2.7	0.4	0	0.1	
Cepaea hortensis (Müller, 1774)	0.2	0.1	12.8	0.2	0	0	*
Cepaea nemoralis (Linnaeus, 1758)	0	0	10	0	0	0	*
Helix pomatia Linnaeus, 1758	0	0	15.8	0.6	0	0	*
Isognomostoma isognomostomos (Schröter, 1784)	0.9	0	0.4	0	0	0	*
Valvatidae							
Valvata cristata Müller, 1774	0	0.3	0	0	0	23.7	G
Valvata piscinalis (Müller, 1774)	0	0	0	0	0	0.6	V

(Table 1. Continued.)

Species	Alb		Hainich		Schorfheide		Red list status for Germany
	F	G	F	G	F	G	
Bithyniidae							
Bithynia tentaculata (Linneaus, 1758)	0	0	0	0	0	4.6	*
Planorbidae							
Bathyomphalus contortus (Linnaeus, 1758)	0.2	0	0	0	0	0	*
Gyraulus crista (Linnaeus, 1758)	0	0	0	0	0	2.4	*
Planorbis carinatus Müller, 1773	0	0	0	0	0	0.9	2
Planorbis planorbis (Linnaeus, 1758)	0	0	0	0	0	2.4	*
Segmentina nitida (Müller, 1774)	0	0	0	0	0	0.6	3
Lymnaeidae							
Galba truncatula (Müller, 1774)	0	0	0	0	0	12.5	*

Notes: Red list abbreviations are as follows: *, no current risk of loss (least concern); G, endangered to unknown extent; R, very rare; V, near threatened; 1, critically endangered; 2, endangered; 3, vulnerable.

† *V. angustior* is listed on the FFH guideline number 1014.

‡ *P. alpicola* following Nekola et al. 2015.

Table 2. Statistical results of type III ANOVA for (A) snail abundances, habitat (forest vs grassland), and region (Swabian Alb, Hainich-Dün, Schorfheide-Chorin), and (B) Shannon diversity, habitat (forest vs grassland), and region (Swabian Alb, Hainich-Dün, Schorfheide-Chorin).

Variable	sum sq	df	*F*	*P*
(A) Abundance (sqrt), ANOVA type III				
Abundance	16982.1	1	187.251	**<0.001**
Habitat	915.2	1	10.096	**0.0017**
Region	2809.2	2	15.488	**<0.001**
Habitat:Region	5637.0	2	31.078	**<0.001**
(B) Shannon diversity, ANOVA type III				
Abundance	164.753	1	517.238	**<0.001**
Habitat	0.963	1	3.024	0.0832
Region	23.261	2	36.514	**<0.001**
Habitat:Region	13.660	2	21.443	**<0.001**

370 ± 155 m^2 (Table 2A, Fig. 1A). While in the Schorfheide, grasslands had over ten-fold higher densities of snails compared to forests (ANOVA, $F_{1,81} = 23.74$, $P < 0.001$), the reverse trend was found for the Alb, where the total number of individuals in forests significantly exceeded the number of individuals in grasslands (Swabian Alb, $F_{1,98} = 14.631$, $P < 0.001$); in the Hainich, density was similar between the habitats.

Diversity of land snails also significantly differed among habitats and regions (Table 2B), mostly consistent with their densities. While in the Schorfheide, grassland plots showed higher diversity ($F_{1,81} = 22.924$, $P < 0.001$), diversity in forests exceeded those of grasslands in the other two regions (Alb: $F_{1,98} = 4.801$, $P = 0.031$; Hainich: $F_{1,98} = 8.711$, $P = 0.004$).

The community composition of land snails differed among habitats and across regions (Fig. 2; PERMANOVA: Exploratory × Habitat, $r^2 = 0.08$, $P < 0.0001$). In general, grassland communities were slightly more similar to one another than forest communities (PERMDISP: $F_{1,\ 275} = 4.27$, $P = 0.040$). Forests in the Schorfheide had the most distinct species composition (Fig. 2A, blue squares), and certain grassland plots in this region also harbored several freshwater snail species (*Valvata cristata*, *V. piscinalis*, *Bithynia tentaculata*, *Bathyomphalus contortus*, *Gyraulus crista*, *Planorbis carinatus*, *P. planorbis, Segmentina nitida*, *Galba truncatula*; Table 1). In addition, grassland plots in the Swabian Alb and the Schorfheide were inhabited by *Vallonia enniensis* (Gredler, 1856) being on the red list for Germany with status 1, and by *Vertigo angustior* Jeffreys, 1830, a species that is protected by the FFH guideline as species #1014.

Within each region, forest and grassland snail communities were clearly separated (Fig. 2B–D; PERMANOVA: $r^2 = 0.17$, $P < 0.0001$). While 18 species were exclusively found in forest habitats, 21 species inhabited grassland areas only. While typical snail species in grasslands in the Swabian Alb and Hainich were species of the genus *Vallonia* and the species *Vertigo pygmaea*, forests were

