




Woody vegetation diversity remains low after extensive forest landscape restoration efforts in a western Rwandan landscape

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ABSTRACT

Ecosystem restoration has emerged as a global priority in tropical regions, where issues like land degradation, biodiversity decline, and climate change are pressing concerns. In Rwanda it is predominantly conducted under the “forest landscape restoration” framework with unclear specifications toward rehabilitation or ecological restoration goals. The extent to which restoration efforts in Rwanda successfully restore the diversity, structure, and function of ecosystems remains largely unknown. This paper examines woody species structure and diversity within different land use types, including homegardens, agriculture mosaics, tree patches, pastures, and Gishwati-Mukura National Park as a reference site. From June to August 2024, data were collected from 159 sites using stratified random sampling and quasi-experimental design to represent the main land use types in the study areas. The findings reveal variations in species richness and composition among the different land use types. We found a notable distinction between native and exotic species proportions, with a dominance of exotic species across most sites: 65% in homegardens, 80% in agricultural mosaics, and 93% in tree patches. Homegardens displayed significantly higher species richness than tree patches, agricultural mosaics, and pastures, but still fell substantially short of the National Park. Our results highlight that while restorative efforts are widespread, the challenge to balance biodiversity conservation with socioeconomic benefits has meant that, to date, restoration practices have favored exotic species, which will have larger implications for trophic interactions and hence wider biodiversity in the region. The study underscores the need to enhance native species richness to promote biodiversity.

1. Introduction

In tropical countries, ecosystem restoration has become a priority due to land degradation, biodiversity loss, and climate change (Aronson and Alexander, 2013). Tropical landscapes are rich in biodiversity and are increasingly under threat from anthropogenic disturbances (Kearsley et al., 2019). The decline in forest cover within the tropics is attributed to factors such as rapid population growth, the expansion of both subsistence and commercial agriculture, and the production of fuelwood and charcoal (Brandt et al., 2017), and prolonged political conflicts which have weakened the enforcement of environmental regulations (Landholm et al., 2019). Forested landscapes are often cleared for agricultural use or targeted for development projects especially in post-conflict countries, the exploitation of forest resources can play an important role in boosting developing economies (Crespo Cuaresma and Heger, 2019).

One country that has experienced many of the above-mentioned conditions is Rwanda. Numerous factors including crop intensification

and commercialization as set out in Rwanda's national development goals (Cantore, 2011), anthropogenic activities (e.g. small-scale mining), and natural disasters threaten Rwanda's biodiversity (Bagstad et al., 2020; Habiyaemye and Jiwen, 2011) and place enormous strains on Rwanda's landscapes and the natural resources upon which its economy is built (Clay, 2019). Driven by historical changes, much of Rwanda has faced serious problems of land degradation in the past decades. In a country where human pressure on the environment was already high, the civil war and Genocide in the mid-1990s exacerbated the loss of natural forests (Gebauer and Doevenspeck, 2015). The combined effects of contemporary climate change and a history of environmental degradation, including soil erosion, deforestation, and loss of ecosystem services, now present significant challenges to Rwanda's economic and social development (Nambajimana et al., 2020). Managing and protecting Rwanda's forest landscapes thus has become a national priority.

Forest landscape restoration, which aims to provide ecological and social benefits as well as mitigate the impacts of climate change

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(Chazdon and Uriarte, 2016) is being implemented in Rwanda as part of numerous national restoration initiatives. Forest landscape restoration efforts have sought to reinforce climate resilience to floods and landslides, and enable local communities to adopt more sustainable land use practices (Arakwiye et al., 2021; Tuyisingize et al., 2022). Especially since the early 2000s, the Rwandan government has implemented several major forest protection and restoration policy initiatives (van Oosten et al., 2018), embarking on a course of economic transformation in which the sustainable use of natural resources, including forests, is considered central to boost the national economy (Republic of Rwanda, 2017, 2017a).

To date, four main types of restoration have been pursued in Rwanda, namely woodlot plantings, agroforestry, watershed protection through erosion control, and natural regeneration (Nash et al., 2020). Due to ecological concerns, the Rwandan government has been encouraging the diversification of tree species in restoration efforts, seeking to balance plantings of *Eucalyptus* and other non-native species with native species to improve outcomes for biodiversity and soil and water conservation (LAFREC, 2021; Ndayambaje and Mohren, 2011). To reduce fuel wood dependency, deforestation, and encourage the use of native trees by the community, some restoration initiatives have also provided improved cookstoves as incentives to households (IUCN, 2024). Existing restoration activities provide benefits to local communities (smallholder farmers and larger-scale plantation owners) (Buckingham et al., 2021) but might harbor low biodiversity, and some species planted in restoration activities demand high levels of water and nutrients, further exacerbating soil degradation and the shortage of cultivable land in the long term (Mugunga et al., 2017). To fully capitalize on the advantages of integrating trees into agricultural landscapes as a component of forest restoration strategies, it is imperative not only to increase their abundance but also to enhance their diversity to meet the growing demand for diverse tree products (Brancaion et al., 2025; Plieninger et al., 2020) and to avoid landscape-scale biotic homogenization (Holl et al., 2022). Woody species recovery in restored and managed landscapes is shaped by a combination of biophysical and socio-spatial factors and environmental gradients that influence disturbance regimes, resource availability, and dispersal process (Austin and Van Niel, 2011; Laurance et al., 2009; Middendorp et al., 2016). Proximity to the national park could enhance native species by facilitating seed dispersal and acting as a source pool for recolonization (Norden et al., 2009), while housing density and tree cover reflect management intensity and may therefore influence restoration trajectories (Jakovac et al., 2021).

Against Rwanda's complex and challenging background, it is vital to understand to what extent past practices have succeeded in restoring woody species diversity within landscapes targeted for restoration. While a frequently stated aim of restoration projects is to restore biodiversity and ecosystem functions and services, it remains unknown whether existing practices actually succeed in reaching this aim on the ground. In this paper, we investigated woody species diversity and structure within more than a hundred randomly selected sites reflecting all major land cover classes throughout a landscape in western Rwanda that has been the target of many different small-scale and large-scale restoration projects. We chose a stratified random sampling approach for two reasons: (1) definitions among local stakeholders of what constitutes "restoration" differ greatly, such that almost every part of the landscape is considered to have been restored to some extent; and (2) our approach presents an unbiased, representative approach to assessing restoration outcomes at the landscape scale to date. We acknowledge that our sampling was a conscious decision to look at "typical" landscape conditions rather than a way to seek out specific best practice sites of restoration. We reasoned that if high diversity restoration activities are somewhat widespread in the landscape, they will show up in our sample of selected sites.

Although we focus on western Rwanda, the general question to what extent "forest landscape restoration" actually delivers forest-like

biodiversity is critically important not only for Rwanda but also for many other landscapes targeted for restoration worldwide. We hypothesized that different land use types would differ significantly in the extent to which they restore woody vegetation diversity and structure relative to natural forest sites. We expected that tree patches would have lower woody species diversity than homegardens, while agricultural mosaics and pastures would have intermediate levels of woody species diversity. Our expectations on species diversity across land-use types come from known patterns of management intensity and planting history in the region. Homegardens are typically managed at the household level, and many farmers incorporate trees around their homes for cultural purposes and other benefits. Tree patches, in contrast, are comprised of small woodlot plantations which are sometimes mixed plantings but often dominated by exotic species.

Our findings enhance understanding of woody species-based restoration and provide valuable insights for ecologically informed decision-making in Rwanda. They can also help to inform restoration strategies in other regions facing similar challenges.

2. Methods

2.1. Study area

The study was conducted in four districts of Western Rwanda: Rubavu, Nyabihu, Rutsiro, and Ngororero (Fig. 1). The area is part of the Albertine Rift biodiversity hotspot in Rwanda and includes three agro-ecological zones: Volcanic Highlands, Congo-Nile Divide, and Plateau and Hills (Arakwiye et al., 2021). The region has a tropical highland climate with two dry seasons (June–September and December–February) and two rainy seasons (March–May and October–November). Mean annual temperatures range between 15 and 20 °C due to mountainous topography (from 800 to 4507 m a.s.l.), and annual rainfall ranges between 1300 and 2000 mm (Akinyemi, 2017; Arakwiye et al., 2021). Major landcover types in Western Rwanda include an agricultural mosaic dominated by subsistence agriculture, pastures, natural and planted forests and plantations, tea farms, and settlements (Hafashimana et al., 2022). Natural forests in the region are dominated by evergreen tree species, while plantations are dominated by exotic species of *Pinus*, *Eucalyptus*, and *Alnus* (Clay, 2019).

