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

KATJA WEHNER,1† CARSTEN RENKER,2 ADRIAN BRÜCKNER,3 NADJA K. SIMONS,1,4 WOLFGANG W. WEISSER,4 AND NICO BLÜTHGEN1

1Ecological Networks, Technische Universität Darmstadt, Schnittspahnstraße 3, 64287 Darmstadt Germany
2Naturhistorisches Museum Mainz/Landesammlung für Naturkunde RLP, Reichklarastraße 1, 55116 Mainz Germany
3Division of Biology and Biological Engineering, California Institute of Technology, 1200 E. California Boulevard, Pasadena, California 91125 USA
4Department of Ecology and Ecosystem Management, Technische Universität München, Hans-Carl-von-Carlowitz-Platz 2, 85350 Freising-Weihenstephan Germany

Citation: Wehner, K., C. Renker, A. Brückner, N. K. Simons, W. W. Weisser, and N. Blüthgen. 2019. Land-use in Europe affects land snail assemblages directly and indirectly by modulating abiotic and biotic drivers. Ecosphere 10(5):e02726. 10.1002/ecs2.2726

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.

Received 19 December 2018; revised 18 March 2019; accepted 19 March 2019. Corresponding Editor: Robert R. Parmenter.
Copyright: © 2019 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
†E-mail: kwehner@gmx.de

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 (Goodfied 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 2004a, 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 land-
scape 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 gradi-
ent 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 sam-
pling method is inappropriate to give a quantita-
tive and qualitative survey.

Shelled snails were subsequently determined
to species level using Welter-Schultes (2012),
Wiese (2016), and Gliöer (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 (Cern-
ohorsky 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/Public
DataSet.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 repre-
sented as empty shells, were standardized to
densities per square meter (Ind/m²), and the
number of species was used for calculating Shan-
non 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 respec-
tive plot.

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

To compare land snail communities among
regions and habitats, multivariate statistical anal-
ysis of the community composition was based on
the standardized densities (Ind/m²) 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 standard-
ization (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·ha⁻¹·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 χ² 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/m²) in forests (F) and grasslands (G) in the Swabian Alb, the Hainich-Dün, and the Schorfheide-Chorin.

