Narrow environmental niches predict land-use responses and vulnerability of land snail assemblages

Katja Wehner1*, Carsten Renker2, Nadja K. Simons1, Wolfgang W. Weisser3 and Nico Blüthgen1

Abstract

Background: How land use shapes biodiversity and functional trait composition of animal communities is an important question and frequently addressed. Land-use intensification is associated with changes in abiotic and biotic conditions including environmental homogenization and may act as an environmental filter to shape the composition of species communities. Here, we investigated the responses of land snail assemblages to land-use intensity and abiotic soil conditions (pH, soil moisture), and analyzed their trait composition (shell size, number of offspring, light preference, humidity preference, inundation tolerance, and drought resistance). We characterized the species’ responses to land use to identify ‘winners’ (species that were more common on sites with high land-use intensity than expected) or ‘losers’ of land-use intensity (more common on plots with low land-use intensity) and their niche breadth. As a proxy for the environmental ‘niche breadth’ of each snail species, based on the conditions of the sites in which it occurred, we defined a 5-dimensional niche hypervolume. We then tested whether land-use responses and niches contribute to the species’ potential vulnerability suggested by the Red List status.

Results: Our results confirmed that the trait composition of snail communities was significantly altered by land-use intensity and abiotic conditions in both forests and grasslands. While only 4% of the species that occurred in forests were significant losers of intensive forest management, the proportion of losers in grasslands was much higher (21%). However, the species’ response to land-use intensity and soil conditions was largely independent of specific traits and the species’ Red List status (vulnerability). Instead, vulnerability was only mirrored in the species’ rarity and its niche hypervolume: threatened species were characterized by low occurrence in forests and low occurrence and abundance in grasslands and by a narrow niche quantified by land-use components and abiotic factors.

Conclusion: Land use and environmental responses of land snails were poorly predicted by specific traits or the species’ vulnerability, suggesting that it is important to consider complementary risks and multiple niche dimensions.

Keywords: Gastropoda, Land snails, Land-use intensity, Biodiversity Exploratories, Forests, Grasslands

Background

Land use disturbs natural environments, changes local geographical landscape structure and alters local biotic and abiotic conditions, e.g. microclimate [1–6].

Reduction of habitat and microhabitat heterogeneity may lead to a homogenization of plant and animal communities, trigger a reduction in functional diversity and thus lower the capacity of an ecosystem to buffer disturbances [7, 8]. Homogenization of animal communities by increasing land-use intensity has been shown for several taxa; e.g., in managed grasslands, 34% of plant- and leafhoppers species were significant losers (i.e. species that were significantly less abundant under conditions of high...
land-use intensity) of land-use intensification, particularly increases in mowing frequency had a negative effect [9].

Land snails are an important macroinvertebrate group that is directly and indirectly involved in ecosystem processes such as litter decomposition or nutrient cycling [10, 11]. There is a natural north–south and west–east gradient of snail species distributions and abundances within Europe; species richness increases from north to south and to a lesser extent from west to east which is linked to regional and ecological differences and the land-use history [12]. Snail species also differ in their tolerance to abiotic factors (pH, soil moisture), and vary greatly in life-history parameters (e.g., lifespan, development, number of offspring, food requirement, shell size) and general behavior [13] which also affect their distribution. Variation in body size and diet seems to be especially important for structuring snail communities [14] as well as the species-specific tolerance to a variety of environmental factors which can result in nested communities at a specific site [15, 16].

Studies on trait composition of snail communities in Sweden pointed to the importance of the species’ niche-width and the importance of local environmental conditions over spatial variables [17]. While tolerance-related traits such as humidity preference or inundation tolerance were positively associated with abiotic soil moisture, a large amount of variation remained unexplained [17], which may be related to land use. The impact of land use and its intensity on land snail communities is less intensively investigated although most land snail species are characterized by a limited mobility and therefore are vulnerable to human introduced habitat changes [15, 18–20]. Changes in abiotic factors such as soil pH, soil moisture, soil calcium content, leaf litter depth, soil surface structure or the type of vegetation have been shown to alter snail communities [15, 21–25]. Also land-use factors such as the proportion of wood harvested in forests or the amount of grazing livestock in grasslands can influence snail communities directly and/or indirectly [20, 26, 27]. In addition, disturbances by different land-use types and intensities may alter the trait composition of snail communities on the regional level; i.e. the presence of coniferous timber may favor snail communities with differing traits than communities in natural deciduous stands.

In the present study, we investigated land snail communities at forest and grassland sites in different regions of Germany, which were characterized by different land-use types and intensities. We aimed to test whether the trait composition of the snail community is influenced by land-use intensity (and soil conditions). We then tested the responses of each snail species to land-use intensity; ‘winners’ significantly increase in abundance and occurrence with land-use intensity, whereas ‘losers’ significantly decrease compared to the null model [9, 39]. We than compared these responses with the snail species’ habitat association; i.e. we asked whether species that only occasionally occur in forests are more affected by forest management than species that are specialized to forest habitats. On the other hand, do species that are grassland specialist suffer less from grassland management than those only occasionally occurring in grasslands? Finally, we compared our findings of the land-use effects and the ‘winner/loser’ status of a species with its putative vulnerability (Red List status), to test if losers of land-use intensifications in forests and grasslands are those species that are classified as vulnerable.

Results

Response to land use

The trait composition of land snail communities differed strongly between forests and grasslands within regions, indicated by a strong differentiation of community-weighted mean trait values (CWMs). Assemblages of forest species consisted of larger species, consistently showed lower light and higher humidity preference, lower drought resistance and mostly lower inundation tolerance than grassland assemblages; differences in the number of offspring were inconsistent among forest and grassland habitats (Fig. 1).

In forests, land-use intensity and abiotic conditions significantly influenced the CWMs of all traits investigated, although often in a different way across regions (Table 1, Additional file 1: Appendix 1; see interaction terms with region). Similarly, in grasslands the trait composition of snail communities was significantly influenced by most land-use components and abiotic conditions (Table 2, Additional file 1: Appendix 1).

In forest habitats, some 4% of all species were ‘losers’ of the combined forest management index (i.e. they were significantly less common in intensively used forests),
a) Shell size (CWM) [mm]
b) Number of offspring (CWM) [per clutch]
c) Light preference (CWM)
d) Humidity preference (CWM)
e) Drought resistance (CWM)
f) Inundation tolerance (CWM)
Table 1 Influence of land-use parameter and abiotic factors on the trait composition of snail communities in forest habitats

| Trait                        | df | Sum Sq  | F      | p     | df | Sum Sq  | F      | p     |
|------------------------------|----|---------|--------|-------|----|---------|--------|-------|
| FORMI                        | 1  | 457.3   | 75.683 | <0.001| 1  | 4692    | 101.500| <0.001|
| Region                       | 2  | 5243.8  | 433.889| <0.001| 2  | 46,655  | 504.612| <0.001|
| FORMI:Region                 | 2  | 285.4   | 23.619 | <0.001| 2  | 753     | 8.142  | <0.001|
| Inonat                       | 1  | 326.4   | 54.282 | <0.001| 1  | 2805    | 66.118 | <0.001|
| Region                       | 2  | 5435.5  | 451.940| <0.001| 2  | 49,336  | 581.538| <0.001|
| Inonat:Region                | 2  | 253.2   | 21.051 | <0.001| 2  | 3652    | 43.046 | <0.001|
|ildcuet                       | 1  | 337.7   | 55.324 | <0.001| 1  | 3128    | 66.613 | <0.001|
| Region                       | 2  | 5351.8  | 438.393| <0.001| 2  | 48,101  | 512.182| <0.001|
| Idlcuet:Region               | 2  | 238     | 19.495 | <0.001| 2  | 166     | 1.766  | <0.01 |
| pH                           | 1  | 82.4    | 13.347 | <0.001| 1  | 1772    | 37.711 | <0.001|
| Soil moisture                | 2  | 5601.9  | 453.818| <0.001| 2  | 49,503  | 526.638| <0.001|
| Soil moisture:Region         | 2  | 177    | 14.353 | 0.220 | 2  | 80      | 0.846  | 0.049 |
| pH                           | 1  | 9       | 1.509  | 0.220 | 1  | 121     | 2.713  | 0.099 |
| pH:Region                    | 2  | 5852.2  | 489.548| <0.001| 2  | 52,165  | 583.257| <0.001|
| Soil moisture                | 2  | 181.3   | 28.714 | <0.001| 2  | 1112    | 23.797 | <0.001|
| Soil moisture:Region         | 2  | 5584.7  | 442.215| <0.001| 2  | 50,664  | 541.944| <0.001|
| pH                           | 1  | 2.750   | 75.899 | <0.001| 1  | 4.707   | 9.739  | <0.001|
| pH:Region                    | 2  | 11,270  | 155.513| <0.001| 2  | 17,493  | 180.564| <0.001|
| Soil moisture                | 2  | 1,948   | 26.884 | <0.001| 2  | 0.801   | 8.293  | <0.001|
| Humidity preference          | 1  | 1,345   | 37.837 | <0.001| 1  | 3.511   | 73.221 | <0.001|
| Drought resistance           | 1  | 1,522   | 37.837 | <0.001| 1  | 1.269   | 37.837 | <0.001|
| Inundation tolerance         | 1  | 1,051   | 26.884 | <0.001| 1  | 0.470   | 9.739  | <0.001|
| pH                           | 1  | 9       | 1.509  | 0.220 | 1  | 1.122   | 22.890 | <0.001|
| pH:Region                    | 2  | 12,937  | 170.392| <0.001| 2  | 16,400  | 167.238| <0.001|
| Soil moisture                | 2  | 0.493   | 6.492  | 0.002 | 2  | 0.560   | 5.714  | 0.003 |
| Soil moisture:Region         | 2  | 0.934   | 24.602 | <0.001| 2  | 1.122   | 22.890 | <0.001|
| pH                           | 1  | 2.750   | 75.899 | <0.001| 1  | 1.269   | 22.890 | <0.001|
| pH:Region                    | 2  | 11,270  | 155.513| <0.001| 2  | 17,493  | 180.564| <0.001|
| Soil moisture                | 2  | 1,948   | 26.884 | <0.001| 2  | 0.801   | 8.293  | <0.001|
| Soil moisture:Region         | 2  | 2.921   | 79.396 | <0.001| 2  | 1.269   | 37.837 | <0.001|
Table 1 (continued)