2.2. Experimental design: Village and site selection

We initially classified the study area into five social-ecological clusters. These were generated based on broad ecological and

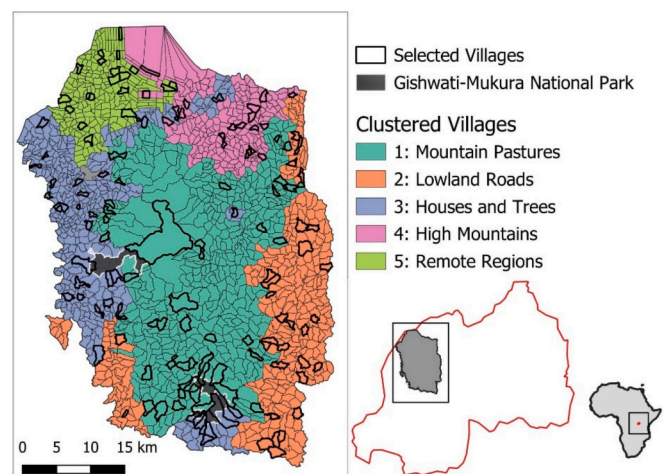


Fig. 1. Study area and identified clusters; Cluster 1: Mountain pastures; Cluster 2: Lowland roads; Cluster 3: Houses and trees; Cluster 4: High mountains; Cluster 5: Remote regions.

socioeconomic conditions, which we expected would influence biodiversity both directly and indirectly through subtly different ways of human land use. For this initial clustering, we conducted a cluster analysis of administrative sectors based on geographical variables (e.g., distance from road, elevation, house density, slope, distance to national park, tree cover, agriculture, and shrub cover; for details see [Baumann et al. \(2025\)](#)).

Cluster I was in the central region of the four districts and was characterized by steep slopes and mountains. It was predominantly covered by pastureland with few scattered trees. Housing density was low, and the Gishwati-Mukura National Park was nearby.

Cluster II was located in the eastern part of the plateau, with a smaller area reaching into the southwestern portion of the study area. It was lower in elevation than the other clusters but was closest to the main roads, which are primarily concentrated around the high plateau region. Similar to cluster one, this cluster also included a substantial area of pastureland.

Cluster III stretched along the western boundary adjacent to Lake Kivu and covered a substantial part of Gishwati-Mukura National Park. A smaller section of this cluster reached into the southern study area. Due to its proximity to the national park, this cluster had the highest tree cover, while pastureland was less prominent. Cluster III also had the highest population density and was relatively close to main roads and towns.

Clusters IV and V were located in the northern region of the study area. Both were far from Gishwati-Mukura national park and had little pastureland. Cluster IV included the highest elevation areas, though slopes were not substantially steeper than those in the southern clusters. Conversely, cluster V was characterized by flatter terrain with more moderate elevation. Cluster IV, bordering a major northern road, was close to population centers and had high tree cover, whereas Cluster V had the lowest tree cover of all clusters but had the highest proportion of arable land within the study area ([Baumann et al., 2025](#)).

From the resulting five clusters of administrative sectors, we then selected individual villages for our field surveys, including 45 villages from cluster I, 24 villages from cluster II, 45 villages from cluster III, 12 villages from cluster IV, and 15 villages from cluster V. Village selection was randomized, with some additional, purposively selected villages selected for sampling near the national park because we were particularly interested in the biodiversity close to the park edge.

We used a quasi-experimental design to capture in an unbiased way all main land use types present in all different sections of the study area. We focused on (i) the agriculture mosaic, which refers to sites where trees and crops grow together (i.e. agroforestry); (ii) tree patches, which we defined as a contiguous site of woody vegetation cover that was typically smaller than 1 ha in size ([Ndayambaje and Mohren, 2011](#); [Richards et al., 2024](#); [Republic of Rwanda, 2017, 2017a](#)). The tree patches in our study do not refer exclusively to exotic plantations. While exotic species dominate, the patches also include mixed plantings, and we use the term to capture the reality of small woodlot plantations commonly established in Rwanda, as distinct from larger-scale tree plantations. These patches are not remnants of natural forests but rather actively planted sites as part of afforestation and reforestation efforts, starting back in the 1980's ([Frietsch et al., 2024](#)). They serve multiple purposes, including firewood, timber provision, and soil erosion control, and are a common landscape feature in rural Rwanda. Third, we included (iii) pastures, which were sites used for livestock grazing ([Republic of Rwanda, 2021](#)). Finally, we considered (iv) homegardens, that is, the area around family homes dominated by traditional agroforestry practices with multiple functions ([Maroyi, 2009](#)). Homegardens are typically managed at the household level, and the farmers incorporate trees around their home for cultural purposes and other benefits ([Jean Baptiste et al., 2009](#)). Homegardens are rarely considered 'restoration sites' but we reasoned that they may play an important role within the larger landscape context, and therefore we were interested in quantifying their biodiversity. Similarly, we included Gishwati-Mukura

National Park as a reference site of near-natural (although disturbed) conditions. To capture the full range of available conditions on the ground, we tried to capture key gradients for a given site type, including agricultural and pasture sites with different densities of trees, and homegardens that were relatively isolated or embedded within larger groups of houses.

2.3. Data collection

We collected data on woody vegetation from June to August 2024. To place our land use types within the selected villages, we selected Homegardens (H), Tree patches (T), Agricultural mosaics (A), and Pastures (P); and we visited Gishwati-Mukura National Park as a reference site. Some villages that were originally randomly selected were not accessible due to poor road conditions or landslides; those were replaced ad hoc in the field from a list of (also randomly generated) replacement villages within the same social-ecological cluster. With the help of village leaders who knew village boundaries, we identified and placed sampling plots near the center of a given village as much as possible. One hectare plots were established in all selected villages apart from the national park, which was too dense to sample an entire 1 ha, and where a 20 m × 20 m plot was used instead. To enable direct comparison, 20 m × 20 m nested plots were also placed within the center of all 1 ha sampling sites. In total, 159 sites were sampled, including 49 Agricultural mosaics, 44 Homegardens, 29 Tree patches, 18 Pastures, and 19 reference sites in Gishwati-Mukura National Park. Data on woody vegetation diversity was obtained by identifying every distinct woody species within the sampling plots and noting its abundance.

Species composition was documented by classifying each species as native or exotic and assigning it to one of three functional groups: pioneer species, forest specialist species, or generalist species. We distinguished these three functional groups based on their ecology and habitat requirements. Pioneer species are early-successional woody species that establish quickly in disturbed or open areas. They are fast growing, light-demanding, and can easily colonize degraded sites; examples include, *Alnus acuminata* and *Eucalyptus species* (all non-native). Generalist species are those capable of thriving across a wide range of habitats and environmental conditions. They are not restricted to disturbed areas, and can persist in diverse environments; examples include *Grevillea robusta* (a non-native species) and *Erythrina abyssinica* (a native species) Forest specialists thrive in intact forest habitats, and are typically slow-growing with narrow ecological requirements, such as, *Carapa grandiflora* and *Symphonia globulifera* (both native) classification is based on different literatures like ([Chazdon, 2014](#); [Corlett and Primack, 2011](#); [Hawthorne, 1995](#); [Ouédraogo et al., 2013](#); [Pascal and Fre, 1984](#); [Sanaphre-Villanueva et al., 2017](#); [White, 1983](#); [World Agroforestry, 2016](#)). A full list of species including their classification as pioneer, generalist or specialist, is provided in the supplementary material (**Table S1**).

Structure was assessed by measuring the diameter at breast height (DBH 1.3 m above ground level) of all live stems within the sampling sites, where stems shorter than 1.3 m in height and those with a DBH less than 1.5 cm were classified as 'seedlings'.

2.4. Data analysis

To analyze species diversity and understand the relationship between sampling effort and the number of species observed, we illustrated the cumulative species richness within the different site types using plot level species accumulation curves for both the 20 m by 20 m and 1 ha sampling plots, using the vegan package in R. Species accumulation curves were generated using the `specaccum()` function from the vegan package in R, using the random method with 100 permutations to estimate mean and confidence intervals. To ensure comparability across land-use types, we additionally computed individual-based rarefaction curves using `rarecurve()` in vegan, allowing richness to be

evaluated at standardized sampling completeness. Richness was rarefied to the minimum number of individuals observed across land use types. Abundance-based Shannon diversity (H') was calculated at the site level using species abundance data and the diversity() function in the vegan package. Tukey-adjusted contrasts were then used to test for statistical differences among land-use types.