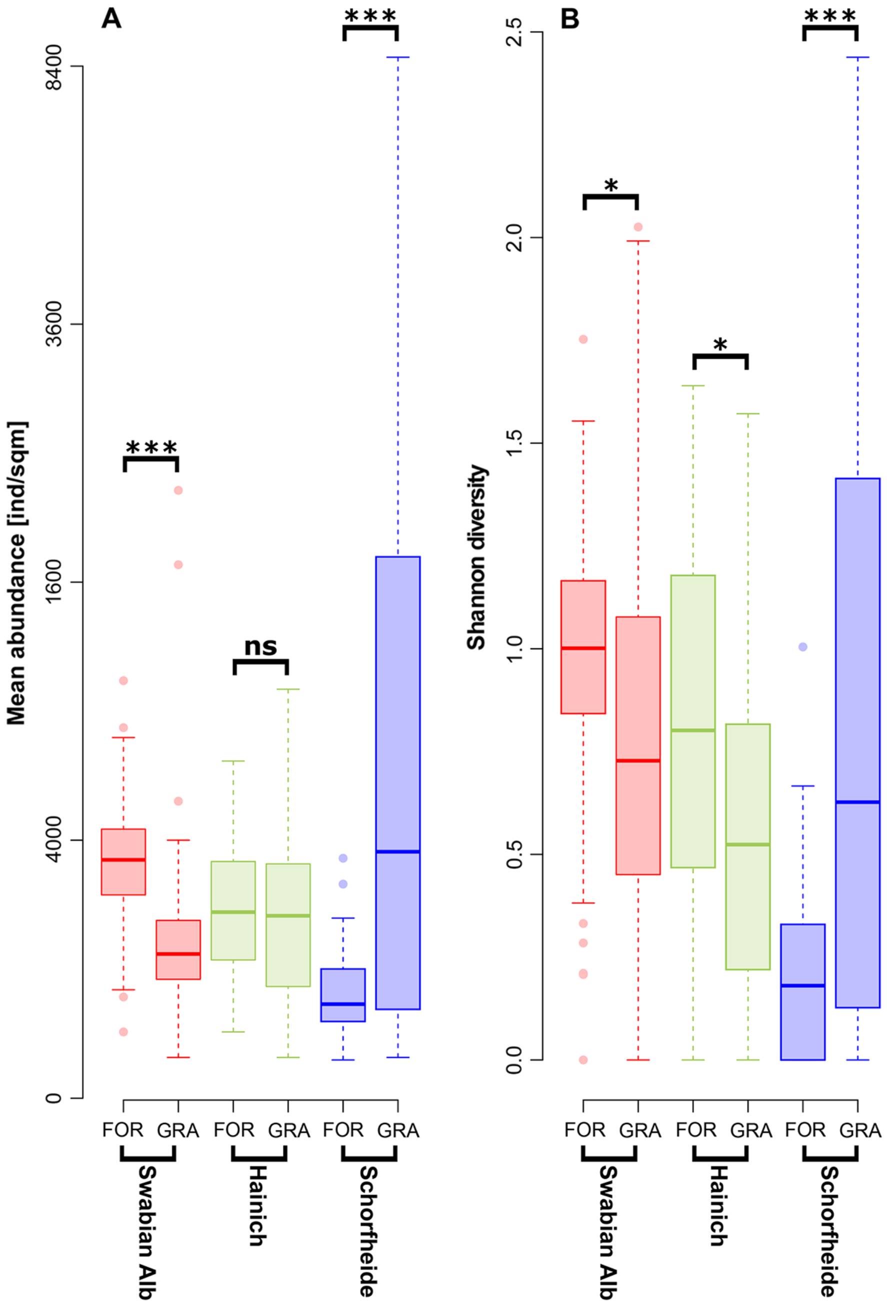
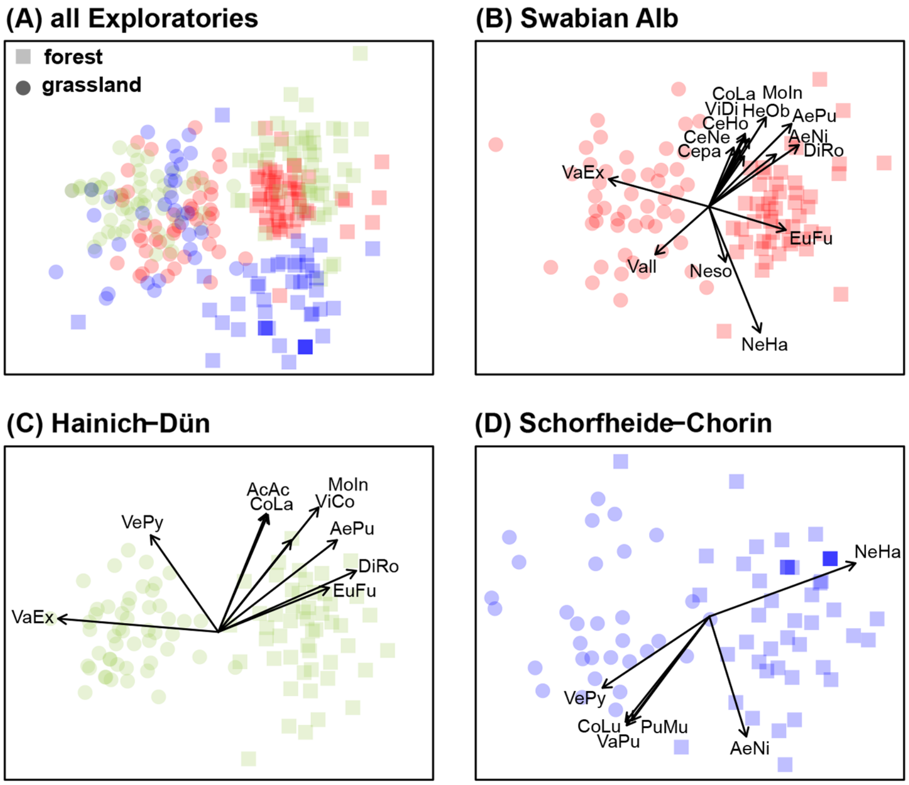


Fig. 1. Snail abundances and diversity in different habitats and regions. (A) Mean abundances of snail individuals per square meter (Ind/m^2) and (B) Shannon diversity in forest (FOR) and grassland (GRA) habitats in the Swabian Alb, the Hainich-Dün, and the Schorfheide-Chorin. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$; ns, not significant.

characterized by the genera *Aegopinella* and *Carychium*, and the species *Discus rotundatus*, *Euconulus fulvus*, *Monachoides incarnatus*, *Nesovitrea*, and *Vitrea* (Fig. 2B, C). In contrast, Schorfheide had only two structuring species in forests (*Aegopinella nitens* and *Nesovitrea hammonis*) but four in grasslands (*Cochlicopa lubrica*, *Pupilla muscorum*, *Vallonia pulchella*, and *Vertigo pygmaea*; Fig. 2D).


(A) all Exploratories

(B) Swabian Alb

(C) Hainich–Dün

(D) Schorfheide–Chorin

Fig. 2. Non-metric multidimensional scaling (NMDS) community analysis of (A) all three regions (2D-stress: 0.17), (B) the Swabian Alb (red; 2D-stress: 0.19), (C) Hainich-Dün (green; 2D-stress: 0.16), and (D) Schorfheide-Chorin (blue; 2D-stress: 0.15). Dots represent grassland plots and squares forest plots; snail species are specific for a certain habitat or region. Abbreviations are as follows: AcAc, *Acanthinula aculeata*; AeNi, *Aegopinella nitens*; AePu, *Aegopinella pura*; Cepa, *Cepaea* sp.; CeHo, *Cepaea hortensis*; CeNe, *Cepaea nemoralis*; CoLa, *Cochlodina laminata*; CoLu, *Cochlicopa lubrica*; DiRo, *Discus rotundatus*; EuFu, *Euconulus fulvus*; HeOb, *Helicodonta obvoluta*; MoIn, *Monachoides incarnatus*; Neso, *Nesovitrea* sp.; NeHa, *Nesovitrea hammonis*; PuMu, *Pupilla muscorum*; Vall, *Vallonia* sp.; VaEx, *Vallonia excentrica*; VePy, *Vertigo pygmaea*; ViCo, *Vitrea contracta*; ViDi, *Vitrea diaphana*.