| Humidity preference (CWM) | df | Sum Sq  | F     | p    | Drought resistance (CWM) | df | Sum Sq  | F     | p    | Inundation tolerance (CWM) | df | Sum Sq  | F     | p    |
|---------------------------|----|----------|-------|------|---------------------------|----|----------|-------|------|-----------------------------|----|----------|-------|------|
| Region                    | 2  | 11.494   | 156.227 | <0.001 | Region                    | 2  | 17.561   | 180.452 | <0.001 | Region                    | 2  | 0.125    | 0.654 | 0.520 |
| Soil moisture:Region      | 2  | 1.020    | 13.867 | <0.001 | Soil moisture:Region      | 2  | 0.529    | 5.441  | 0.004 | Soil moisture:Region      | 2  | 0.935    | 4.881 | 0.008 |

Significant values are given in bold

*FORMI* forest management index, *Inonat* proportion of non-native trees, *Idwcut* proportion of dead wood with saw cuts, *Iharv* proportion of wood harvested
Table 2 Influence of land-use parameter and abiotic factors on the trait composition of snail communities in grassland habitats

| Trait                          | df  | Sum Sq    | F       | p     | Trait                          | df  | Sum Sq    | F       | p     |
|--------------------------------|-----|-----------|---------|-------|--------------------------------|-----|-----------|---------|-------|
| Shell size (CWM)               | 1   | 5.600     | 4.283   | 0.039 | Number of offspring (CWM)      | 1   | 767       | 10.237  | 0.001 |
| Region                         | 2   | 187.31    | 71.659  | <0.001| LUI:Region                      | 2   | 4368      | 29.160  | <0.001|
| Mowing                         | 1   | 1.020     | 0.781   | 0.377 | Mowing                         | 1   | 14        | 0.175   | 0.075 |
| Region                         | 2   | 189.40    | 72.796  | <0.001| Mowing:Region                   | 2   | 1301      | 8.252   | <0.001|
| Grazing                        | 1   | 0.510     | 0.389   | 0.533 | Grazing                        | 2   | 38316     | 268.169 | <0.001|
| Region                         | 2   | 187.06    | 71.464  | <0.001| Grazing:Region                  | 2   | 2356      | 16.489  | <0.001|
| Fertilization                  | 1   | 8.840     | 6.763   | <0.001| Fertilization                   | 1   | 2672      | 33.505  | <0.001|
| pH                             | 1   | 2.120     | 1.664   | 0.197 | pH                             | 1   | 8636      | 140.899 | <0.001|
| Region                         | 2   | 216.91    | 85.099  | <0.001| pH:Region                      | 2   | 35255     | 287.605 | <0.001|
| Soil moisture                  | 1   | 0.490     | 0.488   | 0.540 | Soil moisture                   | 1   | 15105     | 216.410 | <0.001|
| Region                         | 2   | 190.30    | 95.150  | <0.001| Soil moisture:Region            | 2   | 24423     | 174.950 | <0.001|
| Soil moisture:Region           | 2   | 11.580    | 5.791   | 0.012 | Soil moisture:Region            | 2   | 4604      | 32.983  | <0.001|
| Humidity preference (CWM)      | 1   | 2.651     | 14.988  | <0.001| Drought resistance (CWM)       | 1   | 0.002     | 0.082   | 0.774 |
| Region                         | 2   | 123.42    | 348.964 | <0.001| Inundation tolerance (CWM)     | 1   | 1.765     | 25.385  | <0.001|
| LUI:Region                     | 2   | 9.841     | 27.882  | <0.001| LUI:Region                      | 2   | 2.844     | 73.056  | <0.001|
| Mowing                         | 1   | 0.198     | 1.050   | 0.306 | LUI:Region                      | 2   | 0.358     | 9.192   | <0.001|
| Region                         | 2   | 125.79    | 333.045 | <0.001| Mowing                         | 1   | 0.072     | 3.703   | 0.055 |
| Grazing                        | 1   | 0.343     | 1.866   | 0.172 | Grazing                        | 1   | 0.623     | 32.966  | 0.001 |
| Region                         | 2   | 128.55    | 349.785 | <0.001| Grazing:Region                  | 2   | 2.719     | 71.585  | <0.001|
| Fertilization                  | 1   | 3.182     | 16.898  | <0.001| Fertilization                   | 1   | 0.016     | 0.810   | 0.368 |
| Region                         | 2   | 122.80    | 327.885 | <0.001| Fertilization:Region            | 2   | 2.870     | 72.506  | <0.001|
| pH                             | 1   | 4.880     | 31.830  | <0.001| pH:Region                       | 1   | 0.111     | 5.575   | 0.018 |
| Region                         | 2   | 131.88    | 430.070 | <0.001| pH:Region                       | 2   | 2.726     | 68.779  | <0.001|
| Soil moisture                  | 2   | 17.468    | 56.964  | <0.001| Soil moisture                   | 2   | 0.093     | 2.337   | 0.099 |
| Region                         | 2   | 43.980    | 258.049 | <0.001| Soil moisture                   | 2   | 0.496     | 25.671  | 0.001 |

Note: All p-values are significant at the 0.05 level unless otherwise noted.
Table 2 (continued)

|                          | df  | Sum Sq | F    | p   | df  | Sum Sq | F    | p   | df  | Sum Sq | F    | p   |
|--------------------------|-----|--------|------|-----|-----|--------|------|-----|-----|--------|------|-----|
| Humidity preference (CWM)| 2   | 93.991 | 275.743 | <0.001 | 2   | 2.497  | 64.560 | <0.001 | 2   | 30.888  | 229.127 | <0.001 |
| Soil moisture:Region     | 2   | 2.945  | 8.640 | 0.001 | 2   | 0.312  | 8.055 | 0.001 | 2   | 0.018  | 0.131  | 0.877 |

Significant values are given in bold

LUI: land-use intensity
whereas 12% were ‘winners’ and thus increased with forest management intensity (Table 3). The proportions of non-native trees (4% losers vs. 8% winners) and the proportion of dead wood with saw cuts (6% losers vs. 8% winners) revealed a similar pattern, but for the proportion of wood harvested the percentage of losers (12%) exceeded that of winners (8%).

In grasslands, many species were predominantly found at low land-use intensities (LUI); 21% of all species were significant losers and only Monacha cartusiana profited from high LUI (Table 4). However, single land-use components in grasslands had only weak effects. Grazing intensity positively affected Cecilioides acicula and Cepaea hortensis, but showed no negative impact. Similarly, mowing (2% losers and 2% winners) and fertilization (4% losers and 4% winners) had a very little impact compared to the combined LUI.

However, in both forests and grasslands, species’ land-use responses (i.e. their ‘winner/loser’ status) were independent of their traits; i.e. losers in forests or grasslands were neither characterized by a smaller or larger shell size nor by lower or higher numbers of offspring nor by lower or higher light preference etc. (Additional files 2–15: Appendix 2–15).