Second, we used a Generalized Linear Model (GLM) with a Poisson error distribution and log link function to estimate species richness in response to predictor variables. Predictor variables were elevation, land use type, distance from the national park, distance from town, distance to road, slope, house density, tree cover, distance to river, distance to a river stream, and topographic wetness index (TWI). We checked for collinearity among predictor variables by visual inspection of pairwise plots, and excluded highly correlated predictors. Predictors were log-transformed if they were highly skewed. Residual plots were checked to ensure model assumptions of independence and constant variance were met. We selected a final model using manual backward selection, that is, starting with a full model including all predictor variables and removing the least significant variables one by one until only variables were retained that were significant at $P < 0.05$ compared to a null model. We were primarily interested in main effects, and because we had no theoretical expectation of particular interaction effects among predictors, we prioritized model simplicity over complexity, and did not test for significant interaction terms. After fitting the GLM, we used estimated marginal means (using the emmeans package) with Tukey-adjusted contrasts to test for statistical differences among land-use types, including pairwise comparisons of land-use types.

Third, the percentages of stems that were forest specialists, pioneers, and generalists in different land use types, and percentages of stems identified as native or exotic were calculated and visualized. To compare the proportion of exotic versus native woody species across land-use types, we fitted a binomial generalized linear model using the proportion of exotic versus native individuals per site. Post-hoc pairwise comparisons among land-use types were then performed using Tukey-adjusted estimated marginal means (Tukey post-hoc tests, all $p < 0.01$).

Fourth, to illustrate the overlap of species occurring in different land use types, we plotted Venn diagrams. Finally, to analyze vegetation structure, we plotted histograms of diameter at breast height (DBH) for the sum of all stems within a given land use type.

2.5. Limitations

Species diversity was assessed using species richness and the Shannon diversity index, which are widely used and readily interpretable measures in vegetation ecology. We acknowledge that alternative approaches based on Hill numbers as proposed by [Chao and Jost \(2012\)](#) could provide equally meaningful, and potentially more nuanced diversity estimates. However, the metrics used here provide a transparent and widely understood representation of biodiversity patterns across the study landscape.

3. Results

Within our 19 reference sites in the national park, we identified 100 woody plant species, and all of them were native. The most abundant species were *Carapa grandiflora*, *Macaranga kilimandscharica*, *Strombosia scheffleri*, *Xymalos monospora*, and *Symphonia globulifera*. It was dominated by forest specialist species, and 30% of stems were seedlings. Other land use types had lower species richness and were dominated by exotic species ([Fig. 2](#)). Eighty species were identified in Homegardens, with a relatively high proportion of native (35%) species. Here, 23% of stems were seedlings, and *Erythrina abyssinica*, *Vernonia amygdalina* were common species. Sixty species were identified in agricultural mosaics with 20% native and forty-two species were identified in tree patches and, were dominated by exotic species such as *Alnus acuminata*, *Grevillea robusta*, and *Eucalyptus* species. Tree patches were dominated by exotic species (93%) and showed low regeneration, while few woody species (and especially *Alnus acuminata*) were recorded in pastures ([Fig. 2 & Fig. S4](#)). The proportion of exotic species differed significantly across land-use types (binomial GLM, $p < 0.001$; [Fig. 2](#)). Tukey post-hoc comparisons revealed significant differences in DBH distributions among land-use types ($p < 0.001$; [Fig. 6](#)).

Species accumulation curves from the 20 m by 20 m plots ([Fig. 3](#)) showed that reference sites (National Park) had far more species than other types of sites. Of the other land-use types, homegardens exhibited the highest species richness ([Fig. 3; Fig. S1](#)). Rarefied richness based on number of individuals yielded the same pattern as plot-based richness, with homegardens consistently showing higher species richness compared to all other land use types apart from the National Park ([Fig. S2](#)). For species composition, there was substantial overlap in which species occurred in different types of sites. Homegardens, Agriculture mosaics, and Pastures shared 18 species, while Tree patches,

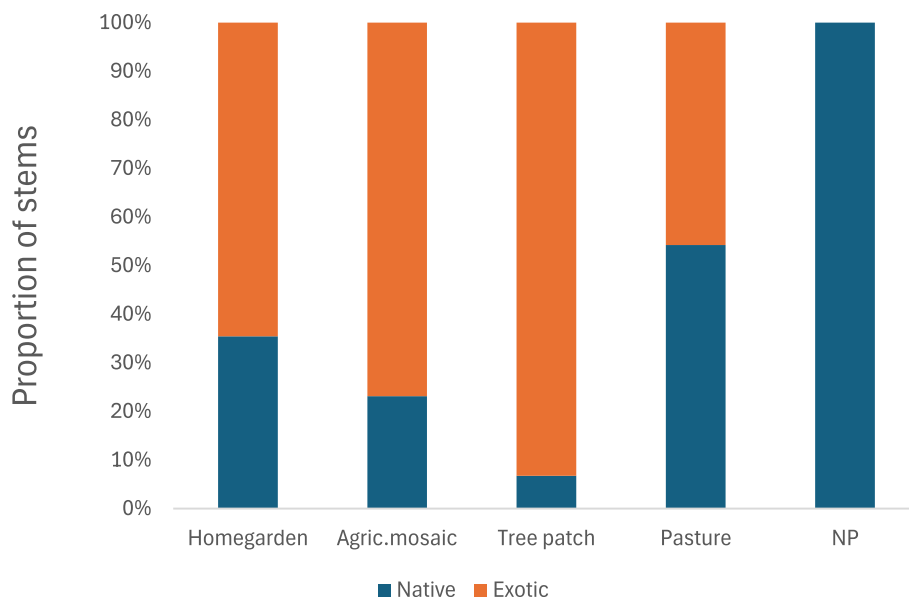


Fig. 2. Woody species classification based on the origin (native or exotic species).

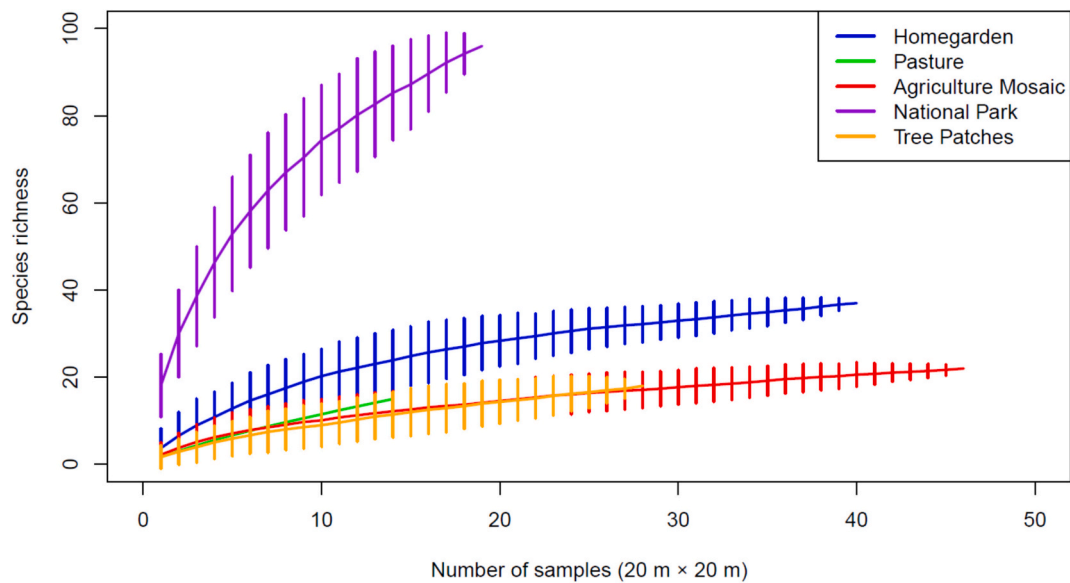


Fig. 3. Species accumulation curve within 20 m by 20 m plots.

Homegardens, and Agriculture mosaics shared 26 species (Fig. S3).

Species richness varied significantly across land-use types (Table 1). From the species richness across land use types, homegardens (H) exhibited the highest species richness, Agriculture mosaics (A) and pasture (P) showed intermediate richness, and tree patches (T) had the lowest species richness (Fig. 5). We found significant differences in Shannon diversity among land-use types ($p < 0.001$). Reference sites exhibited the highest Shannon diversity, followed by homegardens, while agricultural mosaics, pastures, and tree patches had significantly lower values (Fig. 7). Post-hoc Tukey tests confirmed that reference sites differed significantly from all other land-use types, and that homegardens supported significantly higher diversity than agricultural mosaics, pastures, and tree patches ($p < 0.05$ in all cases).

We found significant relationships between species richness and land-use type as well as distance from the National Park (Table 1). Sites closer to the park exhibited lower species richness, but there was high variability among the points (Fig. 4). Estimated marginal means from glm indicated differences in woody species richness among land-use types. Specifically, pairwise comparisons showed that homegardens exhibited the highest richness (Tukey-adjusted $p < 0.01$), tree patches exhibited the lowest richness, and the agricultural mosaic and pasture sites had intermediate levels of richness (Table 2). Histograms of diameter at breast height (DBH) revealed structural differences across land use types. DBH was right-skewed in the National Park, homegardens, and the agriculture mosaic, reflecting many small stems and fewer larger ones. Tree patches, in contrast, showed a slightly bimodal pattern with a few larger stems (Fig. 6).

