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Beyond the forest: terrestrial snails as bioindicators of Afromontane deforestation and land-use change

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ABSTRACT

Tropical Afromontane forest is experiencing rapid deforestation and land-use change, threatening biodiversity in one of the world's richest ecosystems. In Rwanda's Gishwati–Mukura landscape, primary forest has been largely replaced by agroforestry systems, tea plantations, and exotic tree monocultures. Using land snails as bioindicators, we investigated species richness, diversity, and community composition across seven land-use types and five levels of surface degradation. A total of 3235 individuals representing 118 species were sampled from 173 plots using standardized litter and soil collection. Primary forest harbored the highest species richness and diversity, followed by *Alnus* plantations, while *Eucalyptus, Pinus*, and tea plantations supported impoverished communities. Species richness (Hill number $q = 0$) and Shannon diversity (Hill number $q = 1$) declined significantly with increasing surface degradation. Assemblage composition was strongly influenced by land-use type and environmental variables, particularly leaf litter depth and distance to the nearest protected area. Non-metric multidimensional scaling showed that *Alnus* plantations clustered closely with primary forest, indicating structural and compositional similarities. In contrast, other plantation types and home gardens showed greater internal heterogeneity and supported more generalist or disturbance-tolerant species. Morisita–Horn similarity indices revealed that species dominance patterns also varied across land-use types. Our results highlight the ecological importance of remnant primary forest and show that although *Alnus* plantations can support land snail diversity and assemblage composition comparable to primary forest, they exhibit a markedly different dominance structure. This finding reinforces the need to move past traditional species-level metrics when evaluating land-use change, incorporating additional parameters such as species assemblage composition and dominance structure. Effective conservation in the Gishwati–Mukura landscape should prioritize protecting remaining forests while promoting restoration strategies that enhance microhabitat quality and sustain native biodiversity.

1. Introduction

One of the most pressing environmental issues worldwide is the deforestation of tropical rainforest, with approximately 6.7 million hectares of primary forest lost in tropical regions in 2024 alone (World Resources Institute, 2025). Deforestation in tropics is primarily driven by clearing land for agricultural expansion—especially cattle ranching and the cultivation of cash crops—as well as timber logging, mining, and infrastructure development (Hosonuma et al., 2012; Curtis et al., 2018; Gagen et al., 2023). Tropical rainforests are critical for numerous ecosystem functions and services, such as global climate regulation, water cycles and biodiversity (Pan et al., 2011; Gibson et al., 2011; Pillay et al., 2024; Qian et al., 2025). Their destruction contributes significantly to greenhouse gas emissions (10% of global annual emissions; Friedlingstein et al., 2022; Brasika et al., 2025), biodiversity loss, displacement of indigenous communities, and reduced resilience against climate change (Senior et al., 2019; Ometto et al., 2022; Grodofzig et al., 2024; Vallejos et al., 2025). Over the last two decades, forest restoration

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is increasingly viewed as a suitable response to tropical deforestation, but restoration initiatives have placed greater emphasis on expanding tree cover rather than preserving biodiversity (Castro et al., 2021; Brancalion et al., 2025). Even though some restoration initiatives genuinely aim to value biodiversity, they often fail to improve the status of low-profile taxa such as soil invertebrates, fungi, or small terrestrial molluscs that respond strongly to microhabitat conditions and subtle ecological interactions. This is largely because they narrowly focus on species richness—rather than diversity and community structure—of one or a few high-profile plant or animal taxa (e.g., trees and birds that are large, long-lived, and easily observed; Brancalion et al., 2025).

Between 2010 and 2020, Africa lost an average of 3.9 million hectares of forest annually, giving the continent both the highest net forest loss globally and a steadily increasing decadal deforestation rate since 1990 (FAO, 2020). Likewise, Rwanda—the country with the largest proportion of Afromontane Forest in Africa—experienced significant shifts in forest cover over the last three decades (Mlotha, 2018; Arakwiye et al., 2021). Forest covered about 26% of national territory in 1993 but declined—due to conflict and land clearance—to 19% in 2004. Between 2009 and 2019, Rwanda lost around 105,700 ha, i.e., a 15.7% decline in forest area, but planted roughly 139,600 ha of new forests corresponding to a 20.7% increase (REMA, 2021). However, this gain was largely based on exotic tree species such as *Pinus*, *Eucalyptus*, *Grevillea*, and *Alnus* (REMA, 2021; Mugabowindekwe et al., 2023). Typical for this development is the Gishwati–Mukura landscape in western Rwanda, a biodiversity hotspot in the Albertine Rift Valley, which suffered severe deforestation and substantial land use changes transitioning natural forest into a mosaic of cropland, rangeland, tea plantations and agroforestry (Mukuralinda et al., 2016; Mlotha, 2018; Arakwiye et al., 2021; Hagumubuzima et al., 2022). Since 2015, the primary forest of Gishwati and Mukura Forest, are protected as a national park, alongside ongoing efforts to restore the surrounding landscape and preserve biodiversity (Kisioh, 2015; Tuyisingize et al., 2022).

This setting allows a direct comparison of deforested areas against the benchmark of a reference ecosystem, i.e., the primary forest of Gishwati and Mukura forest fragment, which is essential for understanding what follows the Afromontane deforestation and how different land use types support biodiversity recovery (Brancalion et al., 2025). High-profile taxa such as birds and vascular plants (usually trees) are widely used as ecological indicators for assessing the effects of land-use change in tropical landscapes (Gillison et al., 2013; Martin et al., 2020; Dröge et al., 2021; Carvalho et al., 2022; Mugatha et al., 2024). However, assessments based on a few well-studied or charismatic taxa may give only a partial view of biodiversity responses to land-use change. Many restoration and land-management studies focus on species richness while overlooking shifts in community composition, dominance, and less conspicuous but ecologically important taxa. Consequently, it remains unclear how different post-deforestation land-use systems—such as tree plantations and small-scale agriculture—support the recovery of forest-associated biodiversity beyond a few well-studied taxa.

