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RESEARCH ARTICLE

# Home-garden connectivity rather than tree-cover connectivity facilitates biodiversity in fragmented tropical forest landscapes

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**Abstract**

*Context* Forest landscape restoration (FLR) has emerged as a global strategy to address forest fragmentation and degradation, yet, its ecological effectiveness at local scales remains uncertain. Further, many FLR interventions focus on tree planting, while overlooking other tree-rich systems such as home gardens.

*Objectives* This study focused on the Afromontane rainforest landscape of western Rwanda—a biodiversity-rich region under intense anthropogenic pressure. As tree plantations and home gardens represent the dominant land use types in the study area, our research aimed to assess their respective roles in supporting landscape connectivity and biodiversity.

*Methods* First, we evaluated how tree cover and home gardens contribute to landscape connectivity by applying circuit theory through Omniscape. Subsequently, we examined the relationships between tree-cover connectivity, home-garden connectivity, and the richness and diversity of woody plants and birds, using data collected from 91 field sites.

*Results* Tree-cover connectivity was negatively correlated with the richness and diversity of woody plants and birds. This suggested that increased connectivity through mostly exotic trees did not translate into habitat connectivity for biodiversity. In contrast, home-garden connectivity was positively correlated with the richness and diversity of woody plants and birds. This highlighted the possible beneficial role of home gardens as ecological stepping stones.

*Conclusions* We recommend that restoration efforts prioritize the protection of remaining natural forests, which are irreplaceable for sustaining native biodiversity. Complementary FLR strategies should promote the regeneration of secondary forests dominated by indigenous tree taxa and the expansion of biodiverse agroforestry systems, such as home gardens.

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**Keywords** Biodiversity · Forest landscape restoration · Home gardens · Landscape connectivity · Stepping stones

## Introduction

The growing human population and its demand for agricultural land, mineral resources, and spaces to live have dramatically transformed landscapes (Ellis et al. 2021) and disrupted the ecological networks that support the Earth's life-sustaining ecosystems (Hagen et al. 2012; Rudnick et al. 2012; Haddad et al. 2015; Lewis et al. 2015). Landscape fragmentation, degradation, and unsustainable land use have triggered a range of negative ecological consequences, including declines in habitat connectivity and quality (Noss 1991; Perino et al. 2019), detrimental effects on biodiversity (Sala et al. 2000; Fahrig 2003; Fischer and Lindenmayer 2007; Haddad et al. 2015), and disruptions to both ecosystem functioning (Gonzalez et al. 2009; Peh et al. 2014; Hatfield et al. 2018) and the provision of ecosystem services (Tscharntke et al. 2005; Dobrovolski et al. 2011; Mitchell et al. 2015). These negative impacts are particularly apparent in tropical forest landscapes, which are home to more than half of the Earth's terrestrial biodiversity (Jenkins et al. 2013; Lewis et al. 2015; Gibson et al. 2021). Today, less than half of the native tropical forests remain (Lewis et al. 2015), and once continuous ecosystems have been fragmented into more than 50 million forest patches, producing nearly 50 million kilometers of additional forest edges (Brinck et al. 2017). Most tropical forest fragments are embedded in a complex and dynamic matrix of land uses (hereafter referred to as the 'landscape matrix';Gascon et al. 1999; Jules and Shahani 2003; Chazdon et al. 2009), where fragments of natural forest are juxtaposed with croplands, pastures, tree plantations, home gardens, and other land uses. Depending on the type of land use, and associated land cover, the landscape matrix can either enhance landscape connectivity and increase biodiversity or, conversely hinder species' movement and lower biodiversity (Ricketts 2001; Kupfer et al. 2006; Ruffell et al. 2017; Boesing et al. 2018; de Souza Leite et al. 2022). Importantly, a 'soft matrix'—with similar vegetation structure to native areas—typically supports ecological processes such as movement and thus increases overall biodiversity (Anderson et al. 2007; Fischer and Lindenmayer 2007; Chazdon et al. 2009), whereas a 'hard matrix'—with vegetation that greatly differs from native areas—can hinder the movement of many species and causes negative edge effects (Lindenmayer and Fischer 2006).

In recent decades, forest landscape restoration (FLR) has gained traction (Clewell et al. 2004; Maginnis et al. 2012; Chazdon and Guariguata 2018) with the overall aim to foster multifunctional landscapes, balancing ecological integrity and human needs (Lamb 2014; Suding et al. 2015; Reed et al. 2016; Mansourian et al. 2017; Chazdon et al. 2020). In practice, FLR is a broader concept than the traditional notion of 'ecological restoration' (Nyiramvuyekure et al. in review), and it can include many types of ecological interventions, including tree plantations, agroforestry sites, and restoration with native species. Through a combination of interventions, FLR aims to increase tree cover, improve habitat connectivity and biodiversity conservation, enhance landscape resilience to climate change, and improve the well-being of local communities (Brancalion and Chazdon 2017; FAO 2017; Chazdon and Guariguata 2018). Its effectiveness depends on the local context of each landscape (Chazdon et al. 2017; Stanturf et al. 2019), with the spatial configuration of forest fragments and the specific interventions within the landscape matrix being critical parameters for defining and achieving FLR objectives. In the past, FLR interventions in tropical forest landscapes have often involved tree plantations predominantly consisting of non-indigenous tree species. Although tree plantations can support the restoration of basic ecosystem functions (e.g., erosion control, biomass production), they may fall short of effectively protecting biodiversity (Bullock et al. 2011). This is especially the case for commercial tree plantations dominated by monocultures, which are typically established for economic reasons, rather than providing ecological functions and value for biodiversity, especially if they consist of non-native trees (Sayer et al. 2004; Brancalion and Chazdon 2017; Mansourian and Berrahmouni 2021).