Response to abiotic factors
Although niches of common land snail species for soil pH and soil moisture were generally broad, some differentiations were found in the communities of both habitats. In forests, Aegopinella pura, the genus Carychium, Cochlicopa lubrica, Ena montana and Vitrea contracta were significantly associated with higher pH values (Table 3) and Cepaea hortensis, Euconulus fulvus, Nesovitrea hammonis, Vallonia pulchella and Vitrinobrachium breve were found at sites with low pH (Table 3). Furthermore, A. pura and Carychium tridentatum were associated with high soil moisture in forests and Ceciliodes acicula, E. fulvus, N. hammonis, Punctum pygmaeum, Trochulus striolatus and V. pulchella were found at low soil moisture values (Table 3).

Grassland sites had a higher mean pH (6.7) as compared to forest soils, and many snail species (e.g., Candidula unifasciata, the genus Carychium, Granaria frumentum, Pupilla muscorum, Vertigo antvertigo) were associated with higher pH values (Table 4). Only N. hammonis was significantly more common on sites with low pH. Soil moisture niches of grassland species were even broader than those of pH. The genus Carychium, Trochulus hispidus and Vallonia pulchella were found at high moisture values, while C. unifasciata, Discus rotundatus, Truncatellina cylindrica, V. excentrica were associated with low soil moisture (Table 4).

Habitat association
Snail species differed in their habitat association and their distribution among regions (Fig. 2). However, effects of land-use management components and abiotic factors in forests were independent of the species’ habitat association, i.e. species that occurred in forests at low frequencies (e.g., 25% of the individuals in Cochlicopa lubrica; Fig. 2) were equally affected by land-use intensification as species that are exclusively found in forests (e.g., Cepaea hortensis) (F1,49 = 0.14, p = 0.71, Fig. 2, Additional file 14: Appendix 14). In contrast, grassland species that predominantly prefer grassland habitats were less tolerant to fertilization than species that also occur in forests (F1,50 = 5.84, p = 0.019, Fig. 3a, Additional file 15: Appendix 15). Furthermore, grassland “specialists” were significantly associated with higher pH values (F1,49 = 9.21, p = 0.004, Fig. 3b).

Species’ vulnerability
Across forests and grasslands, 75% of the 61 snail species found are currently not threatened or endangered according to their Red List status (Tables 3, 4). Nevertheless, Nesovitrea petronella, Candidula unifasciata and Granaria frumentum are regarded as ‘endangered’ while Vallonia enniensis is ‘highly endangered’ and V. angustior is listed on the FFH directive.

There was no statistical support that a negative response to land-use intensity of a certain species (“loser”) is associated with a high vulnerability of the species, neither in forests nor in grasslands (Table 5). A better predictor for the species’ vulnerability in forests was a relatively low number of sites in which the species occurred, and in grasslands both a low occurrence and a low total abundance corresponded to a higher vulnerability (Table 5). Furthermore, the 5-dimensional niche hypervolume based on the species’ tolerance to land-use components and abiotic conditions was significantly correlated with the species’ vulnerability, hence species with a small niche hypervolume are more vulnerable in both forests (Spearman rank test: S = 20,091, p = 0.0004; Fig. 4a) and grasslands (Spearman rank test: S = 15,547, p = 0.003, Fig. 4b).

Discussion
Response to land use and abiotic factors
Land snail species are slow-dispersing organisms, and historical influences are of general importance for their distribution [28]. Their diversity and heterogeneity is modified by predation, parasitism, competition, abiotic environmental gradients, natural barriers and disturbances [16]. While abiotic and vegetation parameters can be used to predict snail communities, disturbances by
| Species | Red List | Region | Occurrence | FORMI | Inonat | Idwcut | iharv | pH | Soil moisture |
|---------|---------|--------|------------|-------|--------|--------|-------|----|---------------|
| Acanthinula aculeata (O.F. Müller, 1774) | * | AHS | 37 | 61 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Aegopinella nitens (Michaud, 1831) | * | AHS | 62 | 123 | Winner | Neutral | Neutral | Neutral | Neutral | Neutral |
| Aegopinella nitidula (Draparnaud, 1805) | * | AH | 11 | 15 | Neutral | Neutral | Neutral | Loser | Mid-specialist | Mid-specialist |
| Aegopinella pura (Alder, 1831) | * | AHS | 91 | 422 | Neutral | Neutral | Neutral | Neutral | "High" | "High" |
| Arianta arbustorum (Linnaeus, 1758) | * | AH | 14 | 24 | Neutral | Neutral | Loser | Neutral | Neutral | Neutral |
| Carychium minimum O.F. Müller, 1774 | * | AH | 37 | 115 | Winner | Neutral | Winner | Neutral | Neutral | Neutral |
| Carychium tridentatum (Risso, 1826) | * | AHS | 74 | 612 | Neutral | Neutral | Neutral | Neutral | Neutral | "High" |
| Cecilioides acicula (O.F. Müller, 1774) | * | AH | 4 | 4 | Neutral | Neutral | Neutral | Loser | "Low" |
| Capax hortensis (O.F. Müller, 1774) | * | AH | 26 | 82 | Loser | Loser | Loser | Loser | "Low" | Neutral |
| Capax nemoralis (Linnaeus, 1758) | * | H | 15 | 57 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Clausilia bidentata (Strom, 1765) | * | HS | 12 | 14 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Cepaea hortensis (O.F. Müller, 1774) | * | AH | 26 | 82 | Loser | Loser | Loser | Loser | "Low" | "Low" |
| Cepaea nemoralis (Linnaeus, 1758) | * | H | 15 | 57 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Cochlicopa lubrica (O.F. Müller, 1774) | * | AHS | 29 | 62 | Winner | Neutral | Winner | Winner | "High" | Neutral |
| Cochlicopa lubricella (Porro, 1838) | V | A | 1 | 2 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Cochlidina laminata (Montagu, 1803) | * | AH | 19 | 27 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Discus rotundatus (O.F. Müller, 1774) | * | AHS | 97 | 362 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Ena montana (Draparnaud, 1801) | V | AH | 10 | 12 | Mid-specialist | Neutral | Neutral | Neutral | "High" | Neutral |
| Euconulus fulvus (O.F. Müller, 1774) | * | AHS | 52 | 86 | Neutral | Neutral | Mid-specialist | Neutral | "Low" | "Low" |
| Euomphalia striegiella (Draparnaud, 1801) | G | A | 1 | 1 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Helix pomatia Linnaeus, 1858 | H | 24 | 87 | Winner | Winner | Winner | Winner | Neutral | Neutral | Neutral |
| Isognomostoma isognomostomos (Schröter, 1784) | * | A | 3 | 3 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Macrogastria plicatula (Draparnaud, 1801) | V | A | 1 | 1 | Winner | Neutral | Neutral | Neutral | Neutral | Neutral |
| Macrogastria ventricosa (Draparnaud, 1801) | * | AH | 5 | 6 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Monacha cartusiana O.F. Müller, 1774 | * | H | 2 | 2 | Neutral | Neutral | Neutral | Winner | Neutral | Neutral |
| Monachoides incarnatus O.F. Müller, 1774 | * | AH | 46 | 118 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Nesovitrea hammonis (Strom, 1765) | * | AHS | 59 | 169 | Winner | Winner | Neutral | Loser | "Low" | "Low" |
| Nesovitrea petronella (L., Pfeffer, 1853) | 2 | S | 1 | 4 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Oxychilus cellarius (O.F. Müller, 1774) | * | H | 7 | 12 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Oxychilus draparnaudi (Beck, 1837) | * | H | 11 | 15 | Neutral | Neutral | Neutral | Neutral | Neutral | Winner |
| Punctum pygmaeum (Draparnaud, 1801) | * | AHS | 50 | 180 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Pupilla muscorum (Linnaeus, 1758) | V | HS | 2 | 12 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Succinella oblonga (Draparnaud, 1801) | * | A | 2 | 2 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Trochulus hispidus (Linnaeus, 1758) | * | AH | 11 | 16 | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
Table 3 (continued)

| Species                          | RedList | Region | Occurrence | Total abundance | FORMI  | Inonat | Idwcut | Iharv | pH  | Soil moisture |
|----------------------------------|---------|--------|------------|----------------|--------|--------|--------|-------|-----|---------------|
| Trochulus sericeus (Draparnaud, 1801) | *       | AH     | 8          | 12             | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Trochulus striolatus (C. Pfeiffer, 1828) | V       | A      | 16         | 25             | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Urticola umbrosus (C. Pfeiffer, 1828) | V       | S      | 1          | 1              | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vallonia costata (O.F. Müller, 1774) | *       | AS     | 2          | 3              | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vallonia excentrica Sterki, 1893   | *       | AH     | 7          | 25             | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vallonia pulchella (O.F. Müller, 1774) | *       | AHS    | 14         | 38             | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vertigo angustior Jeffreys, 1830  | 3       | A      | 1          | 1              | Neutral| Winner | Neutral| Neutral| Neutral| Neutral       |
| Vertigo pygmaea (Draparnaud, 1801) | *       | HS     | 3          | 9              | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vertigo substrata (Jeffreys, 1833) | 3       | AS     | 2          | 3              | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vitrea contracta (Westerlund, 1871) | *       | AHS    | 40         | 89             | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vitrea crystallina (O.F. Müller, 1774) | *       | AH     | 16         | 30             | Neutral| Neutral| Neutral| Mid-specialist| Neutral| Neutral       |
| Vitrea diaphana (Studer, 1820)     | G       | H      | 11         | 27             | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vitrina pellucida (O.F. Müller, 1774) | *       | S      | 1          | 1              | Winner | Neutral| Neutral| Neutral| Neutral| Neutral       |
| Vitrinobrachium breve (A. Pérussac, 1821) | *       | A      | 2          | 2              | Neutral| Neutral| Neutral| Neutral| Neutral| Neutral       |
| Zonitoides nitidus (O.F. Müller, 1774) | *       | AS     | 2          | 2              | Winner | Neutral| Neutral| Neutral| Neutral| Neutral       |