| Species                  | Alb F | Alb G | Hainich F | Hainich G | Schorfheide F | Schorfheide G | Red list status for Germany |
|--------------------------|-------|-------|-----------|-----------|---------------|---------------|-----------------------------|
| 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             | 7.5           |                             |
| 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 antvertigo (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* (Strom, 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 pygmaea* (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           | *                           |
| Species                  | Alb | Hainich | Schorthheide | Red list status for Germany |
|--------------------------|-----|---------|--------------|----------------------------|
| Euconulidae              |     |         |              |                            |
| *Euconulus fulvus* (Müller, 1774) | 4.4 | 0       | 5.3          | 0                          | *                  |
| Oxychilidae              |     |         |              |                            |
| Aegopinella *sp.*        | 3.4 | 0.3     | 0.7          | 0                          | 0                  |
| Aegopinella *para* (Alder, 1830) | 46.6 | 2.8    | 23.6         | 0.9                        | 0.2                | *                  |
| 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                  |
| Nesiowitrea *sp.*        | 0   | 0.1     | 0            | 0                          | 1.5                | 0                  |
| Nesiowitrea *hammonis* (Ström, 1765) | 5.7 | 1.8    | 2.8          | 0.3                        | 21.2               | 2.1                | *                  |
| Nesiowitrea *petronella* (Pfeiffer, 1853) | 0   | 0      | 0            | 0                          | 0.7                | 0                  | 2                  |
| Oxychilidae              |     |         |              |                            |
| 12.2 Oxychilidae *sp.*   |     |         |              |                            |
| Oxychilus *alliarius* (Müller, 1822) | 0.2 | 0.4     | 2.3          | 0                          | 0                  | 0                  | *                  |
| Oxychilus *draparnaudi* (Beck, 1837) | 0   | 0.2     | 1.3          | 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                  |
| Vitridinae               |     |         |              |                            |
| Vitridina *sp.*          |     |         |              |                            |
| Odebrisia *diaphana* (Draparnaud, 1805) | 0   | 0.2     | 2.3          | 0                          | 0                  | 0                  |
| Vitrina *pellucida* (Müller, 1801) | 0   | 0.7     | 0            | 0                          | 0.7                | 0.3                | *                  |
| Vitrinobrachia *brevicosta* (Férussac, 1821) | 0.4 | 0      | 0            | 0                          | 0                  | 0                  |
| Bradybaenidae            |     |         |              |                            |
| Fructicola *fruticum* (Müller, 1774) | 0   | 0.1     | 0            | 0                          | 0                  | 0                  | *                  |
| Helicodonta *obivoluta* (Müller, 1774) | 3.7 | 0.1     | 10           | 0                          | 0                  | 0                  |
| Hygromiidae              |     |         |              |                            |
| Hygromiidae              |     |         |              |                            |
| Candidula *unifasciata* (Poiret, 1801) | 0   | 0.1     | 0            | 0                          | 0                  | 0                  |
| Euproctus *streigela* (Draparnaud, 1801) | 0.4 | 0       | 0            | 0                          | 0                  | 0                  |
| Helicella *italia* (Linnaeus, 1758) | 0   | 0.8     | 0            | 0                          | 2                  | 0                  |
| Monacha *cartusiana* (Müller, 1774) | 0   | 0.4     | 3.1          | 0                          | 0.4                | *                  |
| Monachoides *incarnatus* (Müller, 1774) | 2.8 | 0.2    | 18.1         | 0.1                        | 0                  | 0                  |
| Pseudotrichia *rubigiosa* (Rossmassler, 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                  |
| Trochulus *hispidus* (Linnaeus, 1758) | 1.2 | 0.9     | 1.4          | 0                          | 0                  | 15                 |
| Trochulus *sericeus* (Draparnaud, 1801) | 1.8 | 0.9     | 0.4          | 0                          | 0                  | 0                  |
| Utriculio *umbrosus* (Pfeiffer, 1828) | 0   | 0       | 0.2          | 0                          | 0                  |
| Helicidae                |     |         |              |                            |
| Helicidae                |     |         |              |                            |
| Arianta *arbusorum* (Linnaeus, 1758) | 0.7 | 0       | 3.6          | 0                          | 0                  |
| Cepaea *sp.*             | 1.2 | 0.1     | 2.7          | 0.4                        | 0                  |
| Cepaea *hortensis* (Müller, 1774) | 0.2 | 0.1     | 12.8         | 0.2                        | 0                  |
| Cepaea *nemoralis* (Linnaeus, 1758) | 0   | 0       | 10           | 0                          | 0                  |
| Helix *pomatia* (Linnaeus, 1758) | 0   | 0       | 15.8         | 0.6                        | 0                  |
| Isognomostoma *isognomostomos* (Schröter, 1784) | 0.9 | 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                  |
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 $r^2 = 0.08$, $P < 0.0001$). 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.

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 m² (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 $r^2 = 0.08$, $P < 0.0001$). 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 $Valonia$ and the species $Vertigo$ pygmaea, forests were...
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).

---

![Figure 1](image.png)

**Fig. 1.** Snail abundances and diversity in different habitats and regions. (A) Mean abundances of snail individuals per square meter (Ind/m²) 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.*
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, $\chi^2$ 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).
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/m² in European forests and 20–200 Ind/m² 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: $\chi^2$ 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 (*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).
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 (Limonidin-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 (Falchner et al. 2001). However, the portion of freshwater specimens was only 1.5% of all specimens found.
Table 5. Pathway coefficients of structural equation modeling analyses of grasslands in the Swabian Alb, the Hainich-Dün, and the Schorfheide-Chorin.