In contrast to exotic monoculture plantations, home gardens that incorporate native tree species and culturally important crops can serve as multifunctional landscapes known to increase biodiversity (Sunwar et al. 2006; Engelen et al. 2017; Gbedomon et al. 2017; Panyadee et al. 2018; Rooduijn et al.

2018; Yinebeb et al. 2022), to support local livelihoods (Maroyi 2009; Galhena et al. 2013; Gifawesen et al. 2020; Hansen et al. 2022), and to contribute to both ecological and social resilience (Kumar and Nair 2006). Known as 'tree home gardens', traditional home gardens are among the oldest agroforestry systems in tropical and sub-tropical regions (Soemarwoto 1987; Kumar and Nair 2006; Nair et al. 2021). These small but highly diversified micro-ecosystems (Galluzzi et al. 2010) are typically managed by local communities across generations, can harbour rich genetic resources, including some indigenous species that may have gone extinct in degraded natural forests (Montagnini 2020). Under some circumstances, home gardens can also provide foraging habitat for forest specialists (Anderson et al. 2007), contribute to biodiversity conservation (Abebe et al. 2013; Engelen et al. 2017; Rooduijn et al. 2018; Vargas-Cárdenas et al. 2024) and function as ecological corridors or stepping stones (Bhagwat et al. 2008; Campera et al. 2021). How home gardens can contribute to overall landscape connectivity, however, remains unclear.

The Afromontane rainforest landscape of western Rwanda is a tropical biodiversity hotspot with exceptionally high endemism (Plumptre et al. 2007; Mittermeier et al. 2011; Kindt 2014). The region also has the highest human population density in mainland Africa (693 inhabitants per square kilometre; National Institute of Statistics of Rwanda 2023), posing massive pressure on the natural landscape. Historically, the landscape experienced severe deforestation and forest fragmentation, but has also seen extensive restoration efforts over the past decade (World Bank 2014). Rwanda's FLR initiative aims to protect and restore natural forests, improve access to clean water, enhance woodlot management, and promote agroforestry to realize a multifunctional landscape (Ministry of Natural Resources 2014). According to the national Restoration Opportunities Assessment Methodology (Ministry of Natural Resources 2014), approximately 2.25 million hectares (Mha) of land are suitable for FLR interventions, including 1.5 Mha prioritized for agroforestry, improved silviculture and the establishment of protective forests on steep slopes (erosion-control plantations). To date, large-scale restoration efforts have primarily focused on increasing tree cover, primarily through the establishment of tree plantations in the matrix adjacent to protected areas (Republic of Rwanda 2012). Almost 90 per cent of restored tree plantations consist of exotic species, and the number of newly planted exotics exceeds the number of native trees manifold (Mugabowindekwe et al. 2023). Moreover, tree plantations are often fragmented, poorly managed and mostly disconnected from natural forests (Nduwamungu 2011). Tree plantations may support some natural biodiversity, however, their role in maintaining biodiversity at the landscape level remains little understood and abides a critical question for restoration and conservation efforts in the region. Conversely, little attention has been allocated to home gardens, despite their potentially high benefits to improve habitat condition, connectivity and ecosystem services provisioning.

Against this background, our study sought to compare two main forms of landscape matrix in western Rwanda: (1) tree plantations largely established through the recent FLR initiative, and (2) home gardens managed by local communities through longstanding traditional practices. We assessed how each type of landscape matrix influences landscape connectivity, and how these, in return, affect biodiversity. We chose woody plants and birds as biodiversity indicators, since they are among the most-studied and data-rich taxa (Stevenson and Fanshawe 2002; Fischer and Killmann 2008; Vande weghe and Vande weghe 2010; Fischer et al. 2024). Specifically, we (i) examined the spatial patterns of tree-cover connectivity versus home-garden connectivity, and (ii) we explored the relationships between connectivity and species richness (and diversity) of woody plants and birds.

## Methods

### Study area

Our study was carried out in the Western Province of Rwanda (hereafter referred to as western Rwanda), encompassing seven administrative districts, namely Karongi, Rutsiro, Rubavu, Nyabihu, Ngororero, Rusizi, Nyamasheke (Fig. 1). Western Rwanda covers an area of 5,877 km$^2$ on both sides of the Congo-Nile Crest (approx. 3,700 km$^2$; Clay and Dejaegher 1987; Ndayambaje et al. 2014; Mukuralinda et al. 2016). The area is part of the Albertine Rift Ecoregion. Once characterized by a continuous forest belt, it has shrunk