Significant values are given in bold

Species responses to land use are assigned as winner, loser or mid-specialist to the following land-use parameters: forest management index (FORMI), the percentage of non-native trees (Inonat), the percentage of dead wood with saw cuts (Idwcut) and the percentage of tree harvesting (Iharv)

Low” and “high” refer to low- and high-gradient species, respectively. Red List status: * = no current risk (least concern), G = endangered to unknown extent, R = very rare, V = near threatened, 1 = critically endangered, 2 = endangered, 3 = vulnerable
Table 4  Red list status, occurrence and total abundance of snail species in the Swabian Alb (A), the Hainich-Dün (H) and the Schorfheide-Chorin (S) in grassland habitats

| Species                      | RedList | Region | Occurrence | Total abundance | LUI | Grazing | Mowing | Fertilization | pH | Soil moisture |
|------------------------------|---------|--------|------------|-----------------|-----|---------|--------|---------------|----|---------------|
| Abida secale (Draparnaud, 1801) | G       | A      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Acanthinula aculeata (O.F. Müller, 1774) | *       | AH     | 2          | 2               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Aegopinella nitens (Michaud, 1831) | *       | AHS    | 9          | 15              | neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Aegopinella nitidula (Draparnaud, 1805) | *       | H      | 1          | 2               | Neutral | Neutral | Winner | Neutral | Neutral | Neutral |
| Aegopinella pura (Alder, 1831) | *       | AH     | 21         | 38              | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Candidula unifasciata (Point, 1801) | 2       | AH     | 9          | 46              | Neutral | Neutral | Neutral | Neutral | "High" | "Low" |
| Carychium minimum O.F. Müller, 1774 | *       | AS     | 23         | 381             | Neutral | Neutral | Neutral | Neutral | "High" | "High" |
| Carychium tridentatum (Risso, 1826) | *       | AHS    | 30         | 142             | Neutral | Neutral | Neutral | Neutral | "High" | "High" |
| Cecloides acicula (O.F. Müller, 1774) | *       | AH     | 2          | 2               | Neutral | Winner | Neutral | Neutral | Neutral | Neutral |
| Cepaea hortensis (O.F. Müller, 1774) | *       | AH     | 3          | 3               | Neutral | Winner | Loser | Neutral | Neutral | Neutral |
| Cepnicola lubrica (O.F. Müller, 1774) | *       | AH     | 77         | 546             | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Cochlidina laminata (Montagu, 1803) | *       | H      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Columella aspera Walden, 1966 | *       | A      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Discus rotundatus (O.F. Müller, 1774) | *       | AHS    | 12         | 28              | Neutral | Neutral | Neutral | Neutral | "Winner" | Neutral | "Low" |
| Eucoberia diaphana (Draparnaud, 1805) | *       | H      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Euconulus fulvus (O.F. Müller, 1774) | *       | S      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Euomphalia strieglia (Draparnaud, 1801) | G       | A      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Granaria frumentum (Draparnaud, 1801) | 2       | A      | 2          | 18              | Neutral | Neutral | Neutral | Neutral | "High" | Neutral |
| Helicella itala (Linnaeus, 1858) | 3       | AH     | 11         | 28              | Neutral | Neutral | Neutral | Neutral | "High" | Neutral |
| Helicodonta obvoluta (O.F. Müller, 1774) | *       | A      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Helix pomatia Linnaeus, 1858 | *       | H      | 3          | 6               | Neutral | Neutral | Neutral | Neutral | "Mid-specialist" | Neutral |
| Macrogastria ventricosa (Draparnaud, 1801) | *       | AH     | 3          | 3               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Monacha cartusiana O.F. Müller, 1774 | *       | HS     | 2          | 34              | Winner | Neutral | Neutral | Neutral | Neutral | Neutral |
| Monachoides incarnatus O.F. Müller, 1774 | *       | AH     | 3          | 3               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Nesovitrea hammonis (Strom, 1765) | *       | AHS    | 16         | 35              | Neutral | Neutral | Neutral | Neutral | "Low" | Neutral |
| Oxychilus draparnaudi (Beck, 1837) | *       | A      | 1          | 2               | Neutral | Neutral | Neutral | "Winner" | Neutral | Neutral |
| Plotyla polita (Hartmann, 1840) | 3       | A      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Pseudotrichia rubiginosa | 2       | S      | 1          | 1               | Neutral | Neutral | Neutral | Neutral | "High" | Neutral |
| Punctum pygmaeum (Draparnaud, 1801) | *       | AHS    | 14         | 28              | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Pupilla muscorum (Linnaeus, 1758) | V       | AHS    | 70         | 1087            | Neutral | Neutral | Neutral | Neutral | "High" | Neutral |
| Pupilla alipica (Clessin, 1871) | R       | S      | 12         | 530             | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Succinea putris Beck, 1837 | *       | S      | 13         | 165             | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Succinella oblonga (Draparnaud, 1801) | *       | AHS    | 25         | 57              | Neutral | Neutral | Neutral | Neutral | Neutral | Mid-specialist |
| Trochulus hispidus (Linnaeus, 1758) | *       | AHS    | 29         | 215             |Neutral | Neutral | Neutral | Neutral | "Winner" | Neutral |
| Trochulus sericeus (Draparnaud, 1801) | *       | AH     | 9          | 14              | Neutral | Neutral | Neutral | Mid-specialist | Neutral | Neutral |
| Species                        | RedList | Region | Occurrence | Total abundance | LUI   | Grazing | Mowing | Fertilization | pH   | Soil moisture |
|-------------------------------|---------|--------|------------|----------------|-------|---------|--------|---------------|------|---------------|
| * Trochulus striolatus (C. Pfeiffer, 1828) | V       | A      | 1          | 1              | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Truncatellina cylindrica (A. Férussac, 1807) | 3       | AH     | 4          | 14             | Loser  | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vallonia costata (O.F. Müller, 1774) | *       | AHS    | 40         | 493            | Neutral | Neutral | Neutral | Neutral | Neutral | Mid-specialist |
| Vallonia enniensis (Gredler, 1856) | 1       | AS     | 5          | 63             | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vallonia excentrica Sterki, 1893 | *       | AHS    | 106        | 1829           | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vallonia pulchella (O.F. Müller, 1774) | *       | AHS    | 96         | 3456           | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vertigo angustior Jeffrey, 1830 | 3       | S      | 9          | 47             | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vertigo antivertigo (Draparnaud, 1801) | V       | AS     | 12         | 102            | Neutral | Neutral | Neutral | Loser | "High" | Neutral |
| Vertigo pygmaea (Draparnaud, 1801) | *       | AHS    | 69         | 355            | Loser  | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vertigo substrata (Jeffrey, 1833) | 3       | S      | 1          | 2              | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vitrea contracta (Westerlund, 1871) | *       | AH     | 5          | 8              | Loser  | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vitrea diaphana (Studer, 1820) | G       | H      | 2          | 2              | Neutral | Neutral | Neutral | Neutral | Neutral | Neutral |
| Vitrina pellucida (O.F. Müller, 1774) | *       | AHS    | 10         | 16             | Loser  | Neutral | Neutral | Neutral | Neutral | Mid-specialist |

Significant values are given in bold.

Species are assigned as winner, loser or mid-specialist to the following land-use parameters land-use index (LUI), grazing, mowing and fertilization intensity. "Low" and "high" refer to low- and high-gradient species, respectively. Red List status: * = no current risk (least concern), G = endangered to unknown extent, V = near threatened, 1 = critically endangered, 2 = endangered, 3 = vulnerable.
human land use are less frequently discussed. Our previous study [27] focused on land snail density, diversity and species composition and emphasized that direct impacts of land use on snail communities were on average lower than the impact of abiotic drivers and biotic substrates. However, unlike several studies on insects, few direct effects have been shown for wood harvesting in forests and mowing in grasslands on snail diversity [27]. How these direct land-use effects influence populations of single species and whether these effects are related to species-specific traits remains largely unclear.