Influence of land-use factors, abiotic parameters and biotic substrates

In forests, variation in abiotic factors had a 2.5 times higher influence on snail density than biotic substrates and even 64 times higher than land-use intensity (Fig. 3A, Table 3). Snail diversity was also strongly affected by biotic substrate, but also the influence of abiotic factors exceeded direct land-use impacts 11-fold (Fig. 3B, Table 3). The relative influence of abiotic factors and biotic substrate on snail community composition was comparably high, and about four times higher than land-use intensity (Fig. 3C, Table 3). In grasslands, the relative influence of abiotic factors and biotic substrate was similar on snail density, diversity, and community structure (Fig. 4A–C, Table 3). The impact of land-use management was on average seven times lower than those of abiotic and biotic factors.

To further elucidate direct and indirect effects of single components of the composite variables abiotic, management and biotic substrate on the snail assemblages, additional SEM analyses were performed (Figs. 5, 6). Snail densities in forests were directly positive and significantly affected by soil pH (abiotic) and the cover of litter (biotic substrate) and indirectly by the proportion of wood harvested (positively) via pH and the proportion of non-native trees (negatively) via the cover of litter (Fig. 5A). Snail diversity in forests was mainly directly affected by soil pH (positive) and negatively by the proportion of non-native

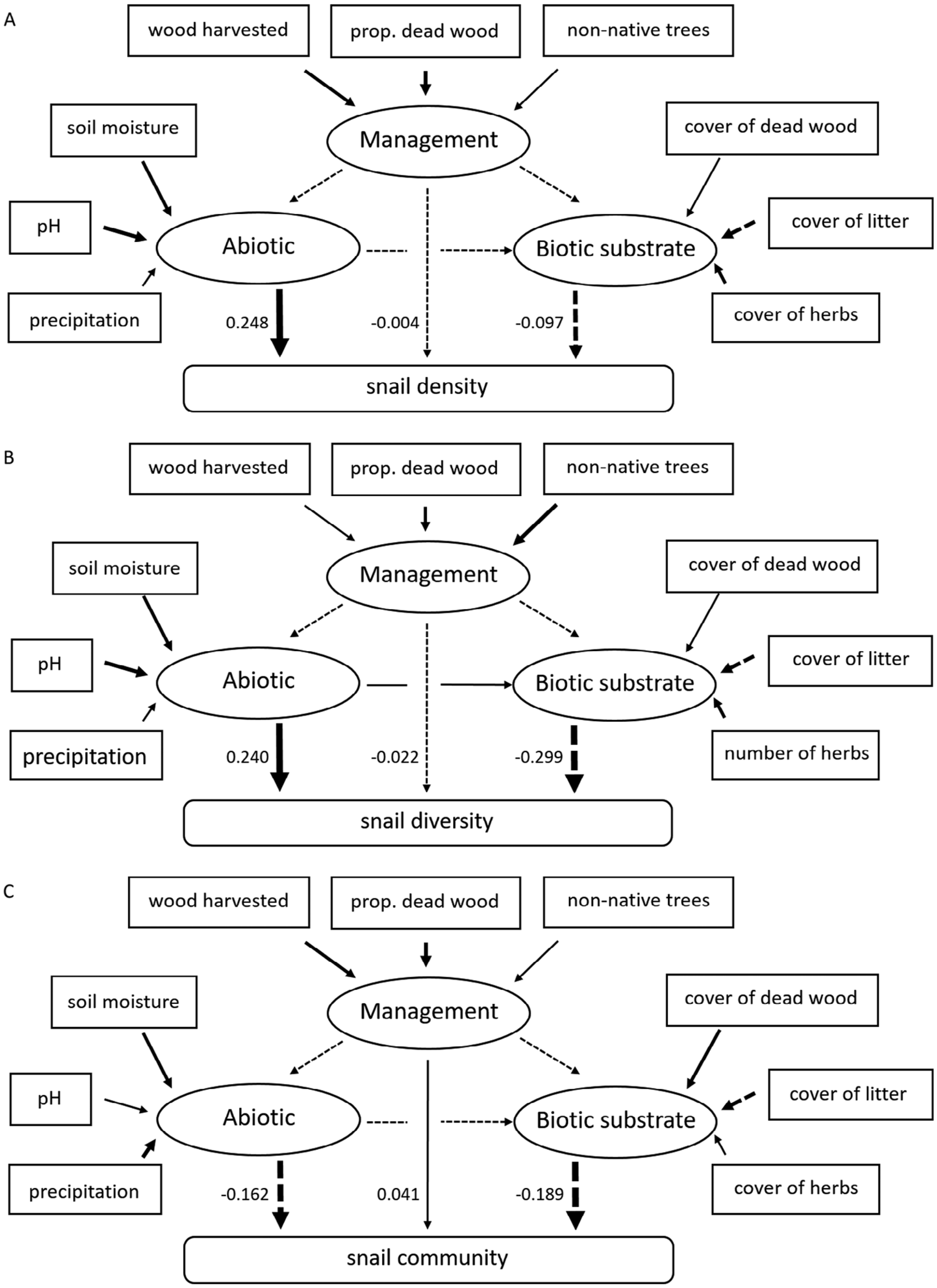


Fig. 3. Structural equation modeling testing the influences of abiotic factors, land-use management, and biotic substrates in forests on snail densities (A, χ^2 = not available; $\chi^2 = 27.561$, df = 30, $P = 0.594$), diversity (B, $\chi^2 = 91.981$, df = 30, $P = 0.000$), and snail community structure (C, $\chi^2 = 105.198$, df = 30, $P = 0.000$). The composite variables Abiotic, Management, and Biotic substrate comprise three measured parameters each, based on a combined dataset of three regions (Swabian Alb, Hainich-Dün, and Schorfheide-Chorin).

Table 3. Percentage of the direct influence of abiotic factors, land-use management, and biotic substrate on snail density, diversity, and community structure in forests and grasslands based on 278 plots.

Habitat	Variable	Abiotic	Management	Biotic substrate
Forest	Density	71.1	1.1	27.8
	Diversity	42.8	3.9	53.3
	Community	41.3	10.5	48.2
Grassland	Density	47.5	8.5	42.7
	Diversity	47.0	6.7	46.3
	Community	48.8	3.9	47.3

tress and indirectly by the proportion of wood harvested (positive) via pH and the cover of litter (Fig. 5B). However, SEM pathway structure for snail community composition was most complex; hence, no significant direct effects were observed (Fig. 5C). The proportion of wood harvested again affected the snail community positively via influencing soil pH.