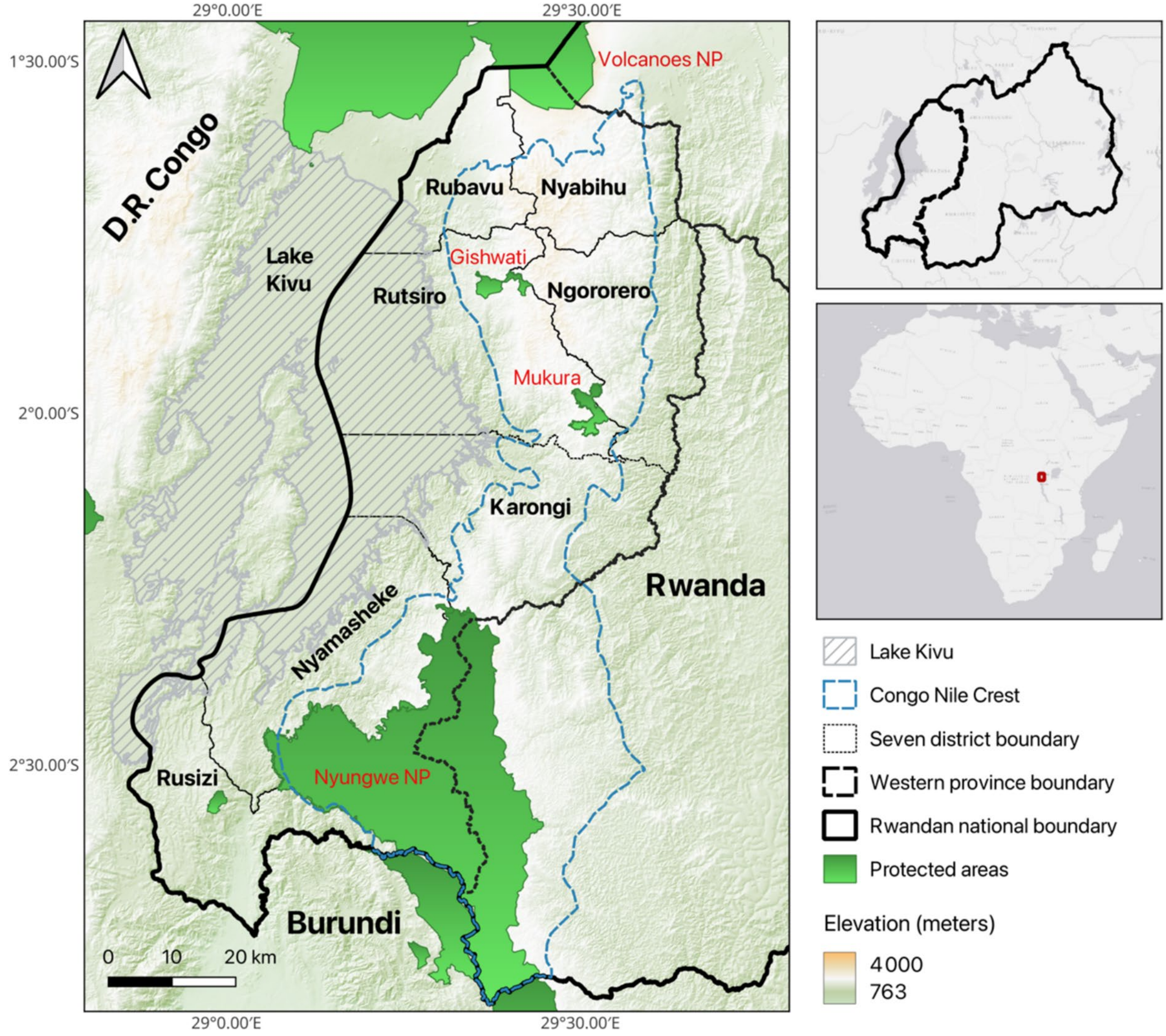

**Fig. 1** Study area in the Western Province of Rwanda, covering seven administrative districts from north to south: Rubavu, Nyabihu, Rutsiro, Ngororero, Karongi, Nyamasheke and Rusizi. The blue dotted line marks the Congo-Nile watershed divide (Congo-Nile Crest), while protected national park areas are highlighted in green color

to a few protected areas, namely Volcanoes National Park (NP), Nyungwe NP, and Gishwati-Mukura NP (UNESCO biosphere reserve since 2020; comprising Gishwati Forest and Mukura Forest; Republic of Rwanda 2020). Despite large parts of previously forested land being cleared, this montane forest ecoregion still provides vital habitat for a diverse biota with a high degree of endemism (Plumptre et al. 2007; Kindt 2014). Elevation in the study area ranges from 2,000 to 4,500 m a.s.l. (Mukashema et al. 2014), with a mean annual precipitation of about 2,000 mm (Vande weghe and Vande weghe 2010), and an average annual mean temperature of 19 °C (World bank 2021).

The land-use history in western Rwanda was largely shaped by political events and socio-economic pressures (Akinyemi 2017), with an estimated 50 to 74% of natural Afromontane forest cleared for subsistence agriculture, livestock grazing, fuelwood, and construction materials (Kanyamibwa 1998; Akinyemi 2017). Today, the landscape matrix in western Rwanda comprises different forms of land use, namely tree plantations (e.g., *Eucalyptus*, *Grevillea, Pinus*, and *Alnus* species), subsistence farming (including small fields and home gardens), cash crop plantations (mainly tea), and pastures (Mukuralinda et al. 2016; Arakwiye et al. 2021). This complex mosaic reflects not only the historical land use patterns but also recent restoration interventions. For instance, in 2014, the government of Rwanda launched the Landscape Approach to Forest Restoration and Conservation (LAFREC) project, as part of the broader FLR initiative, and focused on restoring the Gishwati-Mukura landscape, a critical biodiversity hotspot within Rutsiro District (Republic of Rwanda 2025). To date, Rutsiro District comprises the largest area of tree plantations in Western Province, with FLR efforts adding about 818 hectares of new tree cover each year (Ministry of Environment 2019).