Our study showed that snail assemblages varied consistently in their trait composition (shell size, number of offspring, light and humidity preference, drought resistance and inundation tolerance) across regions and among the two habitats, forests and grasslands. The variation between regions is consistent with a biogeographic gradient of increasing land snail diversity from the north to south caused by historical and ecological factors (temperature, moisture) [12, 22] and snail species responded differently to variable physical environments [13]. Local environmental conditions have been shown to explain about 19% of the trait variability of a snail metacommunity in Sweden [17], where the authors suggested that the unexplained variation may mirror land use. Our results confirmed that land-use intensity significantly influenced the trait distribution of snail communities, a pattern that was more pronounced in forest habitats than in grasslands. Since snail species in forest communities seem to be more specialized than those of grassland communities [12, 28], they may suffer more from habitat changes. For example, as the activity level of snails is temperature-dependent, thinning the canopy by wood harvesting or a high amount of non-native trees can enhance solar irradiance and the enhanced snail locomotion allows the exploitation of ambient heterogeneity [29] and may favor species with higher light preferences. This hypothesis is consistent with results from snail assemblages in our study, since the community-weighted mean (CWM) of light preference increased with the amount of non-native, mainly coniferous trees that may not have a closed canopy. Furthermore, changes of the community trait composition are not only directly caused by land-use parameters, but also by indirectly changing abiotic factors such as soil pH and soil moisture although most snail species exhibit broad niches for these abiotic factors.

In our study, 4% of all forest and 21% of all grassland snail species were significant losers concerning the

---

**Fig. 2** Relation between the responses (abundance-weighted mean) of each snail species to fertilization (a) and soil pH (b) and their proportional occurrence in forests. Indicated species above the line are significant "winners" for fertilization respective soil pH, indicated species below the line (in italic) are significant "losers"
| Species                      | Schorfheide-Chorin | Hainich-Dün          | Swabian Alb     |
|------------------------------|--------------------|----------------------|-----------------|
| Acanthinula aculeata         |                    |                      |                 |
| Aegopinella nitens           |                    |                      |                 |
| Aegopinella pura             |                    |                      |                 |
| Carychium minimum            |                    |                      |                 |
| Carychium tridentatum        |                    |                      |                 |
| Cecilia acicula              |                    |                      |                 |
| Clausilia bidentata          |                    |                      |                 |
| Cochlicopa lubrica           |                    |                      |                 |
| Discus rotundatus            |                    |                      |                 |
| Euconulus fulves             |                    |                      |                 |
| Helicodonta obvoluta         |                    |                      |                 |
| Pseudotrichia rubiginosa     |                    |                      |                 |
| Puncatum pygmaeum            |                    |                      |                 |
| Monarcha cartusiana          |                    |                      |                 |
| Monachoides incarnatus       |                    |                      |                 |
| Nesovitrea hammonis          |                    |                      |                 |
| Nesovitrea petronella        |                    |                      |                 |
| Oxychilus cellarius          |                    |                      |                 |
| Oxychilus draparnaudi        |                    |                      |                 |
| Platyia polita               |                    |                      |                 |
| Pupilla muscorum             |                    |                      |                 |
| Vertigo antivertigo          |                    |                      |                 |
| Vertigo pygmaea              |                    |                      |                 |
| Vertigo substria            |                    |                      |                 |
| Vitrea contracta             |                    |                      |                 |
| Vitrea crystallina           |                    |                      |                 |
| Vitrea diaphana              |                    |                      |                 |
| Vitrea limosa                |                    |                      |                 |
| Vitrea pellucida             |                    |                      |                 |
| Vertigo pygmea               |                    |                      |                 |
| Vertigo antivertigo          |                    |                      |                 |
| Vertigo pygmaea              |                    |                      |                 |
| Vertigo substria            |                    |                      |                 |
| Vitrea contracta             |                    |                      |                 |
| Vitrea crystallina           |                    |                      |                 |
| Vitrea diaphana              |                    |                      |                 |
| Vitrea limosa                |                    |                      |                 |
| Vitrea pellucida             |                    |                      |                 |

Fig. 3 Proportional distribution of land snail species in the Schorfheide-Chorin, the Hainich-Dün and the Swabian Alb. Grasslands are given in light grey, forests in dark grey. The three most abundant species are symbolized by big circles, less abundant species by small circles. Species that are underlined are specific for the respective region. Percentages in brackets indicate the proportional occurrence of species of the same genus.
Table 5  Statistical p values of a general linearized model with Poisson distribution testing the influence of land-use parameters and abiotic factors on species vulnerability

| Species vulnerability | Estimate | p value | Species vulnerability | Estimate | p value |
|-----------------------|----------|---------|-----------------------|----------|---------|
| FORMI                 | −0.224   | 0.689   | LUI                   | −0.511   | 0.256   |
| Occurrence            | −1.441   | 0.002   | Occurrence            | −1.303   | <0.001  |
| Total abundance       | 0.546    | 0.158   | Total abundance       | 0.673    | 0.001   |
| Inonat                | −0.424   | 0.150   | Mowing                | −0.031   | 0.903   |
| Occurrence            | −1.512   | 0.002   | Occurrence            | −1.227   | <0.001  |
| Total abundance       | 0.598    | 0.112   | Total abundance       | 0.638    | 0.001   |
| Idwcut                | −0.094   | 0.945   | Grazing               | −0.049   | 0.339   |
| Occurrence            | −1.454   | 0.005   | Occurrence            | −1.212   | <0.001  |
| Total abundance       | 0.573    | 0.177   | Total abundance       | 0.643    | <0.001  |
| llarv                 | 0.119    | 0.948   | Fertilization         | −0.038   | 0.413   |
| Occurrence            | −1.477   | 0.002   | Occurrence            | −1.224   | <0.001  |
| Total abundance       | 0.594    | 0.103   | Total abundance       | 0.616    | 0.001   |
| pH                    | 0.198    | 0.573   | pH                    | 0.092    | 0.849   |
| Occurrence            | −1.643   | 0.004   | Occurrence            | −2.001   | <0.001  |
| Total abundance       | 0.699    | 0.104   | Total abundance       | 0.615    | 0.012   |
| Soil moisture         | 0.039    | 0.333   | Soil moisture         | −0.043   | 0.330   |
| Occurrence            | −1.719   | 0.002   | Occurrence            | −1.184   | <0.001  |
| Total abundance       | 0.726    | 0.063   | Total abundance       | 0.631    | 0.001   |

Significant values are given in bold.

Fig. 4  Species vulnerability in relation to the five-dimensional niche hypervolume in forest (a) and grassland (b). The hypervolume was the product of the abundance-weighted standard deviations (AWSDs) of all single land-use components as well as pH and soil moisture in forests or grasslands, respectively.
compound indices of land-use intensity, including three land-use components in the forests or in the grasslands, respectively. The proportion of losers among grassland snail species was lower than the level found for grasshoppers (about 52%) [30] and plant- and leafhoppers (about 34%) [9], but similar to that for moths (28%) [31], confirming that snails are a suitable indicator for habitat quality and land-use intensity [17, 22, 32, 33]. The low proportion of loser species may be explained by their ground-living behavior (intangible for combine harvesters), the presence of a shell (protection against exposure and predation) and a larger diet breath compared to insect taxa (omnivory for flexibly changing food resources). However, we may have underestimated the amount of loser species since we did not distinguish between living individuals and empty shells. Empty shells decay at different rates under different ecological conditions [44]. Therefore, in some cases we may have evaluated shells of species which can no longer be found alive in the respective places. Keeping this in mind, our methodological approach may have ramifications on the conclusions drawn.

While increasing land-use intensity in open habitats is known to trigger a decline of pollinator species, and such losses were associated with species-specific trait attributes such as a narrow diet breadth, climate specialization, a large body-size and low fecundity [33–39], we did not find traits for snail species to correspond with their land-use response at species level. This is surprising, given that particularly those traits that are associated with soil moisture (drought resistance, inundation tolerance), body size or reproductive outcome are likely to respond to human-mediated disturbances. Furthermore, land-use effects in forests were independent of the species habitat association (i.e. forests specialists were equally affected as non-forests specialists), but grassland specialists suffered more from land use (i.e. fertilization) and were more dependent on high soil pH.

Note that single land-use parameters and abiotic conditions are often confounded in real landscapes as in our study, and thus responses of some snail species may not always correspond to single environmental dimensions as known from their global distribution or other sources. For example, Cochlicopa lubricella is a xerophilic land snail [42] whereas our data showed a neutral response to soil moisture.

Species' vulnerability
The range of resources and the ecological conditions generally define the niche breadth and determine the geographical area of a species at the small or large scale [40]. Specialists are expected to be more vulnerable to habitat loss and climate change due to synergistic effects of a narrow niche and a small range size.