Generally, SEM pathway structures in grasslands were less complex than those in forests. Soil pH had a significant positive and cover of legumes a significant negative direct effect on snail density (Fig. 6A). While soil moisture and cover of grasses showed a direct but not significant negative effect on snail densities, land-use parameters only had non-significant indirect influences (mowing on soil moisture and the cover of legumes, grazing on soil moisture and the cover of grasses, and fertilization on pH and the cover of legumes). On the other hand, snail diversity in grasslands was positively influenced by soil pH and mowing while biotic substrates had no impact (Fig. 6B). Snail community composition was also positively affected by soil pH and directly negative by fertilization (Fig. 6C). While soil moisture and cover of grasses also directly but not significantly influenced snail community composition, mowing and grazing weakly and non-significantly acted indirectly via soil moisture, soil pH, the cover of grasses, and the cover of legumes.

To test whether the influence pattern of abiotic factors, land-use management, and biotic substrates was consistent among regions, we separately performed SEM analyses for the Swabian Alb, the Hainich, and the Schorfheide. To account for different land-use management types in different regions, land-use factors were combined to a latent variable (see *Materials and Methods*). Generally, regions differed in strength and direction of interaction pathways in both forest and grassland habitats (Tables 4, 5, respectively). For example, the proportion of non-native trees in a forest plot significantly increased the ground cover of deadwood in the Swabian Alb and the Schorfheide but not in the Hainich. Furthermore, a strong negative effect of the proportion of non-native trees on soil moisture was only found in the Schorfheide. On the other hand, there were consistent effects of non-native trees on pH, the cover of litter, and the cover of herbs. Direct effects of parameters on either snail densities, diversity, or community composition were generally rare, however most numerous in the Swabian Alb (significant for the cover of litter and the cover/number of herbs). The proportion of deadwood cut with a saw was the only land-use parameter having a direct effect on snail densities in forests in the Hainich.

Indirect effects in grasslands were less consistent than in forests; only soil moisture affected snail diversity in all three regions and had a positive effect, albeit contradictory, on soil pH in the Swabian Alb and the Schorfheide. However, a consistent direct effect was found for soil pH on snail densities and at least partly on community structure.

DISCUSSION

In general, snail abundances and their local diversity varied across regions and among forest and grassland habitats. Highest values of abundances and diversity did not explicitly match to grassland or forest habitats but rather correlated with habitat conditions. Also the community composition of snail assemblages differed among regions—slightly in grasslands and clearly in forests—and each habitat had some unique inhabitants. While densities in the Swabian Alb and the Hainich correspond well to mean values found in the literature (100–1100 Ind/m^2 in European forests and 20–200 Ind/m^2 in open grasslands; Mörzer Bruijns et al. 1959, Baker 1968, Mason 1970), the Schorfheide with its very high snail densities in grasslands and low densities in forests seems to have more extreme environmental conditions, probably associated with soil types.

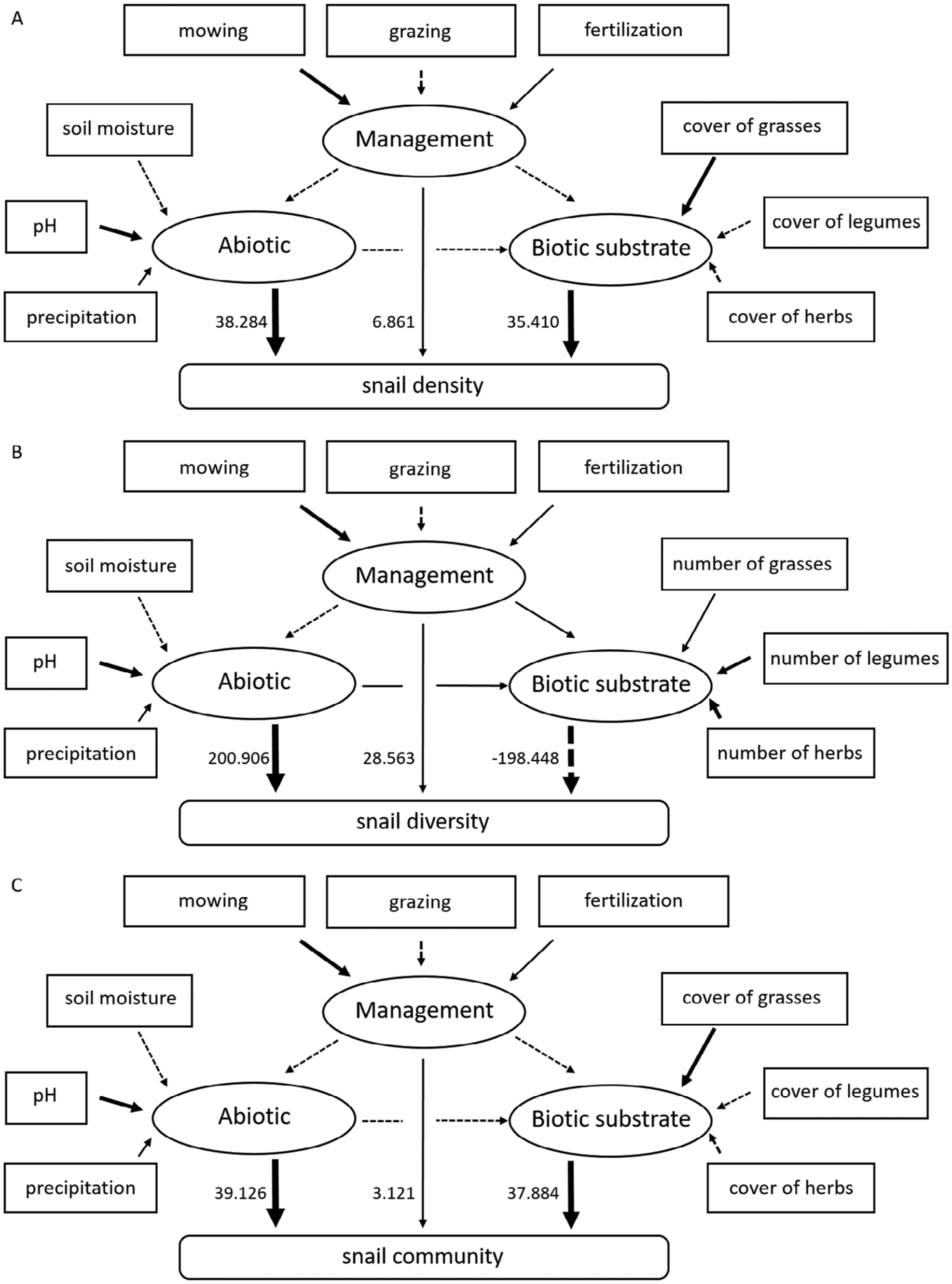


Fig. 4. Structural equation modeling testing the influences of abiotic factors, land-use management, and biotic substrates in grasslands on snail densities (A, $\chi^2 = 27.561$, df = 30, $P = 0.594$), diversity (B, grassland: χ^2 = not available), and snail community structure (C, grassland: $\chi^2 = 24.391$, df = 30, $P = 0.754$). The composite variables Abiotic, Management, and Biotic substrate comprise three measured parameters each, based on a combined dataset of three regions (Swabian Alb, Hainich-Dün, and Schorfheide-Chorin).