Table 1

Modelling results for species richness of woody vegetation. The table shows the terms included in the selected model, their coefficients, standard errors, and p -values. Species richness: $\text{glm5} < - \text{glm}$ (formula = richness ~ logdispark + type, family = "poisson", data = lmdata); where; H: Homegardens; P: Pastures; T: Tree patches; NP: National Park.

Terms	Coefficients	Standard error	p-value
(Intercept)	0.23391	0.26701	0.381
Log (distance to NP)	0.18361	0.02868	1.54e-10 ***
TypeH	0.42558	0.07338	6.65e-09 ***
TypeP	-0.06557	0.15552	0.673
TypeT	-0.60751	0.11200	5.82e-08 ***

4. Discussion

Forest landscape restoration is being implemented worldwide. However, its success in restoring biodiversity varies, as restoration outcomes differ across regions, taxa, and restoration strategies.

(Brançalion et al., 2025; Crouzeilles et al., 2017; Di Sacco et al., 2021). Focusing on woody species in western Rwanda, we showed that a landscape targeted for numerous restoration interventions remains rather poor in species richness compared to reference sites. Perhaps surprisingly, the highest species richness of native species was found in homegardens – locations that are rarely considered in a restoration context. We discuss these findings with respect to four aspects, namely (1) the observed disparities in species richness and diversity among the restored areas; (2) the fact that many forest landscape restoration efforts favor the use of exotic species, potentially at the expense of ecological integrity; (3) and the need for restoration to not only pursue ecological targets but also incorporate the needs and knowledge of the local community to ensure the sustainability and acceptance of the restoration initiatives.

Our findings revealed significant variations in woody species richness and composition across the land use types examined. Homegardens exhibited the highest species richness and diversity among the restored sites, which might be due to traditional and cultural values, medicinal benefits, and the integration of multiple tree species as part of agroforestry practices (e.g. Bouyahya et al., 2017; Hemp, 2006). A recent study in Ethiopia by Mammo and Dereje (2025) similarly highlighted that homegarden agroforestry can contribute to biodiversity conservation, income generation, and food security. Homegardens are widespread in tropical regions and provide essential support to households by supplying food, fodder, traditional medicine, and fuelwood, as well as contributing to income diversification and holding significant cultural and social value (Mohri et al., 2013). Homegardens thus serve as an effective approach for conserving biodiversity by integrating a diverse range of plant species and promoting sustainable land use practices while also balancing ecological considerations with human needs (Eyasu et al., 2020).

In contrast, agriculture mosaics and tree patches in our study area exhibited substantially lower species richness and were dominated by exotic species such as *Eucalyptus* and *Pinus*. These monocultures limit ecological complexity and reduce habitat availability for a broader range of species (Schuler et al., 2017). Native species were generally underrepresented across restored areas on a gradient from homegardens

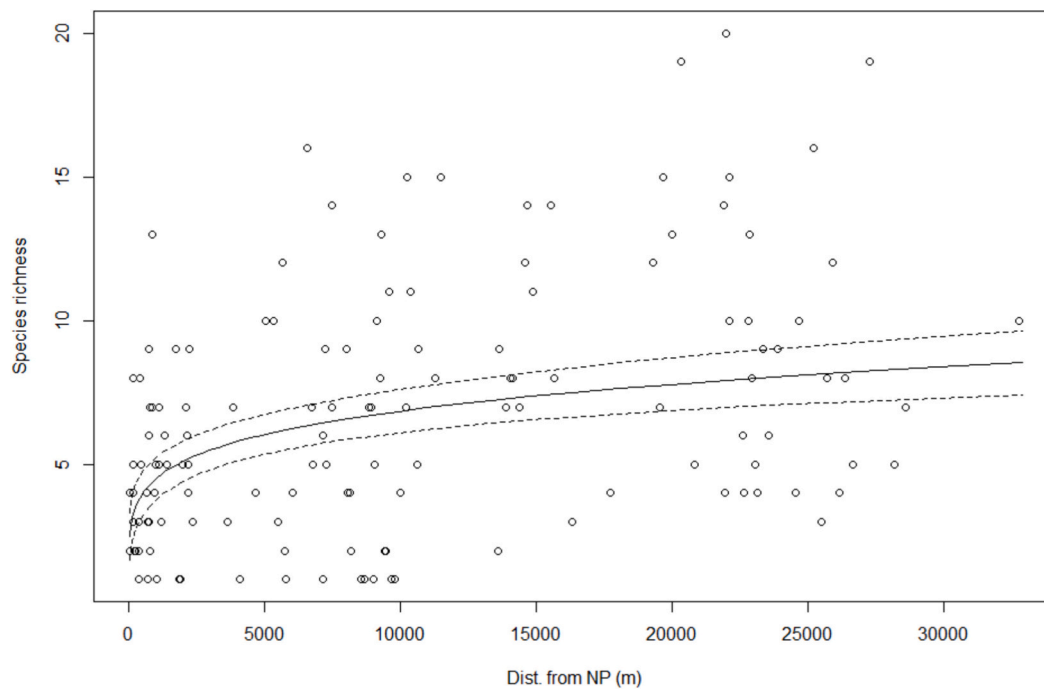


Fig. 4. Scatterplots of species richness against distance from the park (predicted line plotted here is for agricultural mosaic sites).

Table 2

Results for tukey- adjusted pairwise contrasts of estimated marginal means for species richness among land-use types derived from glm, where A: Agriculture mosaic; H: Homegardens; P: Pastures; T: Tree patches.

Contrast	Estimate	SE	z.ratio	p.value
A – H	–0.4256	0.0734	–5.800	<0.0001
A – P	0.0656	0.1560	0.422	0.9748
A – T	0.6075	0.1120	5.424	<0.0001
H – P	0.4912	0.1520	3.225	0.0069
H – T	1.0331	0.1080	9.542	<0.0001
P – T	0.5419	0.1760	3.087	0.0109

(35% native) to agriculture mosaics (25% native) and tree patches (7% native). The dominance of exotic species in Rwanda's restored sites reflects the practical and socioeconomic considerations that have shaped restoration efforts in the country. Exotic species such as *Eucalyptus* are widely planted due to their fast growth, high economic value, readily available planting material, and ability to establish vegetation cover on degraded land quickly (Arakwiye et al., 2021). Tree patches, which may look like restoration success in remote sensing imagery (e.g., for carbon sequestration (Mugabowindekwe et al., 2023)), are particularly species poor. This means on-ground assessments of forest landscape restoration are important – not everything that looks like a 'forest' from satellite images can be considered a natural forest ecosystem, ecologically speaking, on the ground.

Indeed, despite extensive restoration efforts, the landscape in western Rwanda continues to be dominated by exotic species. This might be because large-scale restoration initiatives, especially in the Global South, may officially claim to restore biodiversity, but the specific restoration activities that are being carried out may not primarily target biodiversity – rather, other goals like carbon sequestration or the provisioning of wood may be prioritized by governments or international donors (Forgues et al., 2024; Martin et al., 2021). Indeed, the main focus in Western Rwandan interventions have been situated more on the left hand side of the restorative continuum (Gann et al., 2019), that focuses more on rehabilitation and increasingly ecosystem functions rather than species composition or biodiversity as a key focus.

For example, the Bonn Challenge has been criticized for encouraging

fairly indiscriminate tree planting, with little consideration of which specific actions would be best for biodiversity (Temperton et al., 2019). This, in combination with seed shortages of many native species, has meant that many low-income countries have focused on planting non-native species because their seedlings are readily available in nurseries (Telila et al., 2015), as well as being fast-growing species. In Rwanda, farmers have widely adopted agroforestry practices to retain and integrate trees into their farmlands (Bucagu et al., 2013), Leguminous species within the cropping system were emphasized (Mukangango, 2019; Okogun et al., 2000; Yamoah and Burleigh, 1990), and restoration interventions are routinely designed with a keen awareness of their potential to deliver benefits to the local community. Telila et al. (2015) stated that there was a shift in the initial rehabilitation efforts that primarily utilized *Eucalyptus* to more complex agroforestry systems that increasingly incorporate native species. Still, our results showed that exotic species remain highly dominant to date.