For this reason, it is recommended to base diversity and community structure assessments also on low-profile taxa, such as land snails, a taxonomically diverse and ecologically sensitive invertebrate group that is largely underutilized in environmental assessment and biodiversity monitoring. Land snails are particularly sensitive to habitat changes due to low mobility, small home ranges, and specific habitat requirements, making their community composition a reliable indicator of environmental change (Foltz Jordan and Hoffman Black, 2012; Douglas et al., 2013; Nurinsiyah et al., 2016; Gheoca et al., 2021). Forest-dwelling land snails constitute a functionally important invertebrate group whose diversity, microhabitat specificity, and strong dependence on moisture and leaf-litter conditions make them especially valuable for detecting subtle changes in forest ecosystem integrity (Wehner et al., 2021; Gheoca et al., 2021, 2023). Despite these characteristics, the responses of land snail communities to tropical deforestation and land-use conversion remain poorly understood, especially in Afromontane landscapes. Most studies focused on intact forests, limiting insight into how agricultural systems, plantations, and restoration areas differ in supporting forest-associated invertebrates. It also remains unclear whether alternative land-use types can maintain community structures and dominance patterns similar to those in primary forests. Addressing these gaps is crucial for evaluating restoration outcomes and identifying land-use types that help conserve forest-dependent taxa in human-modified tropical landscapes.

Given this, we studied the land snail fauna of the Gishwati-Mukura landscape, which once had—based on reports from neighboring Nyungwe NP (Boxnick et al., 2015)—a rich land snail fauna of more than 100 species. We explored land snail diversity and community structure in seven dominant land-use types following the destruction of primary forest, including tea plantations, small-scale agricultural (home gardens), tree plantations (including *Alnus, Pinus*, and *Eucalyptus* species, as well as mixed *Pinus–Eucalyptus* stands), and—as a reference system—the primary Afromontane forest of Gishwati and Mukura forest fragment. We focused on the following research questions: (i) How do snail diversity metrics, expressed as the Hill number, $q = 0$ (species richness) and $q = 1$ (Shannon diversity), vary between primary forests and other land-use types, as well as across a gradient of five levels of surface degradation, i.e., decreasing diversity with increasing surface degradation? (ii) What are the environmental and geospatial determinants of snail assemblage composition? and (iii) To what extent are dominance structures—based on both species' presence and relative abundance—similar between the non-native land-use types and the reference system?

2. Methods

2.1. Study area

The Gishwati-Mukura landscape lies within the Congo-Nile Divide Forest complex, extending along the eastern edge of the Albertine Rift Valley in western Rwanda (1°36′S to 2°60′S, 29°18′E to 29°36′E; Fig. 1). Over past decades, the region experienced a dramatic deforestation, leaving only two remaining patches of primary Afromontane rainforest, today protected as the core areas of Gishwati-Mukura National Park (NP; Arakwiye et al., 2021). Together, Gishwati and Mukura Forest cover 34.3 km^2, with Gishwati encompassing 14.4 km^2 and Mukura 19.9 km^2. Both fragments are surrounded by a matrix of home gardens, cattle pastures, and tree plantations, partly included in the national park (Mukuralinda et al., 2016; Arakwiye et al., 2021; REMA, 2021). The terrain is mountainous, with steep slopes, and an elevation range from 1200 to 2800 m above sea level. The climate is temperate, with an average annual temperature of 15 to 17 °C, and a mean annual precipitation of 1200 to 1500 mm, characterized by distinct wet and dry seasons, with rainfall occurring mainly during a long (March to May) and a short (October to December) wet season (Safari, 2012). We investigated primary Afromontane rain forest in Gishwati and Mukura Forest, as well as the surrounding matrix of the Gishwati–Mukura landscape, including—apart from cattle pastures—all land use type present in the area (i.e., tea plantations, home gardens, and four types of tree plantations; Fig. 1). Home gardens are integrated agroforestry systems managed by local communities for subsistence agriculture and household consumption, typically containing crops such as maize, beans, banana, and various fruit trees. Tree plantations consist mainly of exotic species such as *Pinus, Eucalyptus*, and *Alnus* (Mugabowindekwe et al., 2023). These plantations are often fragmented, poorly managed monocultures that are disconnected from primary forest (Nduwamungu, 2011) and are known to provide limited—or in some cases no—biodiversity value (Arakwiye et al., 2021; Sun et al., unpublished data). Tea plantations in the Gishwati-Mukura landscape were established by the Belgian colonial administration in the 1950's and continue to expand until today due to their function as barriers between protected

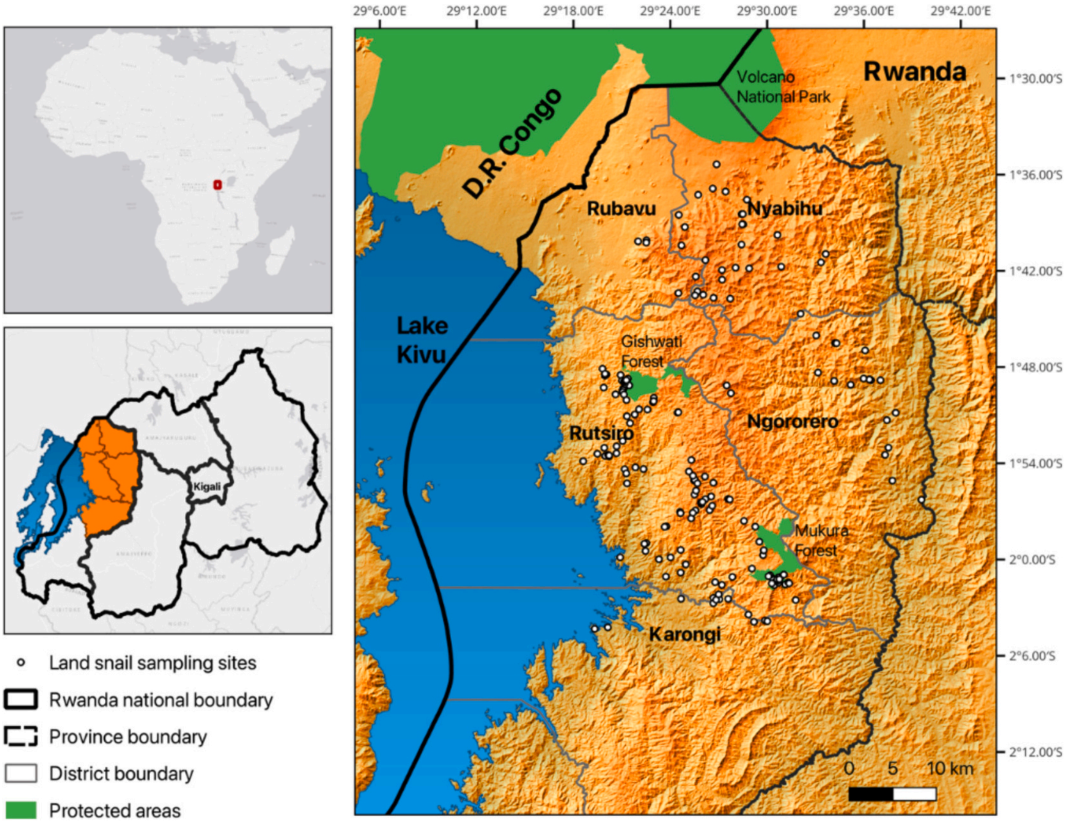


Fig. 1. Study area of the Gishwati-Mukura landscape showing locations of 173 sampling plots across five districts in western Rwanda: Rubavu, Nyabihu, Rutsiro, Ngororero, and Karongi. Inlets show the location of Rwanda in Africa and the position of the Western Province in Rwanda.

areas and cropland to prevent crop-raiding and reduce human-wildlife conflict (Kisioh, 2015).