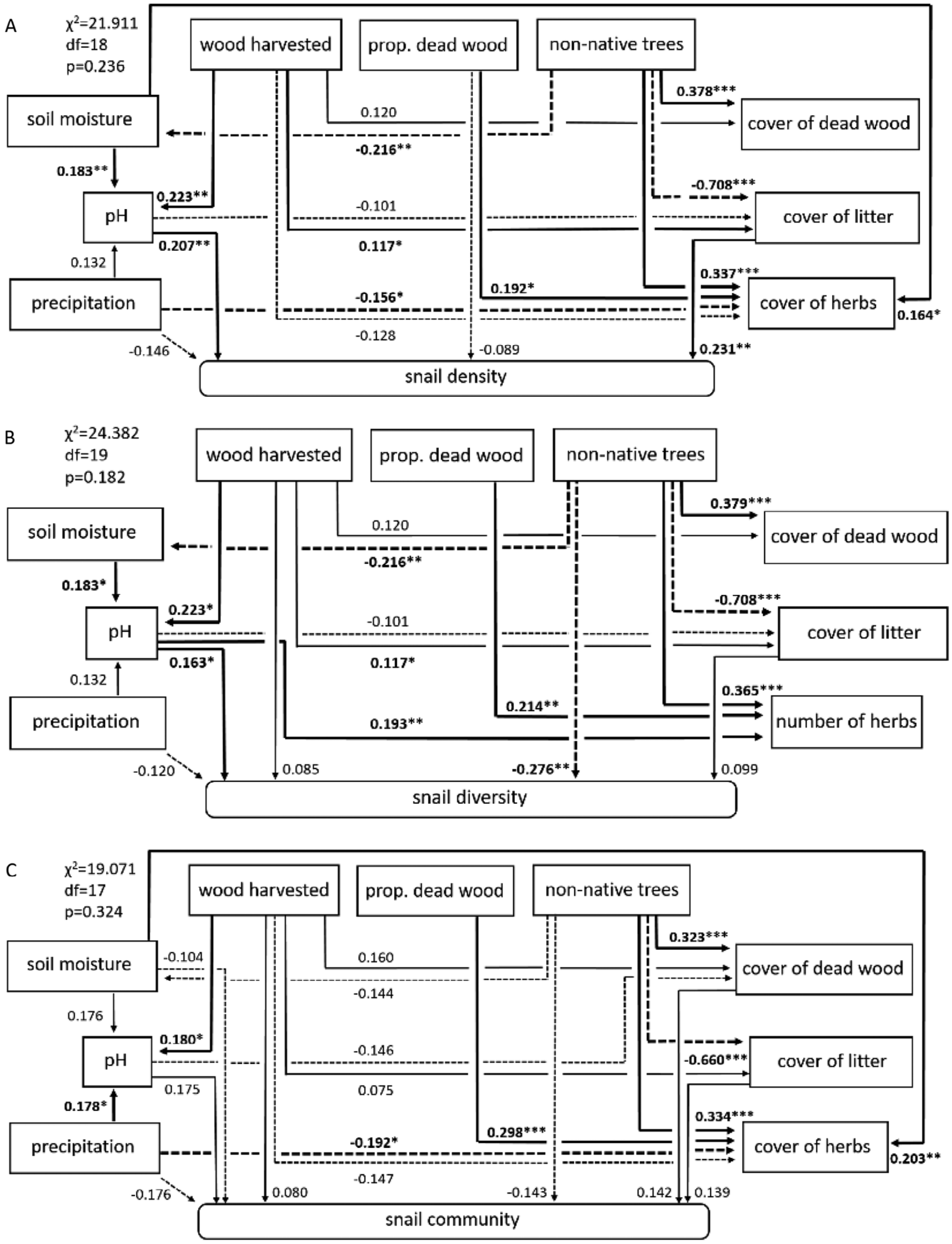


Fig. 5. Structural equation modeling analyses on a combined dataset of three regions (Swabian Alb, Hainich-Dün, and Schorfheide-Chorin). We tested the correlations between abiotic factors (soil moisture, pH, precipitation), land-use management (the proportion of wood harvested, the proportion of deadwood cut with a saw, the proportion of non-native trees), and biotic substrates (cover or number of litter, deadwood, and herbs) on snail density (A), diversity (B), and snail community (C) in forests. Continuous lines indicate a positive correlation and dashed lines a negative correlation. Significances are given in bold ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