The exotic species provide crucial benefits including timber, fuelwood, and erosion control, which aligns with the socio-economic needs of local communities (Taremwa et al., 2022). However, their prevalence comes at the cost of biodiversity and ecological resilience (Fleischman et al., 2020; Iglesias-Carrasco et al., 2025). Exotic monocultures often suppress native species through competition for resources and can alter soil properties, reducing the habitat quality for native species (Chu et al., 2014; Ferreira et al., 2019; Mugunga et al., 2017). A study by Bucagu et al. (2013) found that wealthier farmers who have a large plot of land planted mostly timber trees (*Eucalyptus* species), whereas poor farmers with insufficient land are likely to plant other species like *Grevillea*, which is also introduced but is more compatible with crops and provides a more diverse mixture of benefits. This difference is an influential factor that contributes to exotic woody species preferences, but also suggests that some benefits are possible from using more native species in the future (Bulonvu et al., 2025). Indeed, recent projects have begun to use indigenous species to enhance biodiversity (LAFREC, 2021).

Not least in the context of choosing appropriate native species, restoration activities should be deeply rooted in community involvement, ensuring that local identities, cultures, and traditional connections to the land are respected and integrated into the decision-making process (Gann et al., 2019). The selection of species for restoration not

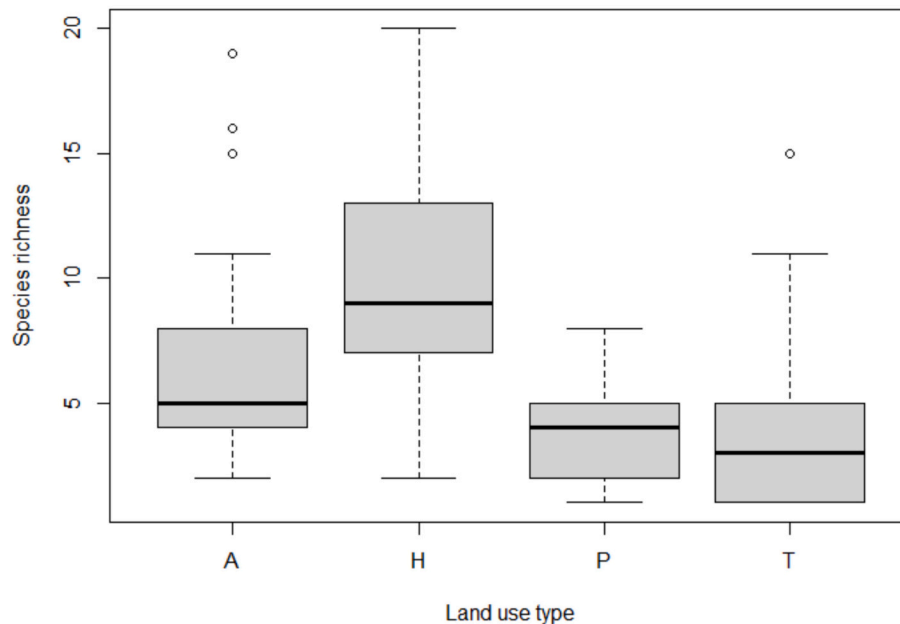


Fig. 5. Boxplot of species richness within land-use type: A: Agriculture Mosaic, H: Homegardens, P: Pastures, and T: Tree patches.

only demands an in-depth understanding but also hinges on the community's profound knowledge of native species (Elias and Fabien, 2024). Community perceptions of adopted approaches in restoration projects influence the success of restoration projects (Abukari and Mwalyosi, 2020). Community perceptions are influenced by a dynamic mix of ecological, social, cultural, economic, and governance factors. Hemmerling et al. (2020) emphasized that restoration strategies, including species selection, must substantially involve local communities, catering to their values and priorities.

Gishwati-Mukura National Park is an important biodiversity reservoir and a potential source of propagules in the region. It harbors by far the highest species richness and maintains structural complexity (Gasore, 2020) that is different from the restored sites. In theory, proximity to the national park can facilitate natural regeneration through seed dispersal. However, the dominance of exotic species in surrounding land-use types at present indicates that native species from the park are not successfully establishing in these areas. This may be due to restricted seed dispersal, intensive land use practices, or the competitive suppression by fast growing exotics. Strengthening ecological connectivity and promoting native regeneration in these areas could substantially enhance the landscape's overall recovery.

Finally, our results suggest that current restoration efforts are far from creating self-sustaining ecosystems. The diameter at breast height (DBH) distribution across different restoration sites highlighted variations in the age of trees, reflecting diverse stages of ecological succession and forest development which are critical for assessing the success of forest restoration efforts. The tree patches tended to be dominated by single age classes, and most consisted of younger or medium-aged trees. Homegardens and agricultural mosaics also showed a prevalence of trees with small DBH, indicating recent planting efforts where young trees dominate and large trees typical of the reference sites are missing. Similar studies like Zahawi et al. (2013) have noted that DBH distribution can serve as a proxy for assessing structural diversity within restored forests, which is crucial for maintaining ecosystem functionality. Natural tree regeneration, to date, appears relatively uncommon in the landscape we studied. The patterns we document including

dominance of exotic species and low levels of natural regeneration suggest that this landscape may constitute a novel ecosystem; where both biotic and abiotic system components are fundamentally altered compared to an original reference state (Hobbs et al., 2013). Recognizing the presence of novel ecosystems is critical for designing appropriate restoration strategies in highly populated and intensively used landscapes like Western Rwanda – rather than aiming for complete ecological recovery of a near-natural reference state, a certain level of novelty may be inevitable in this setting, whilst still aiming to bolster native diversity. This perspective aligns with holistic approaches to ecological restoration (Clewell and Aronson, 2012), that emphasize integrating ecological, social, and cultural dimensions rather than focusing solely on reinstating historical species composition.

5. Conclusion

This study highlighted the complexities of forest landscape restoration in Western Rwanda, showing that even though restoration efforts aim to enhance biodiversity, woody species richness remains very low in restored sites compared to reference sites. By contrast, homegardens, which are traditionally overlooked in restoration initiatives, harbored the highest native woody species richness, suggesting they have hitherto overlooked potential in conservation strategies. The dominance of exotic species in restored areas raises concerns about long-term ecological sustainability, emphasizing the need for new restoration strategies that prioritize native species. Based on our findings, we recommend (1) strengthening efforts to use native species in restoration, (2) including homegardens in restoration strategies because they are important for biodiversity, and (3) conducting further research on the drivers of species selection in restoration. Balancing biodiversity conservation with the socio-economic needs of local communities remains a challenge, requiring more inclusive and adaptive restoration approaches in the future.