2.2. Snail sampling and identification

Snail sampling in Gishwati and Mukura Forests was carried out between October 2013 and March 2014, while sampling in the surrounding landscape matrix took place from July to August 2024 and again from February to March 2025. In total, we selected 173 sampling plots of 20 × 20 m (Supplementary Material A: S1), i.e., 25 plots in primary forest (Gishwati Forest: 10, Mukura Forest: 15), 12 in tea plantation, 78 in tree plantation (*Alnus*: 6, *Pinus*: 17, *Eucalyptus*: 40, *Eucalyptus*/*Pinus*: 15) and 58 in home garden. Plot locations were equally distributed across the study area and arbitrarily chosen within each land-use type but accounting for road accessibility and safety constraints. Sampling involved a combination of visual searching and sorting a standardized volume of litter and soil (Emberton et al., 1996; Cameron and Pokryszko, 2005). All living slugs and snails as well as their empty shells were collected by two researchers for one hour at each plot. Additionally, a fixed volume (3 Liter) of leaf litter and surface soil was collected at each plot, subsequently dried, fractioned by size and sorted. Most specimens were identified to species level using compilations of Pilsbry (1919) and Verdcourt (2006) or original descriptions and revisions cited in Wronski and Hausdorf (2010) and Boxnick et al. (2015). Urocyclid slugs and semi-slugs were sorted into morphospecies and assigned to subfamilies. Specimens collected in 2013/14 are kept at the Leibniz Institute for the Analysis of Biodiversity Change (LIB) in Hamburg, Germany, specimens collected in 2024/25 are deposited in the Centre of Excellence in Biodiversity and Natural Resources Management (CoEB) at the University of Rwanda.

2.3. Ecological and geospatial variables

Nine environmental and geospatial variables were compiled from various sources (Table 1, Supplementary Material A: S1), characterizing topography (elevation, slope, topographic wetness index [TWI]),

Table 1
Sources of environmental and geospatial variables collected in 173 sampling plots in the Gishwati-Mukura landscape.

Variable group	Extracted variable	Source
Topography	Elevation Slope	NASA/METI/AIST/Japan Space systems, U.S./Japan ASTER Science Team (2019)
	Topographic Wetness Index (TWI)	Sörensen et al. (2006)
Landscape	Distance to the nearest protected area	IUCN, UNEP-WCMC (2020)
	Surface degradation (Revised Universal Soil Loss Equation, RUSLE: five levels from very low [1] to very high [5])	RCMRD (2023)
	Land-use type (natural forest; *Alnus* plantation; mixed *Pinus*–*Eucalyptus* plantation; *Pinus* plantation; *Eucalyptus* plantation; home garden; tea plantation)	in situ observations
	Herb height (cm) Shrub height (cm) Leaf litter depth (cm)	All in situ measurements were averaged across ten replicates per 20 × 20 m plot; herb and shrub height was recorded only when plot cover exceeded 20%.

Afromontane rain forests typically have a sparse and patchy herbaceous layer and a relatively low-density shrub layer, largely due to shading from the multi-layered canopy (Friis et al., 2010; Lötter and Beck, 2004).

vegetation structure (herb height, shrub height, leaf-litter depth) and landscape context (distance to the nearest protected area, land-use type, surface degradation level). Surface degradation is a modelled soil degradation risk index based on the Revised Universal Soil Loss Equation (RUSLE), integrating slope, rainfall, soil erosivity, population pressure, and land cover (RCMRD, 2023).

2.4. Species richness, diversity, composition, and similarity

We quantified species richness and diversity within the unified Hill-number framework (Chao et al., 2014), where the Hill number of order $q = 0$ corresponds to species richness, and $q = 1$ corresponds to Shannon diversity (H′). We used a Kruskal–Wallis *H* test to compare land snail species richness ($q = 0$) and Shannon diversity ($q = 1$) across seven land-use types. Post-hoc pairwise comparisons were performed using Dunn's test with Bonferroni correction to identify significant differences between land-use types. We performed a Jonckheere–Terpstra test to assess whether species richness ($q = 0$) or Shannon diversity ($q = 1$) increased or decreased consistently along the surface degradation gradient. Boxplots were generated to illustrate the distribution of species richness ($q = 0$) and Shannon diversity ($q = 1$) across degradation levels and seven land-use types. Additionally, for each land use type, abundance-based rarefaction and extrapolation curves of species richness ($q = 0$) and diversity ($q = 1$) were generated using the ***iNEXT*** package in R (version 4.0.3; Colwell et al., 2012; Chao et al., 2014; Hsieh et al., 2016), with 95% confidence intervals (CIs) estimated using 100 bootstrap replications.

Secondly, to reveal patterns of species assemblage composition in 106 sampling plots from which snails were retained, we established a non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities using the *vegan* package. The final model had a stress value of 0.12, which was well within the acceptable range (< 0.2), indicating that the two-dimensional ordination adequately represented the dissimilarities in the land snail community composition. To further assess the determinants of assemblage composition, we included two landscape variables (land-use type and surface degradation level) as fixed factors and three environmental and geospatial principal components (PCs) as covariates in the NMDS ordination. Principal component analysis (PCA) of seven standardized (z-transformed) environmental and geospatial variables (mean = 0, SD = 1) extracted three PCs with eigenvalues greater than one, collectively explaining 70.75% of the total variance (Table 2). These significant PCs were subsequently fitted as vectors onto the NMDS ordination to visualize both their direction and the strength of their association with species assemblages. We further applied ANOSIM (Analysis of Similarities) to quantify differences in snail assemblages across seven land-use types and five surface degradation levels (Table 2). We tested for homogeneity of multivariate dispersion using Permutational Analysis of Multivariate Dispersions (PERMDISP) and applied the Tukey's HSD test for post hoc pairwise comparisons.

Table 2
Axis loadings of three principal components (demonstrating 70.75% of the total variance), obtained from principal component analysis of seven ecological and geospatial variables obtained from 173 study plots. PC loadings > |0.4| are shown in bold font type.