| Variable 1 | Variable 2 | Density | | | Diversity | | | Community | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | 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 |
| Grazing | −0.437 | −0.243 | −0.195 | −0.437 | −0.243 | −0.195 | −0.437 | −0.243 | −0.195 |
| 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 | −0.120 | 0.208 | 0.434 | −0.415 | −0.120 |
| Grazing | 0.153 | 0.193 | 0.138 | 0.083 | 0.224 | 0.158 | 0.193 | 0.138 |
| Fertilization | 0.125 | 0.235 | −0.261 | −0.591 | −0.125 | 0.146 | 0.235 | −0.261 |
| Soil moisture | −0.121 | −0.118 | 0.405 | 0.024 | −0.120 |
| pH | −0.398 | −0.219 | 0.301 | −0.108 | −0.396 | −0.219 | 0.301 |
| Precipitation | −0.229 | 0.397 | 0.386 | −0.234 | 0.379 |
| Mowing | −0.090 | 0.254 | 0.533 | −0.095 | 0.254 |
| Grazing | −0.148 | | | |
| Fertilization | −0.337 | | | | | | | | | |
| Soil moisture | 0.197 | 0.181 | −0.182 | 0.234 | 0.188 | −0.230 | 0.205 | 0.181 | −0.182 |
| pH | 0.310 | | | | | | | | | |
| Precipitation | −0.225 | 0.119 | 0.414 | −0.178 | 0.167 | −0.225 | 0.119 |
| Soil moisture | 0.174 | | | | | | | | | |
| Grazing | −0.135 | 0.134 | −0.599 | −0.135 | 0.134 | −0.599 | −0.135 | 0.134 | −0.599 |
| Soil moisture | 0.174 | | | | | | | | | |
| Soil moisture | 0.174 | | | | | | | | | |
| pH | 0.174 | | | | | | | | | |
| Mowing | −0.192 | | | | | | | | | |
| Grazing | −0.156 | | | | | | | | | |
| Fertilization | 0.186 | | | | | | | | | |
| Precipitation | 0.180 | | | | | | | | | |
| Soil moisture | 0.249 | 0.643 | 0.249 | 0.643 | −0.249 | 0.643 |
| Snail trait | Mowing | | | | | | | | | |
| Grazing | 0.120 | 0.212 | 0.227 |
| Soil moisture | −0.202 | −0.131 | −0.339 | −0.116 | −0.211 | 0.093 |
| 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 |
| Mowing | −0.095 | 0.112 | −0.135 | 0.264 | 0.129 | −0.056 | −0.183 |
| Grazing | −0.245 | −0.182 | | | | | | | |
| Soil moisture | −0.399 | −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 2004a, 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 above-ground 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 2004b).

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 2004a, 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 2004a, 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 2004b, 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.

ACKNOWLEDGMENTS

We thank the managers of the three Exploratories, Kirsten Reichel-Jung, Iris Steitz, Sandra Weithmann, Juliane Vogt, Miriam Teuscher, and all former managers for their work in maintaining the plot and project infrastructure; Christiane Fischer for giving support through the central office; Andreas Ostrowski for managing the central database; and Markus Fischer, Eduard Linsenmair, Dominik Hessenmöller, Daniel Pratt, Ingo Schöning, François Buscot, Ernst-Detlef Schulze, and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. Many thanks to all research assistants: Kevin Frank, Wiebke Kämper, Jessica Schneider, Andrea Hilpert, Matteo Trevisan, Matthias Brandt, Tewannakit Mermagen, Kathrin Ziegler, Annika Keil, Andreas Kern, Katja Gruschwitz, and Kimberly Adam. We thank Jörg Peil from the State Office for Environment of the Schorfheide-Chorin for providing snail data of the region; Volkmar Wolters for commenting on the manuscript; and Falk Hänsel, Stephan Wöllauer, and Thomas Nauss for the weather data and respective database tool. The work has partly been funded by the DFG Priority Program 1374 ‘Infrastructure-Biodiversity-Exploratories’ (DFG BL608/8-3). Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to §72 BbgNatSchG). We acknowledge the Open Access Publishing Fund of Technische Universität Darmstadt. NB and WWW conceived the ideas. KW collected field data and determined snail species together with CR. KW, AB, NKS, and NB analyzed the data. KW and NB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

LITERATURE CITED

Anderson, M. J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Science 58:626–639.
Anderson, M. J. 2006. Distance-based test for homogeneity of multivariate dispersions. Biometrics 62:245–253.
Baker, R. E. 1968. The ecology of the wrinkled snail, Helicella caperata Mont. on the Brauntun Burrows sand dune system. Journal of Molluscan Studies 38:41–51.
Baur, A., and B. Baur. 1988. Individual movement patterns of the minute land snail Punctum pygmaeum (Draparnaud) (Pulmonata: Endodontidae). Veliger 30:372–376.
Blüthgen, N., et al. 2012. A quantitative index of land-use intensity in grasslands: integrating mowing, grazing and fertilization. Basic and Applied Ecology 13:207–220.
Boschi, C., and B. Baur. 2007. Effects of management intensity on land snails in Swiss nutrient-poor pastures. Agriculture, Ecosystems and Environment 120:243–249.
Boycott, A. E. 1934. The habitats of land Mollusca in Britain. Journal of Ecology 22:1–38.
Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Caldwell, R. S. 1993. Macroinvertebrates and Their Relationship to Coarse Woody Debris: with Special Reference to Land Snails. Pages 49–54 in J. W. McMinn and D. A. Crossley, editors. Biodiversity and coarse woody debris in southern forests. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: effects on Biodiversity Athens, GA. Southeastern Forest Experiment Station, Asheville, North Carolina, USA.