### Assessing landscape connectivity across tree cover and home gardens

Landscape connectivity is defined as the degree to which a landscape facilitates or impedes movement among resource patches (Taylor et al. 1993), and is critical for supporting species movement, gene flow, and long-term biodiversity persistence at the landscape scale (Noss 1991; Rudnick et al. 2012). Connectivity can be conceptualized from multiple perspectives, including structural connectivity (the physical arrangement of vegetation/land-cover elements), functional or habitat connectivity (species-specific responses to landscape structure), and broader ecological connectivity (Lindenmayer and Fischer 2006). For this study, landscape connectivity was defined as the structural connectivity of vegetation/land cover, in our case, with a focus on trees and home gardens. We applied the circuit theory approach (McRae et al. 2016) to assess landscape connectivity across tree cover (here intentionally used as a highly simplified proxy that combines natural forests and tree plantations; Ministry of Environment 2019), and across home gardens. We used a set of openly available satellite-based datasets (see below) on tree cover and building structures. To implement the approach, we used the tool Omniscape which simulates electric current flow across the landscape (McRae et al. 2008, 2016; Dickson et al. 2019). The process starts by identifying the landscape type to be connected and assigning resistance values to landscape features. A moving window procedure then connects all pixels within a given search radius, and the results from different window sizes are aggregated to generate a cumulative current map representing connectivity (McRae et al. 2016).

To map connectivity with a focus on tree cover, we used the ESA World Cover dataset 2021, which provides land-cover classes at a high pixel resolution of 10 m (Zanaga et al. 2022). In a first step, we masked out all classes other than trees. Second, we aggregated the remaining tree cover to a 100-m grid by counting the number of pixels containing trees in each grid cell. This yielded a fractional tree-cover map of trees at a 100-m spatial resolution. Third, we inverted this fractional cover dataset to assign lower resistance values (i.e., 0) to areas of relatively high tree cover, and high resistance values (i.e., 3; Phillips et al. 2021) to areas of low tree cover (e.g., Lake Kivu). We then set moving window radius of 1 km as the cutoff to assess tree-cover connectivity. This buffer was chosen because most birds have an activity radius exceeding 1 km, and they act as seed dispersers for indigenous trees—potentially disseminating seeds over even greater distances (Pejchar et al. 2008; Mueller et al. 2014).

To map connectivity across home gardens, we first identified home gardens in our study area based on Google Open Building polygon datasets collected in May 2023 (Sirko et al. 2021). This dataset contains different types of buildings, which are almost exclusively related to housing structures. Home gardens were operationally defined as the areas within a 15 m radius of each building. This buffer distance was chosen based on field knowledge of the study system, where most households practice subsistence agriculture and typically maintain small plots with woody vegetation—particularly fruit trees—immediately surrounding their homes. Similarly to the tree-cover mapping, we then calculated for each 100-m grid cell the fractional area covered with home gardens and inverted the resulting layer to generate a resistance layer, such that areas with many home gardens show lower resistance values, whereas areas with few home gardens show higher resistance values. Again, a radius of 1 km was assigned to assess the home-garden connectivity. To facilitate interpretation, both connectivity outputs (current flow) were transformed to a scale from 1 to 100, where higher current flow values indicate stronger connectivity, and lower values represent weak or no connectivity. Prior to the modelling process, we applied a 30 km buffer around the study area—equivalent to 50% of the study area's width—to minimize edge effects and reduce bias (Koen et al. 2014; Pelletier et al. 2014). Omniscape modelling was conducted using the 'Omniscape.jl' software package within the 'Julia' programming environment version 0.6.2 (Landau et al. 2021).

### Relating biodiversity metrics to landscape connectivity

Once connectivity landscapes were established, we assessed how tree-cover and home-garden connectivity related to woody plant and bird richness and diversity, respectively. We established woody plant and bird richness and diversity at 91 sampling sites, including 47 tree plantations and 44 home gardens. Tree plantations were only sampled if the area exceeded one hectare and if they were not logged for more than one year. We focused on large plantation patches because they contribute more to landscape tree-cover connectivity and are expected to have stronger effects on biodiversity. Smaller patches vary widely in size and are more influenced by edge effects and disturbance, making consistent landscape-level comparisons difficult. We randomly chose home garden sites across the landscape to minimize spatial autocorrelation but accounted for road accessibility. Each site was sampled twice, once during the long dry season (20 June to 31 July 2024) and once during the short dry season (12 February to 5 March 2025). Woody plant richness was sampled by recording the presence and abundance of all woody plant species within a 20 × 20 m sampling plot at each site. Woody plants were defined as trees and shrubs growing taller than 1.3 m, identified using Fischer and Killmann (2008) and Fischer et al. (2024). For bird surveys, we applied the point count method (Ralph et al. 1995), i.e., standing for 15 min at the centre of each sampling plot to record and identify all birds seen or heard from any direction. Bird species were identified using Stevenson and Fanshawe (2002), Vande weghe and Vande weghe (2010) and Billerman et al. (2025). We conducted bird surveys only during days without rain or strong wind from 5:30 to 10:00 am. Based on habitat use and their functional role in the ecosystem, birds were classified into four categories of forest dependence, namely, forest specialists, forest generalists, forest visitors, and non-forest species following Bennun et al. (1996; Supplementary Material Table 2). Based on the richness and abundance data of woody plants and birds, we calculated the respective Shannon diversity index using the 'vegan' package in R (Oksanen et al. 2001), before applying Mann–Whitney U tests to assess pairwise differences in observed species richness and diversity (for woody plants and birds separately) between tree plantations and home gardens. Finally, we assessed the relationship between both richness and diversity with our connectivity indices using Spearman's rank correlations.