Principal component	PC1	PC2	PC3
Eigen value	1.43	1.28	1.13
Percent variance (%)	29.06	23.59	18.10
Slope	−0.25	0.09	**−0.59**
TWI	0.27	0.06	**0.67**
Elevation	**−0.41**	−0.33	0.02
Distance to protected areas	0.05	**0.67**	0.06
Herb height	**−0.59**	0.16	0.24
Shrub height	**−0.58**	0.13	0.32
Leaf litter amount	−0.01	**−0.61**	0.17

Realistic measures of biodiversity should account not only for relative species abundances but also for differences among species (Leinster and Cobbold, 2012). Therefore, as a third step, we assessed the similarity in dominance structures across 106 sampling plots—for example, whether the most abundant species in home gardens were also dominant in primary forests. To do this, we used the Morisita–Horn similarity index (Horn, 1966), which incorporates both species presence and their relative abundances, providing a nuanced comparison of species composition between primary forest and other land-use types. Following the Morisita–Horn analysis, we performed a Similarity Percentage (SIMPER) analysis based on Bray–Curtis dissimilarities to identify the species contributing most to compositional differences between land-use types.

3. Results

3.1. Species richness and diversity

In total, 3235 specimens representing 118 land snail species (2 caenogastropods and 44 pulmonates) were collected across 173 sampling plots. No snails were recorded in 67 plots, whereas in the remaining 106 plots (Supplementary Material A: S2), abundance ranged from 1 to 475 individuals and species richness from 1 to 33 per plot. The most species-rich families were Streptaxidae (36 species), Achatinidae (27 species, including Subulinidae), and Urocyclidae (19 species). The most abundant families were Achatinidae (34.9% of all specimens), Streptaxidae (23.6%) and Urocyclidae (14.9%). Apart from *Paralaoma servilis,* no other exotic, introduced species was found. However, *Limicolaria martensiana,* a native generalist species more typical for savannah habitats, was likely introduced through agricultural products or livestock.

The Kruskal–Wallis *H* test revealed a significant difference in species richness ($q = 0$) among land-use types ($\chi^2 = 84.88$, $df = 6$, $p < 0.001$), as well as a significant difference in Shannon diversity ($q = 1$; $\chi^2 = 86.67$, $df = 6$, $p < 0.001$). Post-hoc pairwise comparisons using Dunn's test with Bonferroni correction (Supplementary Material B: Table 1) revealed significantly higher land snail species richness ($q = 0$) and diversity ($q = 1$) in primary forest than in other land use types. A Jonckheere-Terpstra test detected a significant monotonic decline along the degradation gradient for both species richness ($q = 0$; JT = 4312, $p = 0.002$) and Shannon diversity ($q = 1$; JT = 4247, $p = 0.001$), indicating that both species richness and the effective number of common species decreased with increasing disturbance level (Fig. 2).

Among land use type, primary forests have higher mean species richness ($q = 0$; 73.46; 95% CI: 61.48–81.53) and higher Shannon diversity ($q = 1$; 29.93, 95% CI: 22.37–36.81) than in home garden (mean richness ($q = 0$): 33.93, 95% CI: 28.48–38.53; Shannon diversity ($q = 1$): 16.18, 95% CI: 11.75–19.67), mixed *Pinus/Eucalyptus* plantations (mean richness ($q = 0$): 19.17, 95% CI: 11–28; Shannon diversity ($q = 1$): 11.15, 95% CI: 4.68–15.99), pure *Eucalyptus* plantations (mean richness ($q = 0$): 16.61, 95% CI: 8.95–23.53; Shannon diversity ($q = 1$): 9.95, 95% CI: 5.59–14.59), tea plantations (mean richness ($q = 0$): 11.33, 95% CI: 4.48–15; Shannon diversity ($q = 1$): 8.96, 95% CI: 4.15–12.19) and pure *Pinus* plantations (mean richness ($q = 0$): 7.29, 95% CI: 1.48–11; Shannon diversity ($q = 1$): 5.62, 95% CI: 1.00–8.85). Bootstrap-derived 95% confidence intervals for species richness ($q = 0$) and Shannon diversity ($q = 1$) indicated substantial overlap among all land-use types, except for primary forests (Fig. 3).

3.2. Determinants of species assemblage composition

Principal component analysis (PCA) reduced seven ecological and geospatial variables to three components capturing the main gradients structuring the study area (Table 2). PC1 (29% of variance) had strong negative loadings for elevation, herb height, and shrub height, indicating that taller vegetation occurs at higher elevations. PC2 (24% of

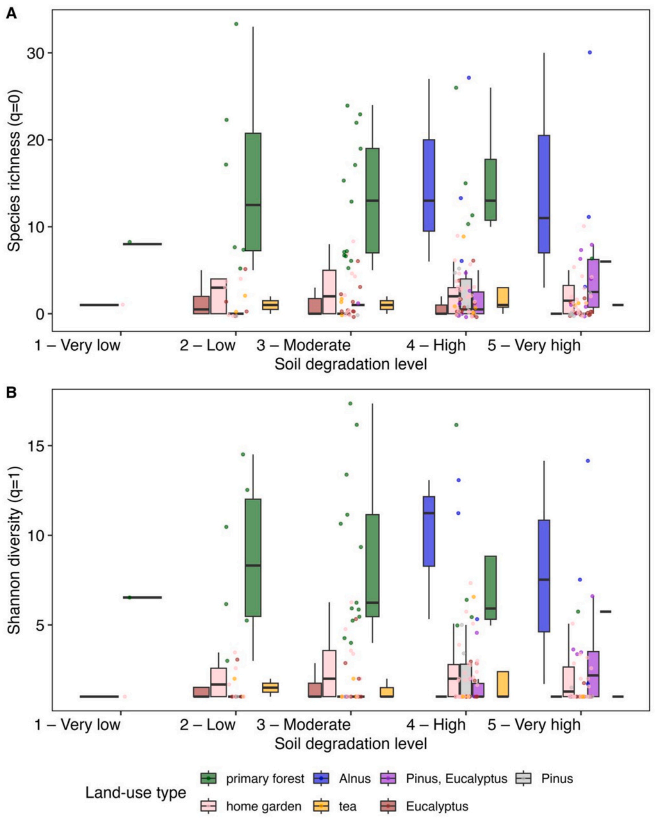


Fig. 2. Boxplots show the distribution of (A) species richness ($q = 0$) and (B) Shannon diversity ($q = 1$) across a gradient of five surface degradation levels, ranging from very low [1] to very high [5] and seven land-use types (primary forest, *Alnus*, *Eucalyptus*, *Pinus*, mixed *Pinus–Eucalyptus* plantations, tea plantation and home garden). A Jonckheere-Terpstra test indicates a significant decline along the degradation gradient for species richness ($q = 0$; JT $= 4312$, $p = 0.002$) and Shannon diversity ($q = 1$; JT $= 4247$, $p = 0.001$). Jittered points represent individual observations.

variance) showed a high positive loading for distance to the nearest protected area and a strong negative loading for leaf litter depth, suggesting that plots farther from protected areas have less leaf litter. PC3 (18% of variance) contrasted steep, well-drained slopes (negative loading for slope) with wetter valley bottoms (positive loading for topographic wetness index, TWI).