Only a few snails in our study across managed forests and grasslands are considered threatened or endangered according to the national Red List. Consistent with the expectation based on their environmental niche breadth, the species’ vulnerability status was significantly predicted by a particularly narrow niche hypervolume—an index that includes single land-use components as well as pH and soil moisture in each habitat. The smaller the hypervolume of a species, the higher its vulnerability according to the Red List. In addition, rarity was important: in forests, the most important predictor for their vulnerable status was a low number of sites in which they occurred. In grasslands, both their restricted occurrence and low total abundance predicted the species’ vulnerability.

Conclusion
In summary, our results indicate that the trait composition of snail communities was significantly altered by land-use intensities and abiotic conditions, and several species especially in grasslands were losers of intensive land use. These land-use and environmental responses were largely independent of specific traits and the species’ Red List status—this suggests that complementary risks may be important for predicting a species’ vulnerability. Instead, species vulnerability was mirrored in the species’ rarity and its overall niche hypervolume including single land-use components and abiotic factors.

Methods
Data origin
Data for this study were already part of a previous analysis of biodiversity and community composition, i.e. Wehner et al. [27] and are available at https://www.bexis.uni-jena.de/PublicData/PublicDataSet.aspx?DataSetId=24986. Wehner et al. [27] collected 15,607 snail individuals belonging to 71 taxa in three regions in Germany in the framework of the Biodiversity Exploratories Project (http://www.biodiversity-exploratories.de) [2]. The collaborative research unit addresses effects of land-use on biodiversity and biodiversity-related ecosystem processes in three regions: the Swabian Alb (ALB), a low-mountain range in South-West Germany (460–860 m a.s.l., 09° 10' 49"–09° 35' 54" E/48° 20' 28"–48° 32' 02" N), the Hainich-Dün (HAI), 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 (SCH), a glacial formed landscape in North-East Germany (3–140 m a.s.l., 13° 23' 27"–14° 08' 53" E/52° 47' 25"–53° 13' 26" N). SCH is characterized by the lowest annual precipitation (520–580 mm), with a mean annual temperature...
of 6–7 °C. It is followed by HAI (630–800 mm, 6.5–8 °C) and ALB (800–930 mm, 8–8.5 °C).

In each region, 100 experimental plots (50 in forests and 50 in grasslands) were setup in 2008 along a land-use gradient covering different management types and intensities including mowing, grazing and fertilization in grasslands and the proportion of non-native trees, the proportion of dead-wood with saw cuts and the proportion of wood harvested in forests (Table 6). Forest plots have a size of 1 ha and grassland plots are 0.5 ha in size.

In June 2017, Wehner et al. [27] took five replicated surface samples from all 50 forest and 50 grassland experimental plots (EPs) in the Swabian Alb and the Hainich, and from 49 forest and 34 grassland plots in the Schorfheide due to constrained accessibility (1415 samples in total). Shelled snails were subsequently determined to the species, genus or family level using [41–43]. Although suggested elsewhere [e.g., 44], [27] did not distinguish between empty shells and living snail individuals.

As our current study focuses on species-level responses, only those individuals that could be assigned to the species level were used (ALB grasslands: 36, ALB forests: 37, HAI grassland: 31, HAI forest: 35, SCH grassland: 24, SCH forest: 21, 61 different land snail species in total). Grassland plots (although not permanently flooded) in one region (Schorfheide) harbored large numbers of aquatic and semi-aquatic snails. In contrast to our previous analysis that covered all snails recorded [27], we excluded aquatic snails from the analyses since their role and responses to terrestrial environmental variables such as land-use in grasslands remain unclear.

**Statistical analyses**

All statistical analyses were performed in R 3.5.2 [45] using the main packages “car” [46], “dplyr” [47], “lme4” [48] and “SMDTools” [49].

**Trait composition of snail communities**

Morphological and life-history trait values for all snail species were obtained from an established trait database by Falkner et al. [50] and compared to findings of [51] whenever possible; see Astor et al. [17] for a similar approach based on [50]. Traits for the set of species in our study are summarized in Table 7. Note that these traits are either continuous variables (size), integers (offspring) or ranks (all others); ranks can be treated as integers or continuous variables for an analysis based on community weighted mean (CWM, see below); the resulting distribution of the CWM in species-rich communities and across a large number of plots typically approach a Gaussian distribution. Moreover, to explore the response to potential environmental filtering, traits with different meaning are treated independently for the following analysis (a common practice, although some traits, e.g. shell size and number of offspring, may be correlated, see [17]).

For comparing snail communities among habitats and regions, the community weighted mean (CWM) of each trait was calculated as CWM per plot $p$.

\[
\text{CWM}_p = \sum_{i=1}^{l} T_i \cdot \frac{a_{i,p}}{A_p}
\]

where $T_i$ is the trait value of species $i$, $a_{i,p}$ is the abundance of species $i$ in plot $p$ and $A_p$ the total abundance of all snails in plot $p$ (total $I$ species).

**Environmental niches**

We characterized the environmental conditions of each forest or grassland plot by its land-use intensity and two abiotic soil parameters (pH and soil moisture; Table 6) [52, 53]. Data were obtained from the BExIS database (Table 6).

We tested the response of the CWM of each trait to variation in environmental conditions using linear regressions. Values for grazing and fertilization were square root transformed before statistical analyses.

In order to characterize the snail species’ responses to environmental conditions (land-use gradient, soil conditions), we calculated each species’ “environmental niche”. The method has been established in the context of the Biodiversity Exploratories and was applied to several taxa such as grasshoppers [30], cicadas, moths [31], bumblebees [54] or plants [55]. The “niche optimum” was calculated as the abundance weighted mean (AWM) for species $i$ as

\[
\text{AWM}_i = \sum_{p=1}^{n_p} L_p \cdot \frac{a_{i,p}}{A_i}
\]

where $n_p$ is the number of plots investigated, $L_p$ is the land-use gradient value of plot $p$, $a_{i,p}$ the abundance of species $i$ in plot $p$ and $A_i$ the total abundance of species $i$ across all 149 forest or 134 grasslands sites, respectively. Hence, the CWM characterizes the plots by the trait distribution of snails, and the AWM characterizes snail species by the environmental conditions of the plot, and the snail abundance $a_{i,p}$ is used to weight either species or plot, respectively.

In addition to the AWM as a niche optimum, we also characterized the “niche breadth” of each species to a single environmental variable using the abundance-weighted standard deviation (AWSD) [30]. To test whether AWMS and AWSDs statistically deviate from an expected random distribution, we compared the calculated values against the expected values obtained from a null model that distributes each species across $N_i$ sites.
| Habitat         | Land-use parameter | Description/unit                                                                 | Range       | References                                      | Dataset ID               | Source/owner                                      | Year used     |
|-----------------|--------------------|-----------------------------------------------------------------------------------|-------------|------------------------------------------------|--------------------------|--------------------------------------------------|---------------|
| Grassland       | Mowing             | Frequency per year                                                                | 0–3         | Blüthgen et al. 2012 [41]                      | 19266 version 1.1.5.12  | Katrin Lorenzen                                   | Mean of 2015/2016 |
|                 | Grazing            | Livestock units x days of grazing x ha\(^{-1}\) x year\(^{-1}\)                  | 0–851       | Blüthgen et al. 2012 [41]                      |                          | Wolfgang Weisser                                  | Mean of 2015/2016 |
|                 | Fertilization      | Kg nitrogen x ha\(^{-1}\) x year\(^{-1}\)                                       | 0–433       | Blüthgen et al. 2012 [41]                      |                          | Manfred Ayasse                                    | Mean of 2015/2016 |
|                 | Land-use index LUI | The compound LUI index adds fertilization plus mowing plus grazing intensities. Each individual LUI component (fertilization, mowing and grazing) was standardized relative to its mean within the corresponding model region | 0.53–452    | Blüthgen et al. 2012 [41]                      |                          | Markus Fischer Juliane Vogt                        | Mean of 2015/2016 |
| Forest          | Proportion of non-native trees | Estimated as the proportion of harvested, living and dead wood volume of non-natural tree species to the sum volume of all tree species | 0–1         | Kahl and Bauhus 2014 [40]                      | 24646 version 1.2.8     | Peter Schall Christian Ammer Jürgen Bauhus          | 2017          |
|                 | Proportion of dead-wood with saw cuts | Represents the proportion of dead wood with saw cuts to the total amount of dead wood | 0–1         | Kahl and Bauhus 2014 [40]                      |                          | 2017                                              |               |
|                 | Proportion of wood harvested | Describes the proportion of harvested tree volume within a stand and is estimated by the presence of cut stumps and calculated as the ratio of harvested volume to the sum of standing, harvested and dead wood volume | 0–1         | Kahl and Bauhus 2014 [40]                      |                          | 2017                                              |               |
|                 | Forest management index Formi | The Formi is the sum of three components taking into account: 1. the proportion of harvested tree volume, 2. the proportion of tree species that are not part of the natural forest community and 3. the proportion of dead wood showing signs of saw cuts. Each component ranges between 0 (no sign of management) and 1 (intensive management) | 0–2.82      | Kahl and Bauhus 2014 [40]                      |                          | 2017                                              |               |
| Grassland/forest| Soil pH            |                                                                                   | 3.0–6.7     | 22246 Verion 1.1.9                             | Ingo Schöning Theresa Klotzing | Mean 2017                                         |               |
### Table 6 (continued)