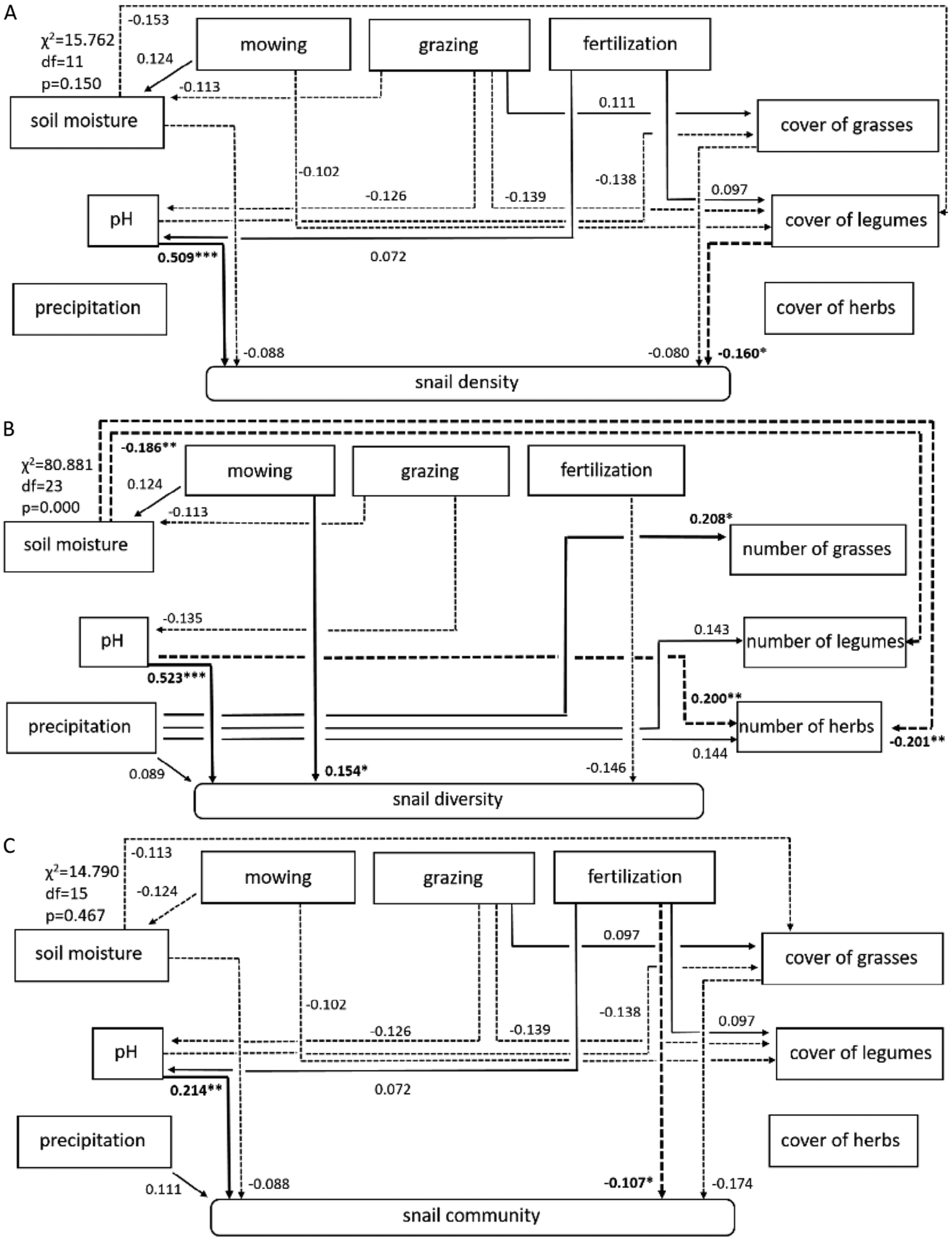


Fig. 6. Structural equation modeling analyses on a combined dataset of three regions (Swabian Alb, Hainich-Dün, and Schorfheide-Chorin). We tested the correlations between abiotic factors (soil moisture, pH, precipitation), land-use management (mowing, grazing, and fertilization in grasslands), and biotic substrates (cover or number of grasses, herbs, and legumes) on snail density (A), diversity (B), and snail community (C) in grasslands. Continuous lines indicate a positive correlation and dashed lines a negative correlation. Significances are given in bold ($^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$).

Table 4. Pathway coefficients of structural equational modeling analyses of forests in the Swabian Alb, the Hainich-Dün, and the Schorfheide-Chorin.

		Density			Diversity			Community		
Variable 1	Variable 2	Alb	Hai	Sch	Alb	Hai	Sch	Alb	Hai	Sch
	Chi-square	9.126	19.546	44.404	23.786	18.464	30.77	13.522	19.465	49.303
	df	18	19	22	21	18	21	19	18	22
	P	0.957	0.422	0.003	0.304	0.425	0.078	0.811	0.364	0.001
Land-use forest	Wood harvested	**0.439**	0.275		**0.439**	0.275		**0.439**	0.275	
Land-use forest	Prop. Deadwood	**1.058**	2.101		**1.058**	2.101		**1.059**	2.101	
Land-use forest	Non-native trees	0.316	0.086		0.316	0.086		0.316	0.086	
Cover of deadwood	Wood harvested	0.208	0.175		0.191	0.175		0.191	0.175	
Cover of deadwood	Prop. Deadwood	−0.214			−0.202			−0.203		
Cover of deadwood	Non-native trees	0.483		**0.541**	**0.495**		**0.543**	**0.495**		**0.519**
Cover of deadwood	Soil moisture	−0.093	−0.170		−0.127	−0.170		−0.127	−0.170	
Cover of deadwood	pH	−0.223	0.157	0.184	−0.190	0.157	0.186	−0.191	0.157	0.189
Cover of deadwood	Precipitation		−0.111	**−0.253**		−0.111	**−0.253**		−0.111	**−0.270**
Cover of litter	Wood harvested	0.135		0.157	0.136		0.157	0.136		0.175
Cover of litter	Prop. Deadwood									
Cover of litter	Non-native trees	**−0.732**	**−0.430**	**−0.823**	**−0.732**	**−0.430**	**−0.823**	**−0.732**	**−0.430**	**−0.806**
Cover of litter	Soil moisture									
Cover of litter	pH		**−0.267**	−0.161		**−0.267**	−0.161		**−0.267**	−0.167
Cover of litter	Precipitation		**0.267**			**0.264**			**0.264**	
Cover/number of herbs	Wood harvested	**−0.275**		−0.182		0.165	−0.181	**−0.275**		−0.170
Cover/number of herbs	Prop. Deadwood	0.222	**0.362**		**0.236**	0.249		0.222	**0.362**	
Cover/number of herbs	Non-native trees	**0.279**	**0.574**	**0.292**	**0.575**	**0.573**	0.177	**0.279**	**0.574**	**0.300**
Cover/number of herbs	Soil moisture	**0.228**	0.220			0.243		**0.228**	0.220	
Cover/number of herbs	pH		−0.231	0.156	0.173	−0.168	**0.443**		−0.231	0.156
Cover/number of herbs	Precipitation	**−0.231**		−0.145			−0.223	**−0.231**		−0.125
Soil moisture	Wood harvested		0.160	−0.148		0.160	−0.147		0.160	−0.123
Soil moisture	Prop. Deadwood									
Soil moisture	Non-native trees		−0.205	**−0.398**		−0.205	**−0.401**		−0.205	**−0.352**
Soil moisture	Precipitation									
pH	Wood harvested	0.225		0.216	0.225		0.216	0.215		0.215
pH	Prop. Deadwood									
pH	Non-native trees	**−0.413**	**0.530**	**−0.272**	**−0.413**	**0.530**	**−0.272**	**−0.418**	**0.530**	**−0.266**
pH	Precipitation	0.160	**0.274**		0.160	**0.274**		0.164	**0.274**	
pH	Soil moisture		**0.504**			**0.504**		−0.082	**0.504**	
Snail trait	Wood harvested		0.223		0.151	0.269			0.133	
Snail trait	Prop. Deadwood		**−0.444**			−0.115		−0.127		
Snail trait	Non-native trees	−0.159	0.221		−0.331		−0.164	−0.093	−0.346	−0.301
Snail trait	Soil moisture	0.226			0.110				**−0.342**	0.192
Snail trait	pH	**0.282**			0.222	0.165			**0.386**	
Snail trait	Precipitation	−0.121	0.149	−0.181		−0.114	**−0.230**	−0.191	−0.141	0.093
Snail trait	Cover of deadwood		−0.101			**−0.205**		0.213		
Snail trait	Cover of litter		0.095	**0.625**	**−0.354**	0.176	**0.413**	**0.401**	−0.146	0.260
Snail trait	Cover/number of herbs	−0.235	0.213	**0.528**	**−0.422**	−0.157	**0.269**	**−0.234**	0.267	0.113