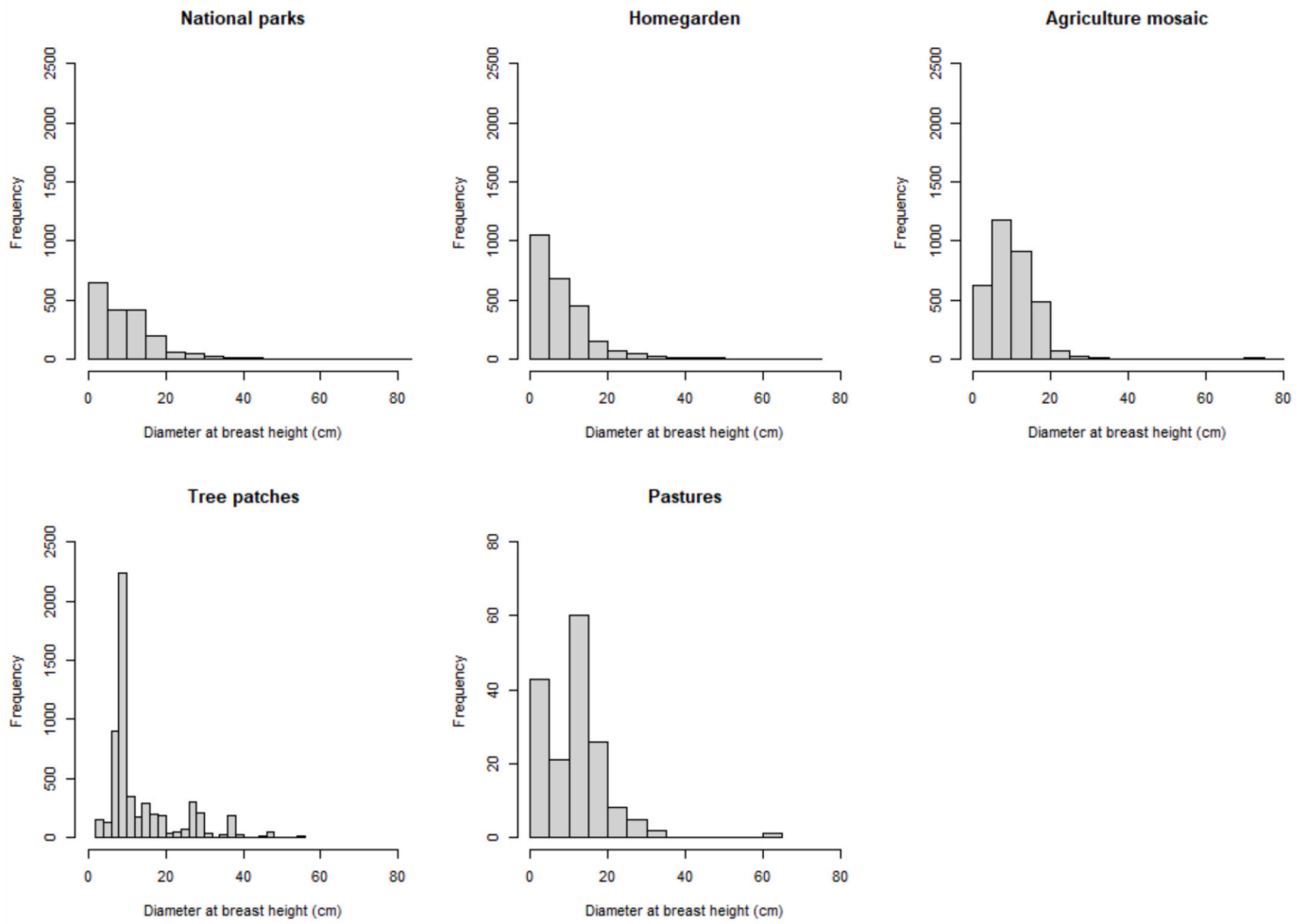


Fig. 6. Diameter at breast height distribution across the land use types. Note that the y-axis on the pastures is different from other land use types because it had fewer stems, indicating a sparse distribution.

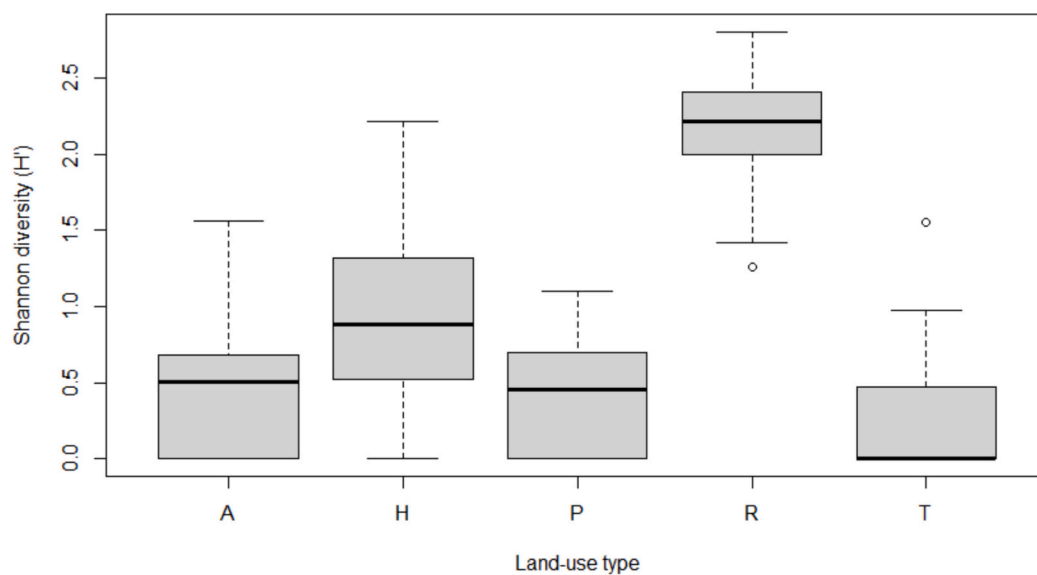


Fig. 7. Abundance-based Shannon diversity (H') among the land-use types; A: Agriculture mosaic, H: Homegarden; T: Tree patches; P: Pastures, and R: Reference (National park).

CRediT authorship contribution statement

Verene Nyiramvuyekure: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Joern Fischer:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Beth A. Kaplin:** Writing – review & editing, Supervision. **Athanase Mukuralinda:** Writing – review & editing. **Vicky M. Temperton:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors have no conflicts of interest to declare.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.111812>.

Data availability

Data will be made available on request.