| Habitat | Land-use parameter | Description/unit | Range      | References                    | Dataset ID | Source/owner                      | Year used       |
|---------|--------------------|------------------|------------|-------------------------------|------------|-----------------------------------|-----------------|
|         | Soil moisture      | Soil moisture in 10 cm depth, as percentage of the volumetric water content | 8.55–55.22 | Weather station | Marion Schrumpf | Antonios Apostolakis, Susan Trumbore | Mean May 2017   |
|         |                    |                  |            | Climate tool                  | Falk Hänsel, Stephan Wöllauer, Thomas Nauss |                      |                  |
with the same probability, with $N_i$ being the number of sites in which species $i$ was found. The null model thus chooses values of the focal land-use parameter (LUI, Formi, single components, pH, soil moisture) of $N_i$ sites and calculates a distribution of predicted AWMs and AWSDs values for each species based on 10,000 iterations. The null model was restricted to the one, two, or three regions in which the species was recorded to consider potential distribution boundaries of each species in Germany that may not be related to plot conditions [30].

As in any randomization model, the proportion of AWMs or AWSDs from 10,000 null models with greater or smaller expected values respectively than the observed value, provides the $p$ value for the significance of the deviation between observed and expected values. A ‘winner’ is defined as a species with an observed AWM larger than the upper 5% of the distribution of AWMs obtained by the null models (i.e. adapted on higher-than average land-use intensity), a ‘loser’ shows an observed AWM smaller than the lower 5% (low land-use intensity specialist). For species which could be classified neither as ‘losers’ nor as ‘winners’, we tested whether they are specialized on intermediate land-use or abiotic levels, that is, whether they have an intermediate AWM with a narrower niche than expected. We standardized the niche breadth as weighted coefficient of variation ($CV = AWSD/AWM$) to account for the increase in SD with increasing mean, and compared observed CV and expected CV from the null models. This comparison allows us to distinguish ‘opportunists’ (observed CV $\geq$ expected CV) from species that are ‘specialized’ on intermediate land-use intensities (observed CV $< $ expected CV and species not only occurring on one site, i.e., CV $\neq 0$) [30]. The environmental niche (AWM, AWSD) and the assignment of low- and high-gradient specialists were also calculated for soil pH and soil moisture, although we did not adopt the ‘loser’/‘winner’ terminology here unlike for land-use intensity.

### Species vulnerability

Vulnerability (classified as a rank variable comparable to IUCN categories: least concern, endangered to unknown extent, very rare, near threatened, critically endangered, endangered, vulnerable) of land snail species was obtained from the Red List 2011 (according to [56]; see Table 3). We tested the relation of vulnerability with the species’ habitat association by calculating the proportional occurrence in either forest or grassland habitats of a certain species’ presence; a ‘specialist’ was defined if more than 90% of all individuals found were present in one habitat (forest or grassland). The relation between vulnerability and species’ habitat association was tested by a linear model using the land-use management components and the abiotic conditions as fixed factors and the proportional occurrence as explanatory factor.

To further test if a species’ vulnerability can be predicted by its land-use response (‘winner’ or ‘loser’ status) and its relation to abiotic soil conditions, we used a general linearized model with Poisson distribution including vulnerability as response factor and the respective land-use parameter or abiotic factor, the number of plots where the species occurred and its total abundance as explanatory factors. Values for grazing and fertilization were square-root transformed prior to statistical analyses and data on abundances and occurrence were log transformed because of data structure.

Finally, we calculated a five-dimensional niche hypervolume (consistent with Hutchinson’s $n$-dimensional niche concept) as a proxy for the total ‘niche breadth’ of each snail species by multiplying the abundance-weighted standard deviations (AWSD) of all three single land-use components as well as of pH and soil moisture, respectively. The hypervolume was defined for forests and grasslands separately.

Whether the total niche breadth can predict vulnerability was tested using a Spearman rank correlation between the vulnerability and the five-dimensional niche hypervolume.
Influence of the abundance-weighted mean (AWM) of soil pH on the maximum shell size, number of offspring, light preference, humidity preference, drought resistance and inundation tolerance in forests. Species in italics are land-use "winners", species in bold are land-use "losers".

Additional file 13: Appendix 13. Influence of the abundance-weighted mean (AWM) of soil moisture on the maximum shell size, number of offspring, light preference, humidity preference, drought resistance and inundation tolerance in grasslands. Species in italics are land-use "winners", species in bold are land-use "losers".

Additional file 14: Appendix 14. Relation of the abundance-weighted means (AWM) of the forest management index, proportion of non-native trees, proportion of dead wood with saw cuts, proportion of wood harvested, pH and soil moisture and the proportional occurrence of a certain species in forests.

Additional file 15: Appendix 15. Relation of the abundance-weighted means (AWM) of the land-use intensity, mowing, grazing, fertilization, pH and soil moisture and the proportional occurrence of a certain species in forests.

Acknowledgements
We thank the managers of the three Exploratories, Kirsten Rechel-Jung, Iris Steitz, and 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 data base, and Markus Fischer, Eduard Lisenmaier, Dominik Heissenmüller, Daniel Prati, Ingo Schöning, François Buscot, Ernst-Detlef Schulte, 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, Sebastian Schmelzle, Twannakit Mermagen, Kathrin Ziegler, Annika Keil, Andreas Kerner, Katja Gruschwitz, and Kimberly Adam.

Authors’ contributions
KW did the fieldwork, collected and determined snail species, performed the statistical analyses and wrote the manuscript. CR assisted in the species determination and commented on the manuscript. NKS assisted in the statistical analyses and commented on the manuscript. WWW and NB designed the study, NB also assisted in the statistical analyses and the paper writing. All authors have approved to the final version.

Funding
Open Access funding enabled and organized by Projekt DEAL. The work has partly been funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (DFG BL860/8-3).

Availability of data and materials
Snail data obtained by [27] and used in this study are available online under https://www.bexis.uni-jena.de/PublicData/PublicDataSet.aspx?DataSetId=24986. Data on snail vulnerability were obtained from the Red List 2011 according to [43] and snail traits were extracted from [38]. Environmental data and those for land-use intensity in grasslands and forests were obtained from the BExIS database (see Table 6).

Ethics approval and consent to participate
The study complied the fundamental principles of the Basel declaration for research in animals. The investigated species are not at risk of extinction.

Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.
Author details
1 Ecological Networks, Technische Universität Darmstadt, Schnittspahnstraße 3, 64287 Darmstadt, Germany. 2 Naturhistorisches Museum Mainz, Landesammlung für Naturkunde RLP, Reichsstraße 1, 55116 Mainz, Germany. 3 Department of Ecology and Ecosystem management, Technische Universität München, Hans-Carl-von-Carlottiz-Platz 2, 85350 Freising-Weihenstephan, Germany.

Received: 30 November 2020 Accepted: 22 December 2020
Published online: 01 February 2021