## Results

### Tree-cover and home-garden connectivity

We obtained maps of tree-cover and home-garden connectivity at 100-m pixel resolution (Figs. 2, 3). Across the tree-cover connectivity map, the highest current flow values, indicating areas of strongest connectivity, were concentrated within the protected areas of Nyungwe NP, Gishwati-Mukura NP, and the Volcanoes NP (Fig. 2a, c-e). Outside these protected areas, strong tree-cover connectivity was observed in the northern part of Gishwati Forest (Fig. 2a, b), an area that received extensive FLR efforts in the past decade. Moderately high connectivity was observed in many parts of the landscape matrix adjacent to protected areas, including the western regions of Gishwati Forest (Fig. 2c), Mukura Forest (Fig. 2d) and Nyungwe NP (Fig. 2e), and some areas southeast of Volcanoes NP (Fig. 2a).

In contrast, home-garden connectivity map exhibited a distinct structural pattern. Strong connectivity was observed in the northern part of Gishwati Forest, along the main road connecting Rubavu in the West and Musanze City in the East (Fig. 3b). Another corridor is apparent along the Lake Kivu shoreline stretching from Rubavu southward to Cyangugu, i.e., an area located west of Gishwati-Mukura and Nyungwe NP (Fig. 3c, e). Moreover, south-eastern part of Volcanoes NP had a moderately high home-garden connectivity (Fig. 3d).

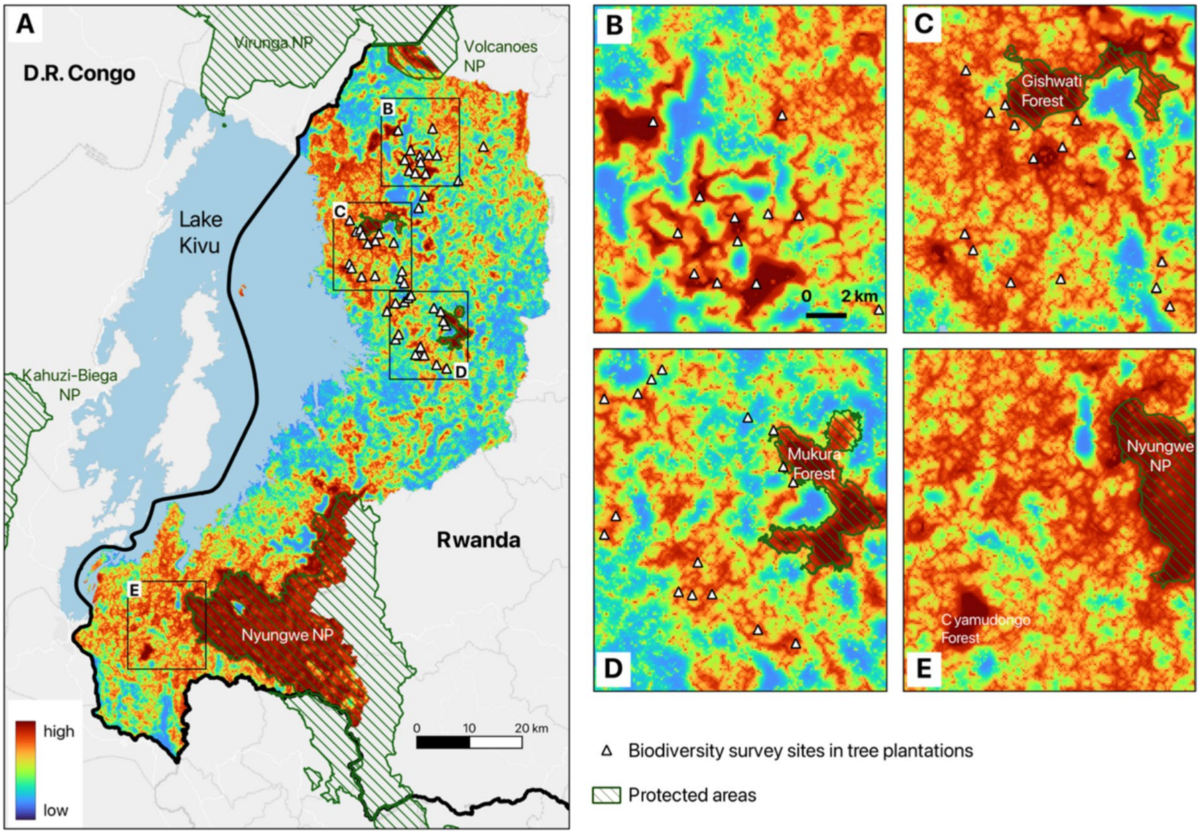

**Fig. 2** Tree-cover connectivity across western Rwanda.Panel **A** was modelled using a 100-m resolution resistance layer, with the moving window radius parameter set to 1 km in Omniscape. Panels **B**–**E** provide zoomed-in views of selected areas, with panels **B**–**D** also showing biodiversity survey sites located within tree plantations. The color gradient shows tree-cover connectivity percentiles for the landscape: red areas indicate high tree-cover connectivity, while blue areas highlight barriers with low or zero connectivity

A moderately high home-garden connectivity was observed across most parts of the landscape matrix.

## Correlation between biodiversity metrics and landscape connectivity

Across the 47 tree plantation sites, we recorded eight woody plant species (7 exotic and 1 native species), with each site containing one to three species (Supplementary Table 1). In contrast, the 44 home garden sites supported a higher diversity of 24 woody plant species (18 exotic and 6 native species), with one to ten species per site (Supplementary Table 1). Furthermore, we recorded 32 bird species at tree plantations and 64 species in the home gardens (Supplementary Table 2). Most bird species observed were small-bodied forest visitors or non-forest species. All species had a conservation status of 'Least Concern' (Billerman et al. 2025).