Notes: We included the abiotic factors soil moisture, soil pH, and precipitation; the land-use management factors proportion of wood harvested, proportion of deadwood cut with a saw, and proportion of non-native trees; and biotic substrates cover or number of litter, dead wood, and herbs. Bold values indicate significant interactions ($P < 0.05$).

While grasslands in the Schorfheide occur mostly on highly organic soils, those of the other regions occur on less organic soils (Socher et al. 2012). Furthermore, also historical biogeographical events (Limondin-Lozouet and Preece 2014) and ancient regional land-use changes (Corsmann 1990) can sustainably affect land snail assemblages. In addition, marsh areas with a high level of groundwater in the Schorfheide enable the establishment of a freshwater snail community which has not been found in any of the other two regions. Furthermore, most of these species brave dry periods by a high desiccation tolerance (Falkner et al. 2001). However, the portion of freshwater specimens was only 1.5% of all specimens found.

Table 5. Pathway coefficients of structural equational modeling analyses of grasslands in the Swabian Alb, the Hainich-Dün, and the Schorfheide-Chorin.

		Density			Diversity			Community		
Variable 1	Variable 2	Alb	Hai	Sch	Alb	Hai	Sch	Alb	Hai	Sch
	Chi-square	9.95	27.302	20.02	56.437	52.185	3.539	5.497	27.124	20.013
	df	23	19	22	19	17	18	18	19	23
	P	0.992	0.098	0.582	0.000	0.000	1.000	0.998	0.102	0.641
Land-use grassland	Mowing	**1.045**	1.498	2.737	**1.045**	1.498	2.737	**1.045**	1.498	2.737
Land-use grassland	Grazing	**−0.437**	−0.243	−0.195	**−0.437**	−0.243	−0.195	**−0.437**	−0.243	−0.195
Land-use grassland	Fertilization	**0.546**	0.437	−0.085	**0.546**	0.437	−0.082	**0.546**	0.437	−0.082
Cover/nr of grasses	Mowing		−0.120		0.208	**0.434**	**−0.415**		−0.120	
Cover/nr of grasses	Grazing	0.153	0.193	0.138		−0.083	−0.224	0.158	0.193	0.138
Cover/nr of grasses	Fertilization	0.125	0.235	−0.261		**−0.591**	−0.125	0.146	0.235	−0.261
Cover/nr of grasses	Soil moisture	−0.121			−0.118	**0.405**	0.024	−0.120		
Cover/nr of grasses	pH	**−0.398**	−0.219	0.301	−0.108			**−0.396**	−0.219	0.301
Cover/nr of grasses	Precipitation	**−0.229**	**0.397**		**0.386**			**−0.234**	**0.379**	
Cover/nr of legumes	Mowing		−0.052			**0.451**	−0.174		−0.052	
Cover/nr of legumes	Grazing	−0.091	−0.148	−0.243	**−0.276**	−0.138		−0.092	−0.148	−0.243
Cover/nr of legumes	Fertilization			**0.333**		**−0.566**	0.141			**0.333**
Cover/nr of legumes	Soil moisture		−0.113	−0.311	**−0.257**	**0.235**	**−0.462**		−0.113	−0.311
Cover/nr of legumes	pH			−0.213			−0.217			−0.213
Cover/nr of legumes	Precipitation	0.170			**0.283**	−0.129		0.171		
Cover/nr of herbs	Mowing	−0.090	0.254			**0.533**		−0.095	0.254	
Cover/nr of herbs	Grazing			−0.148						−0.149
Cover/nr of herbs	Fertilization		**−0.337**			**−0.558**	0.128		**−0.337**	
Cover/nr of herbs	Soil moisture	0.197	0.181	−0.182	**−0.234**	0.188	−0.230	0.205	0.181	−0.182
Cover/nr of herbs	pH	**0.310**			**0.286**	**0.272**	−0.104	**0.292**		
Cover/nr of herbs	Precipitation		−0.225	0.119	**0.414**	−0.178	−0.167		−0.225	0.119
Soil moisture	Mowing		0.174			0.174			0.174	
Soil moisture	Grazing	−0.135	0.134	**−0.599**	−0.135	0.134	**−0.599**	−0.135	0.134	**−0.599**
Soil moisture	Fertilization									
Soil moisture	Precipitation									
pH	Mowing	−0.192			−0.192			−0.192		
pH	Grazing		−0.156			−0.156			−0.156	
pH	Fertilization	0.186		0.228	0.186		0.228	0.186		0.228
pH	Precipitation		0.180	−0.213		0.180	−0.213		0.180	−0.213
pH	Soil moisture	**−0.249**		**0.643**	**0.249**		**0.643**	**−0.249**		**0.643**
Snail trait	Mowing				0.120		0.212		0.227	
Snail trait	Grazing		0.118	−0.125	−0.171		−0.125			
Snail trait	Fertilization			−0.187	−0.127		−0.136	−0.200	−0.258	
Snail trait	Soil moisture	−0.202	−0.131		**−0.339**	−0.116		−0.211	0.093	
Snail trait	pH	**0.485**	**0.308**	**0.636**	**0.384**	**0.356**	**0.645**	0.228		**0.318**
Snail trait	Precipitation		**0.386**		0.117	**0.232**		0.206	0.139	0.115
Snail trait	Cover/nr of grasses		**−0.425**		−0.182				**−0.506**	−0.276
Snail trait	Cover/nr of legumes	−0.095	0.112	−0.135		**0.264**	0.129			−0.183
Snail trait	Cover/number of herbs	−0.149	−0.147	0.182	0.186				**−0.339**	

Notes: We included the abiotic factors soil moisture, soil pH, and precipitation; the land-use management factors mowing, grazing, and fertilization; and the biotic substrates number of grasses, herbs, and legumes. Bold values indicate significant interactions ($P < 0.05$). nr, number.