The NMDS ordination indicated that land snail assemblages across sites were not significantly influenced by PC1 (inset Fig. 4a, $R^2 = 0.04$, $p = 0.15$), PC3 (inset Fig. 4a, $R^2 = 0.02$, $p = 0.41$), or surface degradation level (inset Fig. 4a, $R^2 = 0.07$, $p = 0.10$). In contrast, assemblages were significantly negatively associated with increasing PC2 values (inset Fig. 4a, $R^2 = 0.11$, $p = 0.01$) and differed significantly among land-use types (Fig. 4a, $R^2 = 0.15$, $p = 0.01$). Group ellipses plotted on the NMDS ordination demonstrated a moderate separation among land-use types along compositional gradients, whereby plots located in primary forest and *Alnus* stands clustered closely together, while plantation plots—particularly those dominated by *Eucalyptus* and *Pinus*—were separated from primary forest plots (Fig. 4a). Home gardens exhibited partial overlap with several plantation types (Fig. 4a). Furthermore, ANOSIM revealed moderate yet significant differences in community composition among land-use types ($R = 0.225$, $p = 0.001$; Supplementary Material B: Fig. 1). Tests for homogeneity of multivariate dispersion (PERMDISP) also indicated significant variation in within-group heterogeneity ($F = 3.657$, $p = 0.003$; Table 3). PERMDISP results showed that primary forest and *Alnus* plantations exhibited low within-group dissimilarity, indicated by the shorter distances to their group centroids (Fig. 4b; Supplementary Material B: Figs. 1, 2), suggesting that these land-use types were the most internally cohesive. In contrast, *Eucalyptus*, *Pinus*, and tea plantations, as well as home gardens, showed broader overlap with other land-use types, reflecting greater internal variability. Their within-habitat dissimilarities approached those observed between land-use types (Fig. 4b; Supplementary Material B: Figs. 1, 2), suggesting a high degree of community heterogeneity in these degraded land-use types. Pairwise comparisons further revealed that home gardens exhibited greater variability in species composition than *Alnus* plantations ($p = 0.03$) or primary forest ($p = 0.009$), whereas differences among other land-use types were not significant (Supplementary Material B: Table 2). These findings suggest observed differences in assemblage composition were partly driven by higher within-group heterogeneity in home gardens.

Furthermore, complementary ANOSIM results indicated that community composition did not differ significantly across surface degradation levels ($R = 0.02$, $p = 0.12$; Supplementary Material B: Figs. 3, 4). However, PERMDISP detected significant differences in within-group variability among surface degradation levels ($F = 10.105$, $p = 0.001$; Table 3). Post-hoc Tukey's HSD comparisons showed that degradation level 1 (i.e., very low degradation) exhibited significantly greater dispersion than levels 2 to 5 (all $p < 0.001$), while differences among the remaining levels were not significant (Supplementary Material B: Table 3; Figs. 3, 4). These results suggest that variation in assemblage composition among surface degradation levels may be influenced by both location and dispersion effects.

3.3. *Similarity of dominance structures among land-use types*

Despite a relatively high proportion of shared species between *Alnus* plantation and primary forest (48.24%), the Morisita–Horn similarity index was relatively low (0.3; Figs. 5, 6, Table 4). A similar pattern was observed between home garden and primary forest, which shared a considerable number of species (24.71%) but exhibited a very low Morisita–Horn index (0.09; Figs. 5, 6, Table 4). In contrast, the *Eucalyptus* plantation shared relatively few species with the primary forest (16.47%) yet showed a high Morisita–Horn similarity index (0.5; Figs. 5, 6, Table 4). Pure *Pinus* plots and tea plantations exhibited both low species overlap and low Morisita–Horn similarity values (Figs. 5, 6, Table 4). SIMPER analysis revealed that primary forest differed from plantations and agricultural land mainly due to a few characteristic species. Forest specialist such as *Nothapalus stuhlmanni* and *Thapsia consobrina* were key in distinguishing primary forest from *Eucalyptus*, *Pinus–Eucalyptus*, and *Alnus* stands, while *Gonaxis* spp. further separated it from non-forest land uses. In contrast, *Subulina viridula* and *Subuliniscus lucasi* were more associated with plantation systems, especially *Alnus*, contributing to the distinction from primary forest (Supplementary Material A: Table S3).

4. Discussion

Afromontane forests have undergone extensive deforestation and degradation in recent decades. While forest landscape restoration is increasingly promoted as a key strategy to reverse these trends, its ecological value remains doubtful and insufficiently studied. In our study, we used land snails—a low-profile but ecologically informative taxon—as bioindicators to investigate how biodiversity varies between seven different land-use types following deforestation in western Rwanda, an area recognized as a global biodiversity and forest restoration hotspot. Moreover, we compared species richness, diversity, and assemblage composition between these land-use types and a reference system, i.e., the primary forest of Gishwati and Mukura Forest fragment, as well as along a gradient of increasing surface degradations. We discussed our findings from three perspectives: (i) land snail richness and diversity across different land-use types, (ii) environmental determinants of land snail assemblage composition, and (iii) similarity in dominance structure between primary forest and other land-use types.