Cameron, R. A. D., and B. M. Pokryszko. 2005. Estimating the species richness and composition of land mollusc communities: problems, consequences and practical advice. Journal of Conchology 38:529–548.

Cejka, T., and L. Hamerlik. 2009. Land snails as indicator of soil humidity in Danubian woodland (SW Slovakia). Polish Journal of Ecology 57:741–747.

Cernohorsky, N. H., M. Horsák, and R. A. D. Cameron. 2010. Land snail species richness and abundance at small scales: the effects of distinguishing between live individuals and empty shells. Journal of Conchology 40:233–243.

Chistak, M. N., K. Mody, M. Gossner, N. K. Simons, G. Köhler, W. W. Weisser, and N. Blüthgen. 2016. Losers, winners, and opportunists: how grassland land-use intensity affects orthopteran communities. Ecosphere 7:e01545.

Claassen, C. P. 1998. Shells Cambridge. Cambridge University Press, New York, New York, USA.

Corsmann, M. 1990. Die Schneckengemeinschaften (Gastropoda) eines Laubwaldes: Populationsdynamik, Verteilungsmuster und Nahrungsbiologie. Die Schneckengemeinschaft (Gastropoda) eines Laubwaldes: Populationsdynamik, Verteilungsmuster und Nahrungsbiologie. Berichte des Forschungszentrums Waldökosysteme: Reihe A, Band 58, Forschungszentrum Waldökosysteme.

Denmead, L. H., G. M. Barker, R. J. Standish, and R. K. Didham. 2013. Experimental evidence that even minor livestock trampling has severe effects on land snail communities in forest remnants. Journal of Applied Ecology 52:161–170.

Douglas, D. D., D. R. Brown, and N. Pederson. 2013. Land snail diversity can reflect degrees of anthropogenic disturbance. Ecosphere 4:1–14.

Dourson, D. C. 2010. Kentucky’s land snails and their ecological communities. Goatslug Publications, Bakersville, North Carolina, USA.

Falkner, G., P. Obrdlik, E. Castella, and M. C. D. Speight. 2001. Shelled Gastropoda of Western Europe. Friedrich-Held-Gesellschaft, Munich, Germany.

Fischer, M., et al. 2010. Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. Basic and Applied Ecology 11:473–485.

Foley, J. A., et al. 2005. Global consequences of land use. Science 309:570–574.

Frank, K., M. Hülsmann, T. Assmann, T. Schmitt, and N. Blüthgen. 2017. Land use affects dung beetle communities and their ecosystem service in forests and grasslands. Agriculture, Ecosystems and Environment 243:114–122.

Glöer, P. 2017. Süßwassermollusken. Ein Bestimmungsschlüssel für die Muscheln und Schnecken im Süßwasser der Bundesrepublik Deutschland. Deutscher Jugendbund für Naturbeobachtungen, Göttingen, Germany.

Goodfried, G. A. 1986. Variation in land-snail shell form and size and its causes: a review. Systematic Zoology 35:204–223.

Grace, J. B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge, UK.

Hettenbergerová, E., M. Horsák, R. Chandran, M. Hájek, D. Zelený, and J. Dvoráková. 2013. Patterns of land snail assemblages along a fine-scale moisture gradient. Malacologia 56:31–32.

Horsák, M. 2006. Mollusc community patterns and species response curves along a mineral richness gradient: a case study in fens. Journal of Biogeography 33:98–107.

Hotopp, K. P. 2002. Land snails and soil calcium in Central Appalachian Mountain forest. Southeastern Naturalist 1:27–44.

Hylander, K., C. Nilsson, B. G. Jonsson, and T. Göther. 2005. Differences in habitat quality explain nestedness in a land snail meta-community. Ökos 108:351–361.

Kahl, T., and J. Bauhus. 2014. An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin. Nature Conservation 7:15–27.

Legendre, P., and E. D. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280.

Limondin-Lozouet, N., and R. C. Preece. 2014. Quaternary perspectives on the diversity of land snail assemblages from northwestern Europe. Journal of Molluscan Studies 80:224–237.