Mann-Whiteny U test showed that both species richness and diversity of woody plants and birds differed highly significant between tree plantations and home gardens (woody plant richness: W = 1997, $p<0.001$; woody plant diversity: W = 2068, $p<0.001$; bird richness: W = 1606, $p<0.001$; bird diversity: W = 1576, $p<0.001$). Species richness (mean ± SD) was significantly higher in home gardens (woody plants: 4.16 ± 1.95; birds: 4.84 ± 4.00) than at tree plantations (woody plants: 1.34 ± 0.52; birds: 1.81 ± 1.75; Fig. 4a, c). The Shannon diversity index (mean ± SD) was also significantly higher in home gardens (woody plants: 1.27 ± 0.41; birds: 1.20 ± 0.75) than in tree plantations (woody plants: 0.15 ± 0.25; birds: 0.47 ± 0.62; Fig. 4b, d).

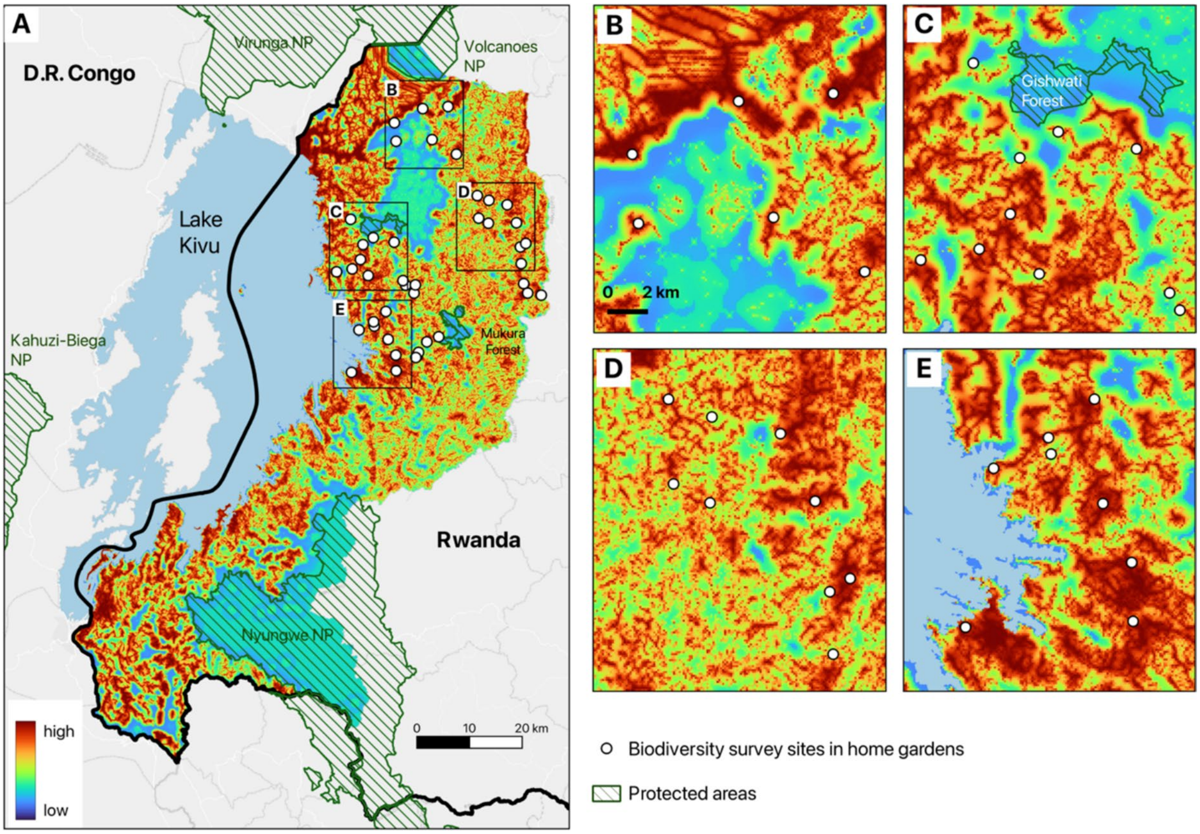

**Fig. 3** Panel **A**. Home-garden connectivity was modelled using a 100-m resolution resistance layer, with the moving window radius parameter set to 1 km in Omniscape. Panels **B**–**E** provide zoomed-in views of areas with relatively high home-garden connectivity. The color gradient represents home-garden connectivity percentiles across the landscape: red areas indicate high home-garden connectivity, while blue areas highlight barriers with low or zero connectivity. White circles show biodiversity survey sites in home gardens

Spearman's rank correlations revealed a significant negative correlation between tree-cover connectivity and home-garden connectivity ($r$ = -0.71, $p < 0.001$, Fig. 5). In general, we observed a higher richness and diversity of woody plants (Fig. 5a, b) and birds (Fig. 5c, d) in home gardens than in tree plantations. Highest bird richness and diversity (Fig. 5c, d) clustered in areas of medium to high home-garden connectivity, associated with low to medium tree-cover connectivity. Conversely, areas with the highest tree-cover connectivity exhibited very low woody plant and bird richness and diversity.