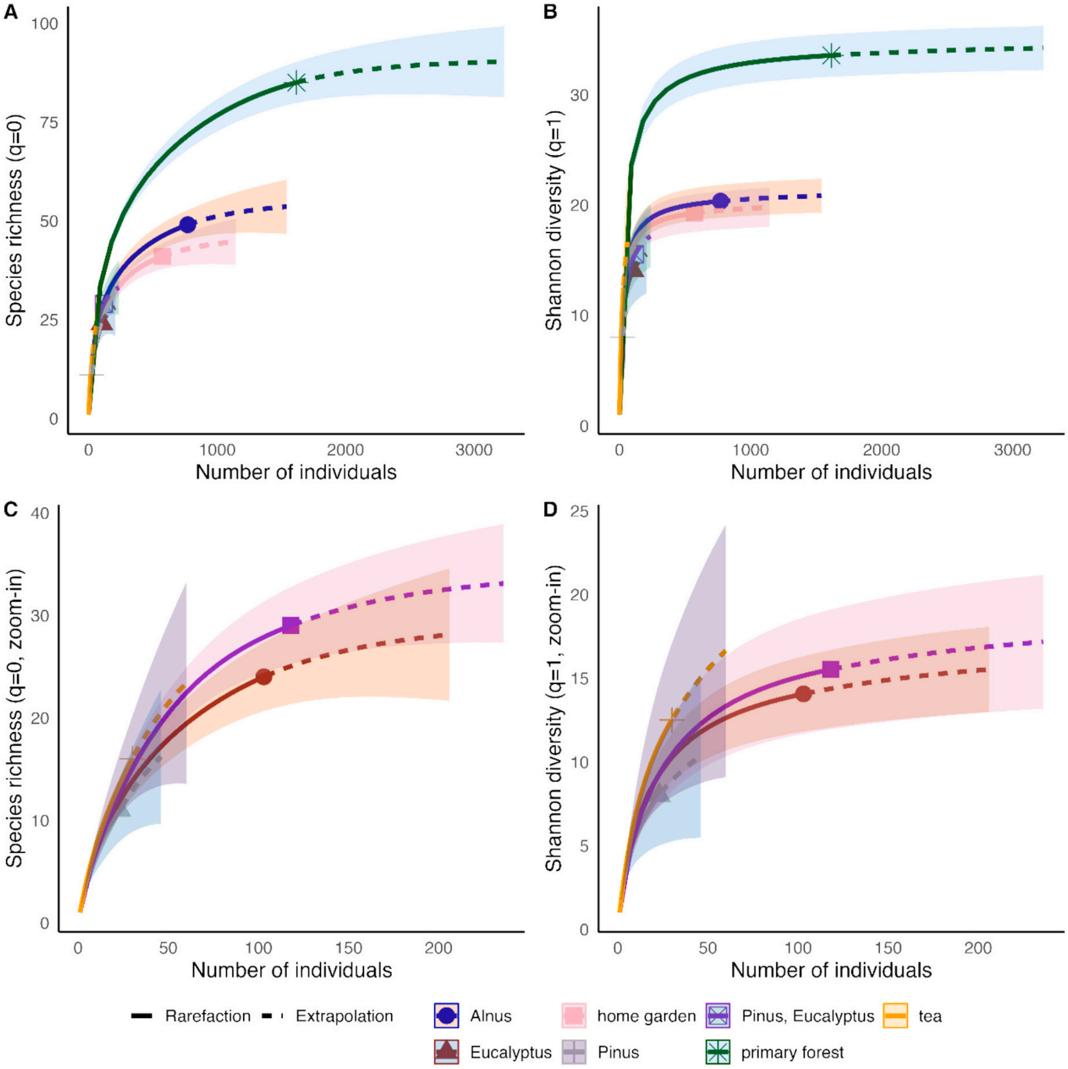


Fig. 3. Abundance-based rarefaction (solid lines) and extrapolation (dashed lines) curves for (A) land snail species richness (Hill number $q = 0$), and (B) Shannon diversity (Hill number $q = 1$) across seven land-use types in the Gishwati-Mukura landscape of western Rwanda (primary forest, *Alnus*, *Eucalyptus*, *Pinus*, mixed *Pinus–Eucalyptus* plantations, tea plantation and home garden). Panels (C) and (D) zoom in on four plantation types (*Eucalyptus*, *Pinus*, mixed *Pinus–Eucalyptus* and tea plantations). Shaded areas show 95% confidence intervals.

4.1. Land snail richness and diversity in different land-use types

Land snail diversity, expressed as the Hill numbers of order $q = 0$ (species richness) and $q = 1$ (Shannon diversity), were highest in primary forest, underscoring the critical importance of intact, moist, and structurally complex Afromontane forest for sustaining diverse assemblages. Diversity declined sharply across modified land-use types and with increasing surface degradation, reflecting habitat simplification and reduced litter and moisture availability. Increasingly degraded surfaces are associated with greater habitat alteration and reduced structural and microclimatic stability, both of which are critical for land snail communities. Among the modified land-use types, *Alnus* plantations supported comparatively high richness and diversity, likely due to their dense canopy and organic-rich litter, which partially mimic primary forest conditions (Tattersfield et al., 2001; Nurinsiyah et al., 2016). A dense canopy reduces direct sunlight and windspeed at the forest floor, lowering evaporation and maintaining higher humidity, while a deep layer of leaf litter (see Supplementary Material A: S1) enhances soil moisture and nutrient availability, together creating a more favorable microclimate for a range of plant and animal species (Aalto et al., 2022). As a result, *Alnus* plantations may function as replacement habitat capable of supporting some snail species typically associated with primary forest. However, this interpretation should be made cautiously, as only a small number of *Alnus* plantations were sampled ($n = 6$). Home gardens also maintained moderate richness and diversity, probably reflecting greater microhabitat heterogeneity (Raheem et al., 2008; Gbedomon et al., 2017). In contrast, *Pinus, Eucalyptus*, and tea plantations supported depauperate assemblages, consistent with their drier microclimates, acidic soils, and poor-quality litter (Tattersfield et al., 2001; Graça et al., 2002; Darmi et al., 2024). The substantial overlap of confidence intervals among these land-use types indicates uniformly low species richness and diversity in degraded habitats.

4.2. Environmental determinants of land snail assemblage composition

Across all plots in which snails were recorded, our results indicate that land-use type is a major driver of species heterogeneity and community structure within the Gishwati–Mukura landscape. Among the environmental variables summarized by the PCA, only PC2—representing increasing distance from the nearest protected area and decreasing leaf-litter depth—significantly influenced assemblage structure. Sites farther from protected areas and with shallower leaf litter supported lower species diversity and exhibited pronounced shifts in community composition. In contrast, vegetation structure, elevation and