References

- Abukari, H., Mwalyosi, R.B., 2020. Local communities' perceptions about the impact of protected areas on livelihoods and community development. *Global Ecology and Conservation* 22, e00909. <https://doi.org/10.1016/j.gecco.2020.e00909>.
- Akinyemi, F.O., 2017. Land change in the central Albertine rift: insights from analysis and mapping of land use-land cover change in North-Western Rwanda. *Appl. Geogr.* 87, 127–138. <https://doi.org/10.1016/j.apgeog.2017.07.016>.
- Arakwiye, B., Rogan, J., Eastman, J.R., 2021. Thirty years of forest-cover change in Western Rwanda during periods of wars and environmental policy shifts. *Reg. Environ. Chang.* 21, 27. <https://doi.org/10.1007/s10113-020-01744-0>.
- Aronson, J., Alexander, S., 2013. Ecosystem restoration is now a global priority: time to roll up our sleeves. *Restor. Ecol.* 21, 293–296. <https://doi.org/10.1111/rec.12011>.
- Austin, M.P., Van Niel, K.P., 2011. Improving species distribution models for climate change studies: variable selection and scale. *J. Biogeogr.* 38, 1–8. <https://doi.org/10.1111/j.1365-2699.2010.02416.x>.
- Bagstad, K.J., Ingram, J.C., Lange, G.-M., Masozera, M., Ancona, Z.H., Bana, M., Kagabo, D., Musana, B., Nabahungu, N.L., Rukundo, E., Rutebuka, E., Polasky, S., Rugege, D., Uwera, C., 2020. Towards ecosystem accounts for Rwanda: tracking 25 years of change in flows and potential supply of ecosystem services. *People and Nature* 2, 163–188. <https://doi.org/10.1002/pan3.10062>.
- Baumann, M., Duguma, D., Vögele, S., Wollni, M., Sun, P., Ndayizwe, G., Fischer, J., 2025. Design principles for social-ecological research at the landscape scale applied to western Rwanda. *PLoS One* 20, e0330704. <https://doi.org/10.1371/journal.pone.0330704>.
- Bouyahya, A., Abrini, J., Et-Touys, A., Bakri, Y., Dakka, N., 2017. Indigenous knowledge of the use of medicinal plants in the north-west of Morocco and their biological activities. *Eur. J. Integr. Med.* 13, 9–25. <https://doi.org/10.1016/j.eujim.2017.06.004>.
- Brancalion, P.H.S., Hua, F., Joyce, F.H., Antonelli, A., Holl, K.D., 2025. Moving biodiversity from an afterthought to a key outcome of forest restoration. *Nat. Rev. Biodivers.* 1, 248–261. <https://doi.org/10.1038/s44358-025-00032-1>.
- Brandt, M., Rasmussen, K., Peñuelas, J., Tian, F., Schurgers, G., Verger, A., Mertz, O., Palmer, J.R.B., Fensholt, R., 2017. Human population growth offsets climate-driven increase in woody vegetation in sub-Saharan Africa. *Nat. Ecol. Evol.* 1, 1–6. <https://doi.org/10.1038/s41559-017-0081>.
- Bucagu, C., Vanlauwe, B., Van Wijk, M.T., Giller, K.E., 2013. Assessing farmers' interest in agroforestry in two contrasting agro-ecological zones of Rwanda. *Agrofor. Syst.* 87, 141–158. <https://doi.org/10.1007/s10457-012-9531-7>.
- Buckingham, K., Arakwiye, B., Ray, S., Maneerattana, O., Anderson, W., 2021. Cultivating networks and mapping social landscapes: how to understand restoration governance in Rwanda. *Land Use Policy* 104, 104546. <https://doi.org/10.1016/j.landusepol.2020.104546>.
- Bulonvu, F., Imani, G., Mujawamariya, M., Kaplin, B.A., Mutabazi, P., Cuni-Sanchez, A., 2025. The importance of native trees and forests: smallholder farmers' views in South-Western Rwanda. *Forests* 16, 1234. <https://doi.org/10.3390/f16081234>.
- Cantore, N., 2011. *The Crop Intensification Program in Rwanda: A Sustainability Analysis*.
- Chao, A., Jost, L., 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93, 2533–2547. <https://doi.org/10.1890/11-1952.1>.
- Chazdon, R.L., 2014. *Second growth: the promise of tropical Forest regeneration in an age of deforestation*. University of Chicago Press. <https://doi.org/10.7208/9780226118109>.
- Chazdon, R.L., Uriarte, M., 2016. Natural regeneration in the context of large-scale forest and landscape restoration in the tropics. *Biotropica* 48, 709–715. <https://doi.org/10.1111/btp.12409>.
- Chu, C., Mortimer, P.E., Wang, H., Wang, Y., Liu, X., Yu, S., 2014. Allelopathic effects of *Eucalyptus* on native and introduced tree species. *For. Ecol. Manag.* 323, 79–84. <https://doi.org/10.1016/j.foreco.2014.03.004>.
- Clay, N., 2019. Fixing the ecosystem: conservation, crisis and capital in Rwanda's Gishwati Forest. *Environment and Planning E: Nature and Space* 2, 23–46. <https://doi.org/10.1177/2514848619826576>.
- Clewell, A.F., Aronson, J., 2012. *Ecological Restoration: Principles, Values, and Structure of an Emerging Profession*. Island Press.
- Corlett, R.T., Primack, R.B., 2011. *Tropical Rain Forests: An Ecological and Biogeographical Comparison*. John Wiley & Sons.
- Crespo Cuarema, J., Heger, M., 2019. Deforestation and economic development: evidence from national borders. *Land Use Policy* 84, e347–e353. <https://doi.org/10.1016/j.landusepol.2018.12.039>.
- Crouzeilles, R., Ferreira, M.S., Chazdon, R.L., Lindenmayer, D.B., Sansevero, J.B.B., Monteiro, L., Iribarrem, A., Latawiec, A.E., Strassburg, B.B.N., 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Sci. Adv.* 3, e1701345. <https://doi.org/10.1126/sciadv.1701345>.
- Di Sacco, A., Hardwick, K.A., Blakesley, D., Brancalion, P.H.S., Breman, E., Cecilio Rebola, L., Chomba, S., Dixon, K., Elliott, S., Ruyonga, G., Shaw, K., Smith, P., Smith, R.J., Antonelli, A., 2021. Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Glob. Chang. Biol.* 27, 1328–1348. <https://doi.org/10.1111/gcb.15498>.
- Elias, M., Fabien, R., 2024. Perception and knowledge of local community on the use of indigenous tree species for ecosystem restoration in Gasabo District, Rwanda. *Rwanda Journal of Engineering, Science, Technology and Environment* 6, 1–19.
- Eyasu, G., Tolera, M., Negash, M., 2020. Woody species composition, structure, and diversity of homegarden agroforestry systems in southern Tigray, Northern Ethiopia. *Heliyon* 6. <https://doi.org/10.1016/j.heliyon.2020.e05500>.
- Ferreira, V., Boyero, L., Calvo, C., Correa, F., Figueroa, R., Gonçalves, J.F., Goyenola, G., Graça, M.A.S., Hepp, L.U., Kariuki, S., López-Rodríguez, A., Mazzeo, N., M'Erimba, C., Monroy, S., Peil, A., Pozo, J., Rezende, R., Teixeira-de-Mello, F., 2019. A global assessment of the effects of Eucalyptus plantations on stream ecosystem functioning. *Ecosystems* 22, 629–642. <https://doi.org/10.1007/s10021-018-0292-7>.
- Fleischman, F., Basant, S., Chhatre, A., Coleman, E.A., Fischer, H.W., Gupta, D., Güneralp, B., Kashwan, P., Khatri, D., Muscarella, R., Powers, J.S., Ramprasad, V., Rana, P., Solorzano, C.R., Veldman, J.W., 2020. Pitfalls of tree planting show why we need people-centered natural climate solutions. *BioScience* 70, 947–950. <https://doi.org/10.1093/biosci/biaa094>.
- Forgues, K., Carignan, M.-C., Marchena, B., Mancilla, Lady, Pacheco, C., Pacheco Ortega, E., Guainora, A., Potvin, C., 2024. Comparing carbon offsets and livelihood benefits in a long-term reforestation project: Agroforestry versus native timber versus enrichment planting. *Ecological Solutions and Evidence* 5, e12372. <https://doi.org/10.1002/2688-8319.12372>.
- Frietsch, M., Pacheco-Romero, M., Temperton, V.M., Kaplin, B.A., Fischer, J., 2024. The social-ecological ladder of restoration ambition. *Ambio* 53, 1251–1261. <https://doi.org/10.1007/s13280-024-02021-8>.
- Gann, G.D., McDonald, T., Walder, B., Aronson, J., Nelson, C.R., Jonson, J., Hallett, J.G., Eisenberg, C., Guariguata, M.R., Liu, J., Hua, F., Echeverria, C., Gonzales, E., Shaw, N., Declerck, K., Dixon, K.W., 2019. International principles and standards for the practice of ecological restoration. *Restor. Ecol.* 27(S1): S1–S46, 27, S1–S46. doi:<https://doi.org/10.1111/rec.13035>.
- Gasore, B., 2020. Gishwati-Mukura Landscape Designated UNESCO Biosphere Reserve. Official Rwanda Development Board (RDB) Website. URL <https://rdb.rw/gishwati-mukura-landscape-designated-unesco-biosphere-reserve/> (accessed 12.22.25).
- Gebauer, C., Doevenspeck, M., 2015. Adaptation to climate change and resettlement in Rwanda. *Area* 47, 97–104. <https://doi.org/10.1111/area.12168>.
- Habiyaremye, G., Jiwen, G., 2011. *Demographic Pressure Impacts on Forests in Rwanda*.
- Hafashimana, N., Sebego, R.J., Kenabatho, P.K., Lekoko, R.N., Maphanyane, J.G., 2022. Assessing the effects of LULC change on landslide hazards in Rwanda: a case study in Nyabihu District. *Journal of Environmental Geography* 15, 23–30. <https://doi.org/10.14232/jengeo-2022-44169>.
- Hawthorne, W.D., 1995. *Ecological Profiles of Ghanaian Forest Trees*.
- Hemmerling, S.A., Barra, M., Bienn, H.C., Baustian, M.M., Jung, H., Meselhe, E., Wang, Y., White, E., 2020. Elevating local knowledge through participatory modeling: active community engagement in restoration planning in coastal