Moreover, Spearman's rank correlations revealed a significant negative relationship between tree-cover connectivity and woody plant richness ($r$ = -0.63, $p < 0.001$), as well as between tree-cover connectivity and bird richness ($r$ = -0.46, $p < 0.001$). We also found a significant negative correlation between tree-cover connectivity and woody plant diversity ($r$ = -0.67, $p < 0.001$) and between tree-cover connectivity and bird diversity ($r$ = -0.45, $p < 0.001$). In contrast, we found a significant positive relationship between home-garden connectivity and woody plant richness ($r = 0.64$, $p < 0.001$), as well as between home-garden connectivity and bird richness ($r = 0.44$, $p < 0.001$). Our analysis further revealed a significant positive correlation between home-garden connectivity and woody plant diversity ($r = 0.68$, $p < 0.001$), and between home-garden connectivity and bird diversity ($r = 0.41$, $p < 0.001$).

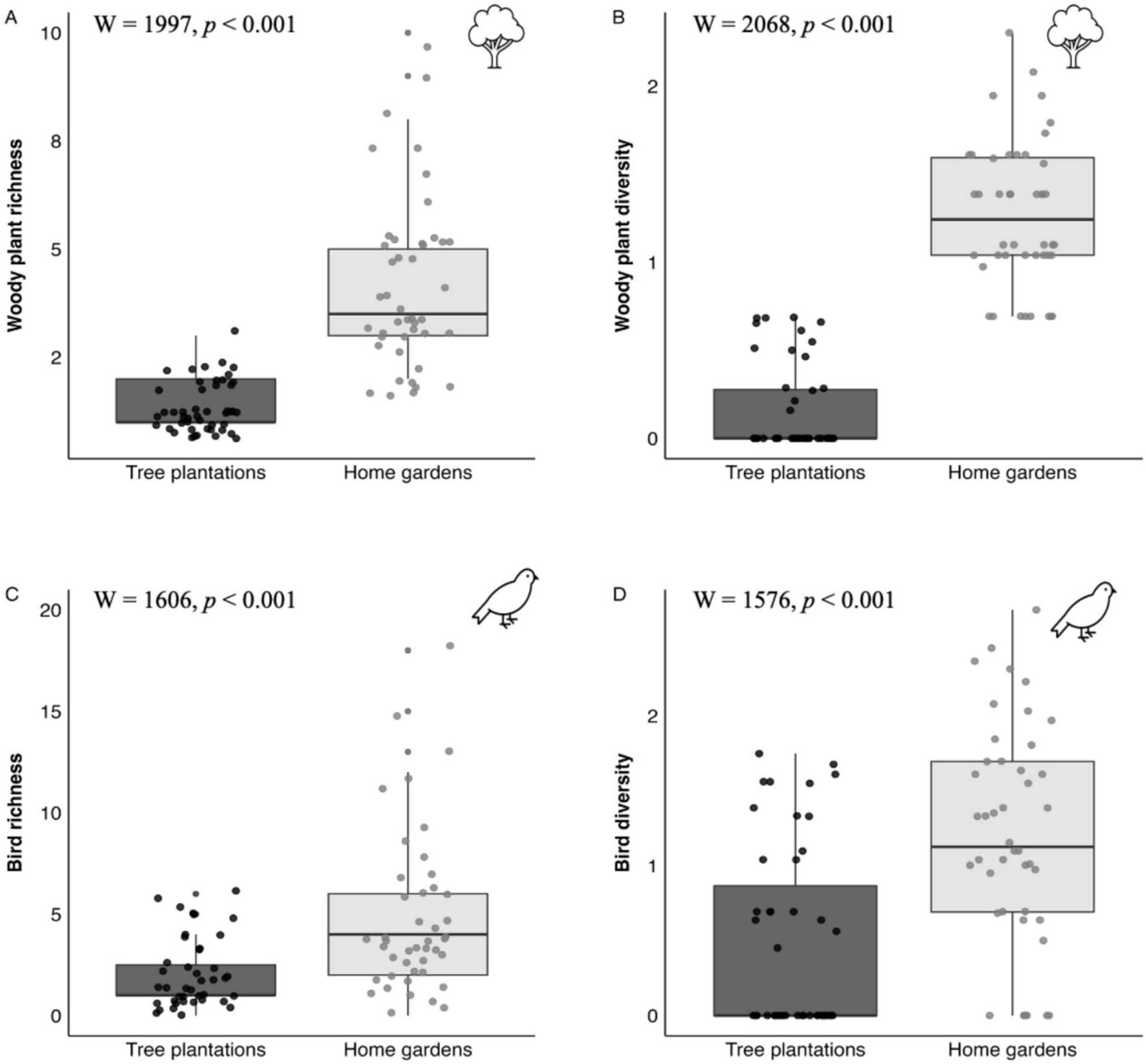

**Fig. 4** Boxplots showing the species richness and diversity of woody plants and birds recorded in tree plantations (black color) and home gardens (grey color): **A** woody plant richness; **B** Shannon index of woody plant diversity; **C** bird species richness; **D** Shannon index of bird diversity. Results of pairwise comparisons using Mann–Whitney U tests are indicated within each plot

## Discussion

Many regions in the tropics have suffered from considerable forest loss, fragmentation, and degradation in the past, and tree planting efforts seek to reverse this. How such tree plantations contribute to this goal, and what their value is relative to other land uses that contain tree cover, such as home gardens, remains poorly understood. Here, in a global hotspot of tropical forest restoration, we assessed connectivity of two different forms of land use (i.e., recently established tree plantations and traditional home gardens) in relation to two biodiversity metrics (i.e., woody plant and bird richness and diversity). By comparing connectivity maps for both forms of land use, and by relating connectivity to diversity metrics, we found tree plantations to function like a ‘hard matrix’, offering only limited habitat value and