Land snails are usually characterized by a low mobility and a non-migratory behavior which make them vulnerable to changing environmental conditions (Baur and Baur 1988, Douglas et al. 2013). Factors influencing snail abundances, snail diversity, and community composition in different habitats of different regions comprise abiotic parameters, differences in land-use management, and biotic substrates. While abiotic and biotic factors have been frequently linked to snail assemblages (Caldwell 1993, Martin and Sommer 2004*a*, *b*, Hylander et al. 2005, Horsák 2006, Douglas et al. 2013), variation in land-use intensity of different management types has been rarely studied. Results of our study indicate that direct effects (e.g., those that destroy shells by trampling or wood harvesting, those that destroy biotopes) of land-use factors on snail densities, diversity, and community structure in forests and grasslands exist, but that they are of minor importance as compared to abiotic and biotic parameters. However, additional indirect effects occur, allowing land-use factors to act via abiotic (i.e., soil pH) and/or biotic substrate parameters (i.e., cover of litter or cover of grasses), also indirectly affecting regional microclimate, water resources, soil properties, vegetation characteristics, and other environmental parameters.

Therefore, land-use factors and environmental parameters are not independent from each other, but changes in one factor directly or indirectly influence another which has also indirect effects on snail assemblages. In our study, the proportion of non-native trees on our EPs, which is defined by the proportion of planted coniferous trees (pine trees in the Schorfheide and spruce in the Swabian Alb and Hainich; Fischer et al. 2010), influenced soil moisture and the soil cover (deadwood) in general and had an impact on the cover of herbs and soil pH in three regions. Although the direct effects of non-native trees by providing a different kind of litter substrate on snail assemblages were non-significant, coniferous trees acted indirectly via changing environmental conditions. Former studies also show that mollusk communities are more abundant and species-rich in broad-leaved than in coniferous forests (Wäreborn 1969), which also correlates with the calcium conditions. Coniferous trees have a lower leaf calcium content than broad-leaved trees and therefore influence the calcium content of the upper soil horizon (Vesterdal and Raulund-Rasmussen 1998).

In addition, the proportion of timber harvesting also mediates changes in soil calcium (Hotopp 2002) and anthropogenic wood harvesting in temperate forests reduces the amount of deadwood, homogenizes the range of tree sizes, and reduces the presence of old trees, all factors that are potentially negative for land snail abundance and diversity (Oliver and Larson 1996). Whereas we did not find strong direct effects of deadwood cover, we confirmed a general impact of harvesting intensity on soil pH, the cover of litter, and the cover of deadwood.

In grasslands, soil pH was the strongest determinant of snail assemblages. It influenced densities and diversity and community composition in general and almost significantly in all regions. Grasslands showed fewer direct effects of land-use factors than forests. Their proportional influence on snail assemblages was seven times lower on average as compared to abiotic or biotic substrate factors (in forests, land-use impact was nine times lower). Mowing positively affected snail diversity and consistently altered soil moisture. Mowing usually strongly affects aboveground plant material, and the removal of harvested biomass reduces the nutrient level of soil (Oelmann et al. 2009, Socher et al. 2012) which seems slightly important for snail assemblages in our study although the applied extensive fertilization, that is, the change of nutrient level, did not show explicit consequences. Usually, snail densities and diversity are higher at unmown sites, especially concerning semiarid grasslands which are deeply mown (Pech et al. 2015). However, high soil moisture (i.e., on sedge grasslands) in combination with a rough ground profile enhances the mowing setup and the surviving of snails (Martin and Sommer 2004*b*).

The effects of grazing were of minor importance in our study. There was no direct influence, but a weak effect on soil moisture, pH, and the cover of legumes. However, trampling effects of grazing livestock on snail assemblages have been investigated in forest remnants (Denmead et al. 2013). Besides effects on litter depth and quality, soil moisture, and nutrient availability, there were also negative effects of mechanical disturbance (Martin and Sommer 2004*a*, Denmead et al. 2013). Furthermore, grazing patchily changes aboveground parts of plants and consequently changes microhabitat heterogeneity for snails and has been shown to be negative for snail density and diversity in Swiss nutrient-poor pastures (Boschi and Baur 2007).

The impact of fertilization on snail assemblages was also weak, but consistently negative. In general, fertilization (with variation between 0 and 333 kg N/ha on different plots) may significantly increase the soil nitrogen content (Socher et al. 2012) and increases plant biomass by enhancing plant productivity. However, Socher et al. (2012) showed that fertilization intensity had different effects on plants in different regions, which we can confirm by our study (see Table 4). Again, the strongest impact of this land-use factor in our study was not directly altering snail assemblages but rather worked indirectly by changing environmental conditions. The increase of plant biomass causes an increase of the resistance snails have to face; intensive high-grass meadows are usually sparsely populated. Furthermore, denser vegetation reduces the light penetration to the ground and enhances the soil moisture level (Boschi and Baur 2007). Dry nutrient-poor grasslands that are inhabited by xerophile, often threatened snail species, are often characterized by a short vegetation (Boschi and Baur 2007).

Furthermore, anthropogenic land-use in grasslands often changes open landscapes to fragmented habitats with a drier microclimate (Douglas et al. 2013). Moisture conditions may also be responsible for differences in community compositions among regions in our study since we found a high amount of freshwater species on several grassland plots in the Schorfheide. Snail assemblages suffer from habitat fragmentation and desiccation since they depend on humidity and soil moisture which determine their time of feeding and breeding (Boycott 1934, Martin and Sommer 2004*a*, *b*, Hylander et al. 2005, Douglas et al. 2013, Hettenbergerová et al. 2013). Many snail species show a large moisture range, and land snail composition tightly responds to soil moisture (Martin and Sommer 2004*b*, Cejka and Hamerlik 2009, Hettenbergerová et al. 2013).

In summary, abiotic factors and the biotic substrates in forest and grassland habitats play an important role in shaping land snail assemblages. The impacts of land-use factors of different management types on snail assemblages in our study were direct or indirect, but rather weak as compared to environmental parameters. We conclude that both direct and indirect effects of environmental parameters and land-use management need to be included for painting a more realistic picture of natural complexity. Finally, our study confirms that land snails strongly respond to environmental gradients and add an important indicator taxon to the current evidence of land-use impacts in Central Europe.

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