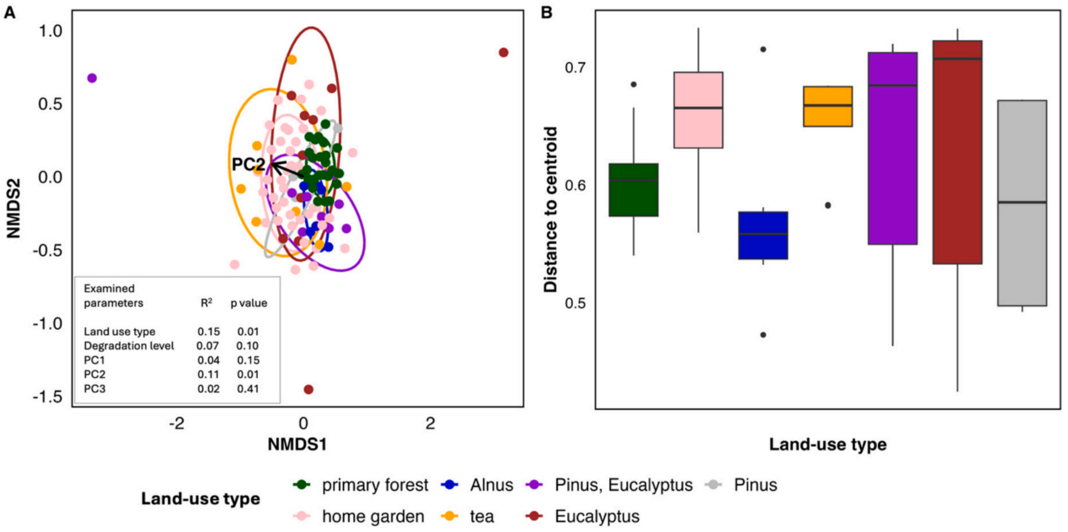


Fig. 4. A) Non-metric multidimensional scaling (NMDS) ordination depicting variation in community composition of land snails across 106 sampling plots. Vector indicates significant correlations between significant determinants (PC2: distance to nearest protected area and leaf litter depth) and the assemblage composition. Group ellipses represent confidence intervals (95%) around the centroid of each group. The inset table summarizes R^2 and p-values for all variable (PCs) tested. B) Whisker-box plots show distances of samples to group centroids for each land-use type by the Permutational Analysis of Multivariate Dispersions (PERMDISP).

Table 3
Results of tests for homogeneity of multivariate dispersions (PERMDISP) based on NMDS ordination. Model 1 compares seven land-use types, and model 2 compares five surface degradation levels. Each test was performed with 999 permutations. Significant differences in dispersion among groups are indicated by permutation p-values ($p < 0.05$).

Model 1	*df*	Sum of squares	Mean squares	*F*	Permutation *p* value
Land-use type	6	0.09	0.02	3.66	0.003
Residuals	99	0.42	0.00		
Model 2					
Surface degradation level	4	0.06	0.02	10.11	<0.001
Residuals	98	0.15	0.00		

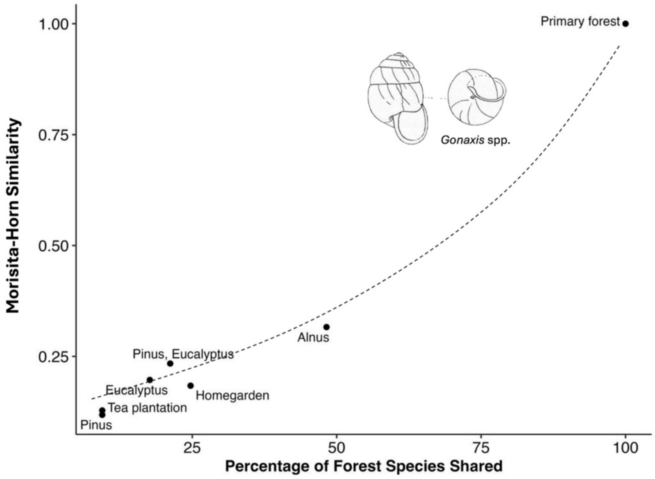


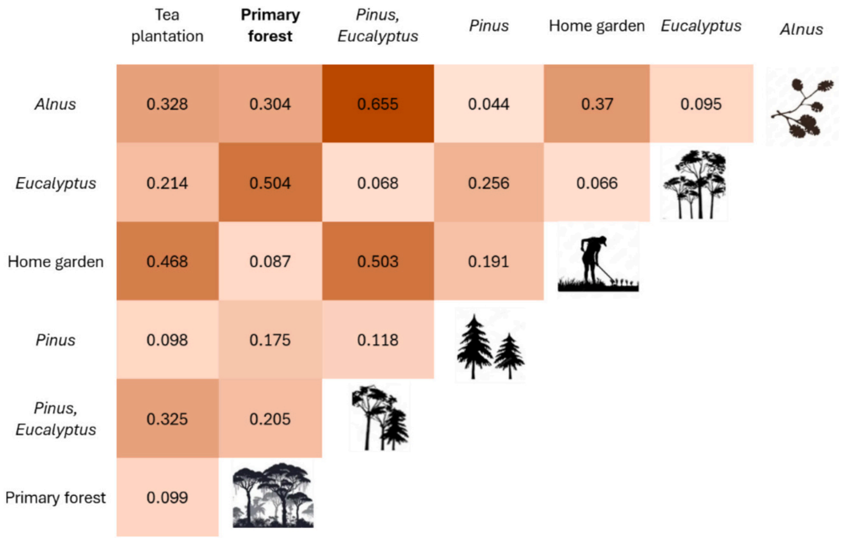
Fig. 5. Relationship between the proportion of shared land snail species and Morisita–Horn similarity for six land-use types relative to primary forest. Each point represents one land-use type. X-axis shows the percentage of species shared with primary forest, and y-axis shows the Morisita–Horn similarity index, which is weighted by species abundances.

topography (PC1, PC3), as well as surface degradation, had little effect on land-snail assemblages, a pattern consistent with findings from other regions (Wehner et al., 2021; Martínez-De León et al., 2022; Gheoca et al., 2023; Schmera et al., 2023). Distance to the nearest protected area likely serves as a proxy for the time since deforestation and ongoing surface degradation (Ryan et al., 2017; Guerra et al., 2019). Accordingly, sites farther from primary forests appear to have experienced longer periods of disturbance, resulting in impoverished assemblage composition. However, distance may also indicate reduced migration likelihood, as remote sites receive fewer migrants that might have otherwise increased richness or stabilized gene pools.