Lyeard, C., et al. 2004. The global decline of non-marine mollusks. BioScience 54:321–330.

Martin, K., and M. Sommer. 2004a. Relationships between land snail assemblage patterns and soil properties in temperate humid ecosystems. Journal of Biogeography 31:531–545.

Martin, K., and M. Sommer. 2004b. Effects of soil properties and land management on the structure of grassland snail assemblages in SW Germany. Pedobiologia 48:193–203.
Mason, C. F. 1970. Snail populations, beech litter production, and the role of snails in litter decomposition. Oecologia 5:215–239.

Morris, N., and J. Taylor. 2000. Global events and biotic interactions as controls on the evolution of gastropods. Pages 149–501 in S. J. Culver and P. F. Rawson, editors. Biotic response to global change: the last 145 million years. Cambridge University Press, Cambridge, UK.

Mörzer Brujin, M. F. M., C. Altena, and L. J. M. Butot. 1959. The Netherlands as an environment for land Mollusca. Basteria 23:135–162.

Nekola, J. C., B. F. Coles, and M. Horsák. 2015. Species assignment in Pupilla (Gastropoda: Pulmonata: Pupillidae): integration of DNA-sequence data and conchology. Journal of Molluscan Studies 81:196–216.

Newbold, T., et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Nurinsiyah, A. S., H. Fauzia, C. Henning, and B. Hausdorf. 2016. Native and introduced land snail species as ecological indicators in different land use types in Java. Ecological Indicators 70:557–565.

Oelmann, Y., G. Brodl, N. Hölzel, T. Kleinebecker, A. Vogel, and P. Schwarze. 2009. Nutrient impoverishment and limitation of productivity after 20 years of conservation management in wet grasslands of north-western Germany. Biological Conservation 142:2941–2948.

Oksanen, J., et al. 2018. ‘vegan’ - Community Ecology Package. https://cran.r-project.org, https://github.com/vegandevs/vegan

Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics. McGraw Hill, New York, New York, USA.

Pearce, T. A. 2008. When a snail dies in the forest, how long will the shell persist? Effect of dissolution and micro-bioerosion. American Malacological Bulletin 26:111–117.

Pech, P., J. Dolanský, R. Hrdlička, and J. Leps. 2015. Differential response of communities of plants, snails, ants and spiders to long-term mowing in a small-scale experiment. Community Ecology 16:115–124.

Perrins, C. M. 1996. Eggs, egg formation and the timing of breeding. International Journal of Avian Science 138:2–15.

Poschlod, P., J. P. Bakker, and S. Kahmen. 2005. Changing land use and its impact on biodiversity. Basic and Applied Ecology 6:93–98.

R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosseel, Y. 2012. lavaan: an R Package for Structural Equation Modeling. Journal of Statistical Software 48:1–36.

Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Schilthuizen, M., T.-S. Liew, B. B. Elahan, and I. Lackman-Ancrenaz. 2005. Effects of karst forest degradation on pulmonate and prosobranch land snail communities in Sabah, Malaysian Borneo. Conservation Biology 19:949–954.

Simons, N., et al. 2014. Resource-mediated indirect effects of grassland management on arthropod diversity. PLoS ONE 9(9):e107033.

Socher, A. S., D. Prati, S. Boch, J. Müller, V. H. Klaus, N. Hölzel, and M. Fischer. 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. Journal of Ecology 100:1391–1399.

Stohlgren, T. J., T. N. Chase, R. A. Pielke, T. G. Kittels, and J. S. Baron. 1998. Evidence that local land use practices influence regional climate, vegetation, and stream flow patterns in adjacent natural areas. Global Change Biology 4:495–504.

Vesterdal, L., and K. Raulund-Rasmussen. 1998. Forest floor chemistry under seven tree species along a soil fertility gradient. Canadian Journal of Forest Research 28:1636–1647.

Wäreborn, I. 1969. Land molluscs and their environments in an oligotrophic area in southern Sweden. Oikos 20:461–479.

Wäreborn, I. 1992. Changes in the land mollusc fauna and soil chemistry in an inland district in southern Sweden. Ecography 15:62–69.

Welter-Schultes, F. 2012. European non-marine molluscs. A guide for species identification. Planet Poster Editions, Göttingen, Germany.

Wiese, V. 2016. Die Landschnecken Deutschlands, Second edition. Quelle & Meyer, Wiebelsheim, Germany.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2726/full