- Louisiana. *J. Geogr. Syst.* 22, 241–266. <https://doi.org/10.1007/s10109-019-00313-2>.
- Hemp, A., 2006. The Banana forests of Kilimanjaro: biodiversity and conservation of the Chagga Homegardens. *Biodivers. Conserv.* 15, 1193–1217. <https://doi.org/10.1007/s10531-004-8230-8>.
- Hobbs, R.J., Higgs, E.S., Hall, C.M., 2013. Defining Novel Ecosystems, in: *Novel Ecosystems*. John Wiley & Sons, Ltd, pp. 58–60. doi:<https://doi.org/10.1002/9781118354186.ch6>.
- Holl, K.D., Luong, J.C., Brancalion, P.H.S., 2022. Overcoming biotic homogenization in ecological restoration. *Trends Ecol. Evol.* 37, 777–788. <https://doi.org/10.1016/j.tree.2022.05.002>.
- Iglesias-Carrasco, M., Torres, J., Cruz-Dubon, A., Candolin, U., Wong, B.B.M., Velo-Antón, G., 2025. Global impacts of exotic eucalypt plantations on wildlife. *Biol. Rev.* 100, 1734–1753. <https://doi.org/10.1111/brv.70022>.
- IUCN, 2024. Restoring Soil and Land Health in Rwanda Using a Community Centered Approach - Blog | IUCN [WWW Document]. URL: <https://iucn.org/blog/202401/restoring-soil-and-land-health-rwanda-using-community-centered-approach>. (Accessed 21 January 2025).
- Jakovac, C.C., Junqueira, A.B., Crouzeilles, R., Peña-Claros, M., Mesquita, R.C.G., Bongers, F., 2021. The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biol. Rev.* 96, 1114–1134. <https://doi.org/10.1111/brv.12694>.
- Jean Baptiste, N., K. Ruffo, C., Minani, V., Em, M., 2009. Know Some Useful Trees and Shrubs for Agricultural and Pastoral Communities of Rwanda.
- Kearsley, E., Hufkens, K., Verbeeck, H., Bauters, M., Beeckman, H., Boeckx, P., Huygens, D., 2019. Large-sized rare tree species contribute disproportionately to functional diversity in resource acquisition in African tropical forest. *Ecol. Evol.* 9, 4349–4361. <https://doi.org/10.1002/ece3.4836>.
- Landholm, D.M., Pradhan, P., Kropp, J.P., 2019. Diverging forest land use dynamics induced by armed conflict across the tropics. *Glob. Environ. Chang.* 56, 86–94. <https://doi.org/10.1016/j.gloenvcha.2019.03.006>.
- Landscape Approach to Forest Restoration and Conservation (LAFREC), 2021. *Implementation Completion and Results Report (No. ICR00005783)*.
- Laurance, W.F., Goosem, M., Laurance, S.G.W., 2009. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* 24, 659–669. <https://doi.org/10.1016/j.tree.2009.06.009>.
- Mammo, S., Dereje, Y., 2025. Woody species diversity of homegarden agroforestry and their contribution to livelihoods improvement in Dendi District, Central Ethiopia. *Agrofor. Syst.* 99, 59. <https://doi.org/10.1007/s10457-025-01157-0>.
- Maroyi, A., 2009. Traditional homegardens and rural livelihoods in Nhemba, Zimbabwe: a sustainable agroforestry system. *Int. J. Sustain. Dev. World Ecol.* 16, 1–8. <https://doi.org/10.1080/13504500902745895>.
- Martin, M.P., Woodbury, D.J., Doroski, D.A., Nagele, E., Storace, M., Cook-Patton, S.C., Pasternack, R., Ashton, M.S., 2021. People plant trees for utility more often than for biodiversity or carbon. *Biol. Conserv.* 261, 109224. <https://doi.org/10.1016/j.biocon.2021.109224>.
- Middendorp, R.S., Pérez, A.J., Molina, A., Lambin, E.F., 2016. The potential to restore native woody plant richness and composition in a reforesting landscape: a modeling approach in the Ecuadorian Andes. *Landscape Ecol.* 31, 1581–1599. <https://doi.org/10.1007/s10980-016-0340-7>.
- Mohri, H., Lahoti, S., Saito, O., Mahalingam, A., Gunatilleke, N., Irham, Hoang, V.T., Hitinayake, G., Takeuchi, K., Herath, S., 2013. Assessment of ecosystem services in homegarden systems in Indonesia, Sri Lanka, and Vietnam. *Ecosyst. Serv.* 5, 124–136. <https://doi.org/10.1016/j.ecoser.2013.07.006>.
- Mugabowindekwe, M., Brandt, M., Chave, J., Reiner, F., Skole, D.L., Kariryaa, A., Igel, C., Hiernaux, P., Ciais, P., Mertz, O., Tong, X., Li, S., Rwanyiziri, G., Dushimiyimana, T., Ndoli, A., Uwizeyimana, V., Lillesø, J.-P.B., Gieseke, F., Tucker, C.J., Saatchi, S., Fensholt, R., 2023. Nation-wide mapping of tree-level aboveground carbon stocks in Rwanda. *Nat. Clim. Chang.* 13, 91–97. <https://doi.org/10.1038/s41558-022-01544-w>.
- Mugunga, C.P., Giller, K.E., Mohren, G.M.J., 2017. Tree-crop interactions in maize-eucalypt woodlot systems in southern Rwanda. *Eur. J. Agron.* 86, 78–86. <https://doi.org/10.1016/j.eja.2017.03.004>.
- Mukangango, M., 2019. Potential of *Acacia angustissima*, *Leucaena pallida* and *Mimosa scabrella* in agroforestry systems on a Rwandan Ferralsol. *Acta Universitatis Agriculturae* 73, 63–69.
- Nambajimana, J. de D., He, X., Zhou, J., Justine, M.F., Li, J., Khurram, D., Mind'je, R., Nsabimana, G., 2020. Land use change impacts on water erosion in Rwanda. *Sustainability* 12, 50. <https://doi.org/10.3390/su12010050>.
- Nash, C., Carvalho, S., Raes, L., Ndoli, A., Karangwa, C., Imanirareba, E., Njue, J., Nicholas, B., Toovey, D., 2020. How Rwanda became a restoration leader | IUCN [WWW document]. URL: <https://iucn.org/news/forests/202003/how-rwanda-became-a-restoration-leader> (accessed 1.20.25).
- Ndayambaje, J.D., Mohren, G.M.J., 2011. Fuelwood demand and supply in Rwanda and the role of agroforestry. *Agrofor. Syst.* 83, 303–320. <https://doi.org/10.1007/s10457-011-9391-6>.
- Norden, N., Chave, J., Belbenoit, P., Caubère, A., Châtelet, P., Forget, P.-M., Riéra, B., Viers, J., Thébaud, C., 2009. Interspecific variation in seedling responses to seed limitation and habitat conditions for 14 Neotropical woody species. *J. Ecol.* 97, 186–197. <https://doi.org/10.1111/j.1365-2745.2008.01444.x>.
- Okogun, J.A., Sangina, N., Mulongoy, K., 2000. Nitrogen contribution of five leguminous trees and shrubs to alley cropped maize in Ibadan, Nigeria. *Agrofor. Syst.* 50, 123–136. <https://doi.org/10.1023/A:1006471303235>.
- Ouédraogo, D.-Y., Mortier, F., Gourlet-Fleury, S., Freycon, V., Picard, N., 2013. Slow-growing species cope best with drought: evidence from long-term measurements in tropical semi-deciduous moist forest of Central Africa. *J. Ecol.* 101, 1459–1470. <https://doi.org/10.1111/1365-2745.12165>.
- Pascal, J.-P., Fre, I.F. de P., 1984. Les forêts denses humides sempervirentes des Ghats occidentaux de l'Inde: ecologie, structure floristique, succession.
- Plieninger, T., Muñoz-Rojas, J., Buck, L.E., Scherr, S.J., 2020. Agroforestry for sustainable landscape management. *Sustain. Sci.* 15, 1255–1266. <https://doi.org/10.1007/s11625-020-00836-4>.
- Republic of Rwanda, 2017. In: Ministry of Natural Resources (Ed.), *Rwanda National Forest Policy*.
- Republic of Rwanda, 2017a. *Forest Investment Program for Rwanda*.
- Republic of Rwanda, 2021. *How Silvopastoralism approach is contributing to sustainable and efficient livestock production around Gishwati-Mukura National Park*.
- Richards, D., Allen, K., Graham, S., Harcourt, N., Kirk, N., Lavorel, S., McNally, S., Polyakov, M., Whitehead, D., 2024. Carbon stocks and sequestration from small tree patches in grassland landscapes in Aotearoa-New Zealand. *Clim. Pol.* 0, 1–19. <https://doi.org/10.1080/14693062.2024.2427710>.
- Sanaphre-Villanueva, L., Dupuy, J.M., Andrade, J.L., Reyes-García, C., Jackson, P.C., Paz, H., 2017. Patterns of plant functional variation and specialization along secondary succession and topography in a tropical dry forest. *Environ. Res. Lett.* 12, 055004. <https://doi.org/10.1088/1748-9326/aa6baa>.
- Schuler, L.J., Bugmann, H., Snell, R.S., 2017. From monocultures to mixed-species forests: is tree diversity key for providing ecosystem services at the landscape scale? *Landscape Ecol.* 32, 1499–1516. <https://doi.org/10.1007/s10980-016-0422-6>.
- Taremwa, N.K., Gasingirwa, M.-C., Nsabimana, D., 2022. Unleashing traditional ecological knowledge for biodiversity conservation and resilience to climate change in Rwanda. *Afr. J. Sci. Technol. Innov. Dev.* 14, 204–215. <https://doi.org/10.1080/20421338.2020.1821948>.
- Telila, H., Hylander, K., Nemomissa, S., 2015. The potential of small Eucalyptus plantations in farmscapes to foster native woody plant diversity: local and landscape constraints. *Restor. Ecol.* 23, 918–926. <https://doi.org/10.1111/rec.12257>.
- Temperton, V.M., Buchmann, N., Buisson, E., Durigan, G., Kazmierczak, L., Perring, M. P., de Sá Dechoum, M., Veldman, J.W., Overbeck, G.E., 2019. Step back from the forest and step up to the Bonn challenge: how a broad ecological perspective can promote successful landscape restoration. *Restor. Ecol.* 27, 705–719. <https://doi.org/10.1111/rec.12989>.
- Tuyisingize, D., Eckardt, W., Caillaud, D., Ngabikwiye, M., Kaplin, B.A., 2022. Forest landscape restoration contributes to the conservation of Primates in the Gishwati-Mukura landscape, Rwanda. *Int. J. Primatol.* 43, 867–884. <https://doi.org/10.1007/s10764-022-00303-0>.
- van Oosten, C., Uzamukunda, A., Runhaar, H., 2018. Strategies for achieving environmental policy integration at the landscape level. A framework illustrated with an analysis of landscape governance in Rwanda. *Environ. Sci. Pol.* 83, 63–70. <https://doi.org/10.1016/j.envsci.2018.02.002>.
- White, F., 1983. *The Vegetation of Africa*.
- World Agroforestry, 2016. *Tree Functional and Ecological Databases*.
- Yamoah, C.F., Burleigh, J.R., 1990. Alley cropping Sesbania sesban (L) Merril with food crops in the highland region of Rwanda. *Agrofor. Syst.* 10, 169–181. <https://doi.org/10.1007/BF00115365>.
- Zahawi, R.A., Holl, K.D., Cole, R.J., Reid, J.L., 2013. Testing applied nucleation as a strategy to facilitate tropical forest recovery. *J. Appl. Ecol.* 50, 88–96. <https://doi.org/10.1111/1365-2664.12014>.