References
1. Poschold P, Bakker JP, Kahrmen S. Changing land use and its impact on biodiversity. Basic Appl Ecol. 2005;6:93–8.
2. Fischer M, Bosdorff O, Gockel S, Hansel F, Kempf A, Sassenmüller D, Weisser WW, et al. Implementing large-scale and long-term functional biodiversity research: the biodiversity exploratories. Basic Appl Ecol. 2010;11:473–85.
3. Steinhaüßer R, Siebert R, Steinfuhrer A, Hellmich M. National and regional land-use conflicts in Germany from the perspective of stakeholders. Land Use Policy. 2015;49:183–94.
4. Axelsson R, Angelstam P, Svensson J. Natural forest and cultural woodland with continuous tree cover in Sweden: how much remains and how is it managed? Scand J Forest Res. 2007;22:545–58.
5. Socher AS, Prati D, Boch S, Müller J, Klaus VH, Hölzel N, Fischer M. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. J Ecol. 2012;100:1391–9.
6. Simons NK, Gossner MM, Lewinschohn TM, Boch S, Lange M, Müller J, Weisser WW, et al. Resource-mediated indirect effects of grassland management on arthropod diversity. PLoS ONE. 2014;9:e107033.R.
7. Hooper DU, Chapin FS, Ewel JJ, Hector A. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr. 2005;75:3–35.
8. Dornman CF, Schweiger O, Augustin I, Bailey D, Billerle R, De Blust G, Zobel M, et al. Effects of landscape structure and land-use intensity on similarity of plant and animal communities. Global Ecol Biogeogr. 2007;16:774–87.
9. Chisté MN, Mody K, Kunz G, Guenzj J, Blüthgen N. Intensive land use drives small-scale homogenization of plant- and leafhopper communities and promotes generalists. Oecologia. 2018;186:529–40.
10. Astor T, Lenor L, Berg MP. Measuring feeding traits of a range of litter-consuming terrestrial snails: leaf litter consumption, faeces production and scaling with body size. Oecologia. 2015;178:833–45.
11. Cameron R. Slugs and Snails. Collins New Naturalist Library, Book 133; HarperCollins Publishers, ePUB edition, 2006.
12. Limondin-Lozouet N, Preece RC. Quaternary perspectives on the diversity of land snail assemblages from northwestern Europe. J Mollus Stud. 2014;80:224–37.
13. Randolph PA. Influence of environmental variability on land snail population properties. Ecology. 1973;54:933–55.
14. Schamp B, Horsák M, Hjäkem M. Deterministic assembly of land snail communities according to species size and diet. J Anim Ecol. 2010;79:803–10.
15. Hylander K, Nilsson C, Jonsson BG, Götter T. Differences in habitat quality explain nestedness in a land snail meta-community. Oikos. 2005;108:351–61.
16. Hoyermann JT, Davis CJ, Werner EE, Skelly DK, Relywczuk E, Relywczuk KL. Environmental gradients and the structure of freshwater snail communities. Ecoscience. 2011;18:450–58.
17. Astor T, von Puschowitz T, Strengbom J, Berg MP, Bengtsson J. Importance of environmental and spatial components for species and trait composition in terrestrial snail communities. J Biogeogr. 2017;44:1362–72.
18. Goodfellow GA. Variation in land-snail shell form and size and its causes: a review. System Zool. 1986;35:204–23.
19. Baur A, Baur B. Individual movement patterns of the minute land snail Punctum pygmaenum (Draparnaud) (Pulmonata: Endodontidae). Veliger. 1988;30:372–3.
20. Kappes H, Jordens K, Hendrickx F, Maelfait J-P, Lens L, Backeljau T. Response of snails and slugs to fragmentation of lowland forests in NW Germany. Landsc Ecol. 2009;24:685–97.
21. Wärendt I. Changes in the land mollusc fauna and soil chemistry in an inland district in southern Sweden. Ecoscience. 1992;9:56–9.
22. Nekola JC. Large-scale terrestrial gastropod community composition patterns in the Great Lakes region of North America. Divers Distrib. 2003;9:55–71.
23. Martin K, Sommer M. Relationships between land snail assemblage patterns and soil properties in temperate humid ecosystems. J Biogeogr. 2004a;31:531–45.
24. Martin K, Sommer M. Effects of soil properties and land management on the structure of grassland snail assemblages in SW Germany. Pedobiologia. 2004b;48:193–203.
25. Horsák M. Mollusc community patterns and species response curves along a mineral richness gradient: a case study in fens. J Biogeogr. 2006;33:98–107.
26. Denmead LH, Barker GM, Standish RJ, Dutham RK. Experimental evidence that even minor livestock trampling has severe effects on land snail communities in forest remnants. J Appl Ecol. 2013;50:161–70.
27. Wehner K, Renker C, Brückner A, Simons NK, Weisser WW, Blüthgen N. Land-use affects land snail assemblages directly and indirectly by modulating abiotic and biotic drivers. Ecosphere. 2019;10(5):e02726.
28. Cameron RAD, Down K, Pannett DJ. Historical and environmental influences on hedgerow snail faunas. Biol J Linn Soc. 1980;13:75–87.
29. Chappelon C, Seuront L. Space-time variability in environmental thermal properties and snail thermoregulatory behavior. Funct Ecol. 2011;25:1040–50.
30. Chisté M, Mody K, Gossner MM, Simons NK, Köhler G, Weisser WW, Blüthgen N. Lossers, winners, and opportunists: How grassland land-use intensity affects orthopteran communities. Ecosphere. 2016;7(11):e01545.
31. Mangels J, Fiedler K, Schneider FD, Blüthgen N. Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists. Biodivers Conserv. 2017;26:3385–405.
32. Čejeta T, Hamrlik L. Land snails as indicator of soil humidity in Danubian woodlands (SW Slovakia). Pol J Ecol. 2009;57:741–7.
33. Banaszak-Cibicka W, Zmiłorski M. Wild bees along an urban gradient: winners and losers. J Insect Conserv. 2011;15:331–43.
34. Douglas DD, Brown DR, Pederson N. Land snail diversity can reflect degrees of anthropogenic disturbance. Ecosphere. 2013;4:1–14.
35. McKinney ML, Lockwood JL. Biotic homogenization: a few winners replacing many losers in the next mass extinction. TREE. 1999;11:450–3.
36. Williams P, Colla S, Xie Z. Bumblebee vulnerability: common correlates of winners and losers across three continents. Conserv Biol. 2008;23:391–40.
37. Rader R, Bartomeus I, Tylianakis JM, Lalibertè E. The winners and losers of land use intensification: pollinator community disassembly is non-random and alters functional diversity. Divers Divers. 2014;20:908–17.
38. Weiner CN, Werner M, Linsemar M, Blüthgen N. Land use impacts on mutualistic networks: disproportional declines in specialized pollinators via changes in flower composition. Ecology. 2014;95:466–74.
39. Kühsel S, Blüthgen N. High diversity stabilizes the thermal resilience of pollinator communities in intensively managed grasslands. Nat Commun. 2015;6:7989.
40. Slattery RA, Hirst M, Sexton JP. Niche breadth predicts geographical range size: a general ecological pattern. Ecol Lett. 2013;16:1104–14.
41. Welter-Schulz F. European non-marine molluscs. A guide for species identification. Gottingen: Poster Editions, 2012.
42. Wiebe V. Die Landschneecken Deutschlands. 2nd ed. Wiebelsheim: Quelle & Meyer, 2016.
43. Süßwassermollusken GP. Ein Bestimmungsschluessel für die Muscheln und Schnecken im Süßwasser der Bundesrepublik Deutschland. Göttingen: Deutscher Jugendbund fuer Naturbeobachtungen, 2017.
44. Pearce TA. When a snail dies in the forest, how long will the shell persist? Effect of dissolution and micro-bioerosion. Am Malacol Bull. 2008;26:111–7.
45. R Core Team. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing, 2010.  http://www.R-project.org/. ISBN 3-900051-07-0.
46. Fox J, Weisberg S. An R companion to applied regression. 2nd ed. Thousand Oaks: Sage; 2011.
47. Wickham H, Francois R, Henry L, Muller K. dplyr: A grammar of data manipulation. 2019.  https://dplyr.tidyverse.org, https://github.com/tidyverse/dplyr.
48. Bates D, Maechler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Softw. 2015;67(1):1–48.
49. VanDerWal J, Falconi L, Januchowski S, Shoo L, Storlie C. `SMDTools` - species distribution modelling tools: tools for processing data associated with species distribution modelling exercises. 2014. http://tidyverse.tidyverse.org, https://github.com/tidyverse/tidyr.
50. Falkner G, Obrdlik P, Castella E, Speight MCD. Shelled gastropoda of Western Europe. Munich: Friedrich-Held-Gesellschaft; 2001.
51. Fromming E. Biologie der mitteleuropäischen Landgastropoden. Berlin: Duncker & Humblot; 1954.
52. Kahl T, Bauhus J. An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin. Nat Conserv. 2014;7:15–27.
53. Blüthgen N, et al. A quantitative index of land-use intensity in grasslands: integrating mowing, grazing and fertilization. Basic Appl Ecol. 2012;13:207–20.
54. Kämper W, Weiner C, Kühsel S, Storm C, Thomas ELTZ, Blüthgen N. Evaluating the effects of floral resource specialisation and of nitrogen regulation on the vulnerability of social bees in agricultural landscapes. Apidologie. 2017;48(3):371–83.
55. Busch V, Klaus VH, Schäfer D, Prati D, Boch S, Müller J, Hölzel N, et al. Will I stay or will I go? Plant species-specific response and tolerance to high land-use intensity in temperate grassland ecosystems. J Veg Sci. 2019;30(4):674–86.
56. Jungbluth J, von Knorre D, Rößneck U, Groh K, Hackenberg E, Kobialka, Zettler M, et al. Rote Liste und Gesamtartenliste der Binnenmollusken (Schnecken und Muscheln; Gastropoda et Bivalvia) Deutschlands. 6. überarbeitete Fassung, Stand Februar 2019. Naturschutz Biolog Vielfalt. 2011;70(3):647–708.

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