In addition, the association between higher PC2 values and reduced species diversity highlights the importance of litter-rich, moist microhabitats for sustaining diverse snail communities (Wronski et al., 2014; Denmead et al., 2015; Gheoca et al., 2021; 2023). Our community assemblage analyses (NMDS, ANOSIM) revealed clear differentiations among land-use types. Primary forest and *Alnus* plantations clustered closely, indicating similar structural conditions and species assemblages. Conversely, *Eucalyptus, Pinus*, and tea plantations supported distinct, compositionally simplified communities, likely reflecting the constraints imposed by drier and more homogeneous environmental conditions (Tattersfield et al., 2001; Douglas et al., 2013). Home gardens overlapped with several plantation types, reflecting mixed and variable assemblages dominated by generalist species such as reported from other tropical forest habitats in Sri Lanka and Java (Rahem et al., 2008; Nurinsiyah et al., 2016). Although ANOSIM indicated no significant differences in overall community assemblage composition across surface degradation levels, PERMDISP detected significant variation in within-group dispersion, with the least degraded habitats showing the highest variability. Together, these results suggest that differences in snail assemblages are driven not only by land-use type but also by within-habitat heterogeneity. Intact or structurally complex habitats tend to support more cohesive communities, whereas degraded or intensively managed habitats favor compositionally variable assemblages dominated by generalist species. This finding highlights the potential of land snails to serve as reliable indicators of habitat disturbance.

4.3. *Similarity of dominance structures*

Consistent with previous studies investigating the effects of land-use change on soil invertebrate communities in tropical forests (Wang and



	Tea plantation	**Primary forest**	*Pinus, Eucalyptus*	*Pinus*	Home garden	*Eucalyptus*	*Alnus*
Alnus	0.328	0.304	0.655	0.044	0.37	0.095	
Eucalyptus	0.214	0.504	0.068	0.256	0.066		
Home garden	0.468	0.087	0.503	0.191			
Pinus	0.098	0.175	0.118				
Pinus, Eucalyptus	0.325	0.205					
Primary forest	0.099						

Fig. 6. Pairwise similarity values between different land use types established using the Morisita-Horn index (ranging from 0 to 1), whereby higher values indicate greater similarity in species assemblage composition between respective land use types.

Table 4
Land snail similarity in species composition between primary forest and other land-use types in the Gishwati-Mukura landscape of western Rwanda. The Morisita-Horn index measures the similarity of species assemblage composition and abundance between primary forest and all other land-use types.

Land-use type	Total number of species	Shared species% with primary forests	Moristia-Horn index
Alnus plantation	49	48.24	0.30
Eucalyptus plantation	20	16.47	0.50
Pinus plantation	11	8.24	0.18
Pinus/Eucalyptus plantation	28	20.0	0.20
Tea plantation	15	9.41	0.10
Home garden	41	24.71	0.09
Primary forest	84	100	1.00

Foster, 2015; Galli et al., 2025), Morisita–Horn similarity indices indicated that land-use change influenced both species composition and dominance patterns. Although species pools overlapped substantially between *Alnus* plantations and primary forest, the relative abundance of dominant species differed markedly. A similar pattern was observed in home gardens, where species richness was relatively high (mainly due to introduced savannah species such as *Limicolaria martensiana* and *Burtoa nilotica*), but species similarity with primary forest remained low. In contrast, differences between *Eucalyptus* plantations and primary forest were largely driven by rare species (e.g., Streptaxidae species), as dominant species were largely shared and exhibited comparable relative abundances. *Pinus* and tea plantations exhibited both low species overlap and low similarity relative to primary forest, indicating highly distinct snail assemblages that differed not only in composition but also in the relative abundances of shared taxa.

SIMPER analysis further highlighted that generalist species such as *Subulina viridula, Subuliniscus lucasi, Kaliella iredalei*, and *Gulella* (*Wilmattina*) *disseminate* contributed disproportionately to dissimilarity between primary forest and tree plantations. When combined with the next few contributing species, cumulative contributions frequently exceeded 40–50%, indicating a highly uneven structure whereby a few widespread or disturbance-tolerant taxa dominated compositional differences. In contrast, differences involving primary forest were driven by forest-associated species such as *Nothapalus stuhlmanni, Thapsia consobrina*, and *Gonaxis* spp., which were reduced or absent in tree and tea plantations, as well as home gardens. Comparisons among plantation types (e.g., *Eucalyptus* vs. *Pinus*) showed little differentiation, suggesting homogenized communities under similar environmental conditions. Home gardens showed intermediate patterns, i.e., both generalists (e.g., *Subulina viridula*) and some semi-natural species, such as *Varicostele rutshuruensis*, contributed to dissimilarity, but key forest taxa remained absent. Overall, land-use intensification shifts communities from forest-specialist species to a few widespread, disturbance-adapted taxa, leading to biotic homogenization and highlighting the importance of structurally complex habitats for conservation.

The idea that species differ in their sensitivity to habitat change is well established. For example, Le Provost et al. (2021) or Socolar et al. (2025) reported that some species depend on stable, semi-natural habitats (such as *Alnus* plantation), whereas others persist across a broader range of land-use intensities. In our study, the marked decline in diversity and the shifts in community composition along the degradation gradient are consistent with this general pattern of differential species responses to environmental change. However, as our analyses do not explicitly test underlying mechanisms or species-specific responses, these patterns should be interpreted cautiously. Finally, it should be noted that biodiversity may recover relatively quickly in terms of species richness, reaching levels comparable to primary forests, whereas the recovery of diversity and community composition can take much longer—potentially centuries—especially where forest-dependent species have disappeared locally or cannot disperse into regenerating forests (Rozendaal et al., 2019).

5. Conclusion

Our study highlights the high sensitivity of land snails to land-use change and underscores their value as effective ecological indicators for monitoring ecosystem dynamics in tropical Afromontane landscapes. We demonstrate that land snails respond strongly to microhabitat conditions—particularly to leaf-litter availability and proximity to primary forest—revealing fine-scale environmental gradients that might otherwise go undetected. Habitat characteristics selectively favor different taxa, resulting in distinct community assemblages across land-use types within the Gishwati–Mukura landscape. Notably, land snail richness and diversity were highest in primary forest. Although *Alnus* plantations supported some levels of richness and community composition broadly comparable to those of primary forest, their dominance structure differed markedly. This divergence highlights the importance of examining multiple dimensions of biodiversity—including species richness, diversity indices, assemblage composition and dominance patterns—-when assessing the ecological consequences of land-use change using land snails. Collectively, our findings position land snails as a promising yet underutilized bioindicator group for evaluating habitat integrity and guiding conservation and restoration efforts in tropical montane ecosystems.

AI statement

During the preparation of this work the authors used Chat GBT (Open AI) to check grammar, spelling and references. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

CRediT authorship contribution statement

Ping Sun: Writing – original draft, Visualization, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Bernhard Hausdorf:** Writing – review & editing, Supervision, Conceptualization. **Torsten Wronski:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary Materials A & B

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2026.114981.

Data availability

All data used in this study are available in the Supplementary Materials A and B of this article.

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