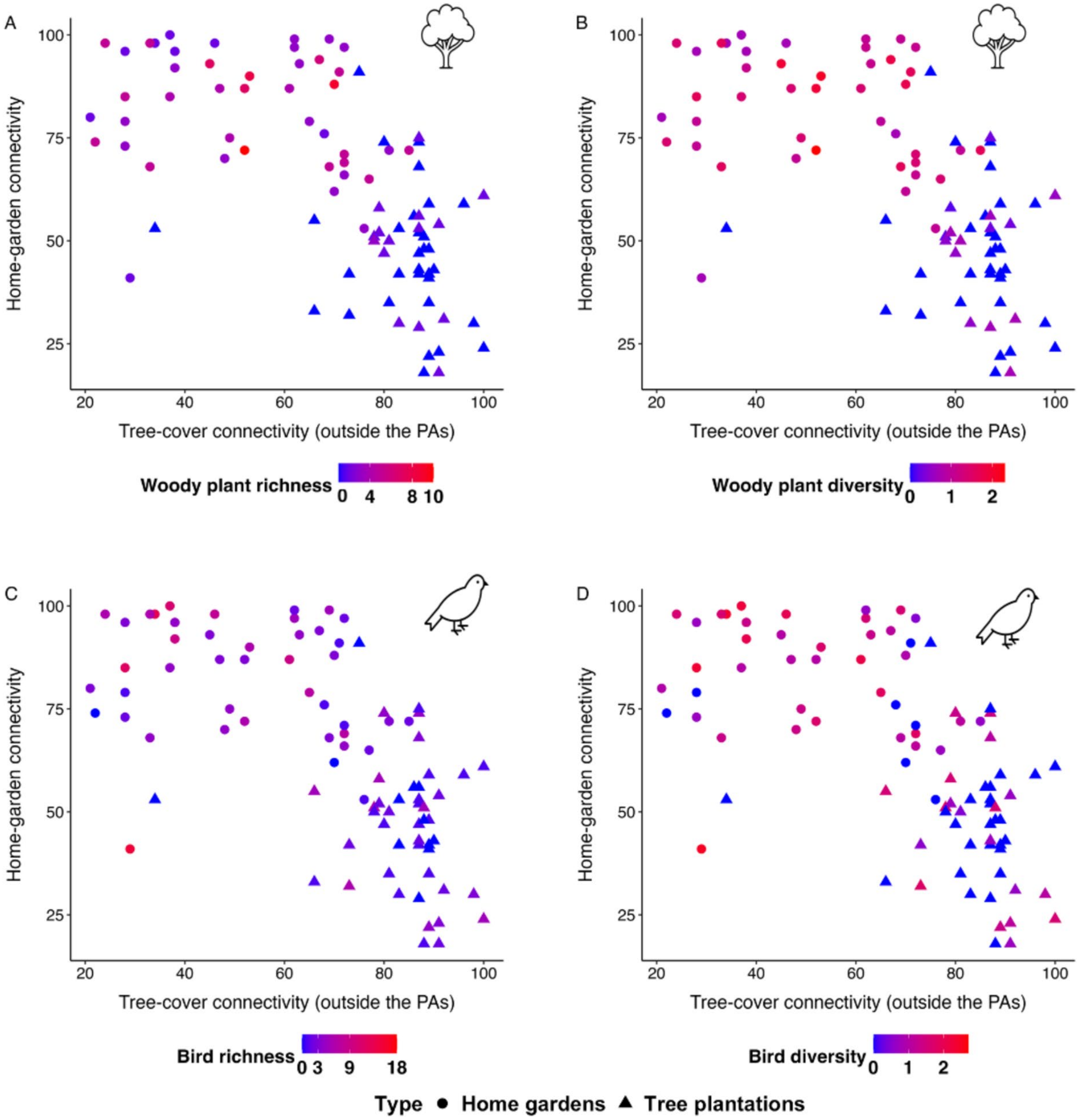

**Fig. 5** Scatterplots showing the relationships between tree-cover connectivity and home-garden connectivity, with **A** woody plant richness; **B** Shannon diversity index of woody plants; **C** bird richness; **D** Shannon diversity index of birds represented by a color gradient ranging from blue (low richness) to red (high richness). Points represent different land matrix types: circles for home gardens and triangles for tree plantations

restricted permeability, while home gardens serve as a 'soft matrix' allowing organisms to disperse (sensu Franklin 1993; Lindenmayer and Fischer 2006). Our findings challenge conventional tree plantations in FLR practice and underscore the need to actively incorporate home gardens in restoration strategies. We discuss our findings in the context of two implications for FLR policy and practice: (i) tree plantations increase tree-cover connectivity but not biodiversity, and (ii) home gardens may serve as stepping stones for species dispersal and thus benefit biodiversity conservation.

## Tree plantations increase tree-cover connectivity but not biodiversity

FLR practice has contributed to achieving Rwanda's national target of 30% forest cover, as outlined in the Vision 2020 (Republic of Rwanda 2012). Our analyses indicate that FLR-led restoration efforts have successfully increased tree cover in the landscape, leading to high tree-cover connectivity around protected areas (Fig. 2a-e). However, well-connected areas of trees supported significantly lower richness and diversity of woody plants and birds than less well-connected areas (Fig. 5a-d). As such, it appears that tree planting efforts to date have increased connectivity but failed to enhance habitat quality and thus biodiversity. Compared to previous studies (e.g., Crouzeilles et al. 2019) that identified tree-cover and tree-cover connectivity as key indicators for the recovery of tropical biodiversity (and as indicators of restoration success), our findings offer a contrasting view.

Sustainably managed tree plantations that do not replace natural or semi-natural ecosystems could contribute to the conservation of native biodiversity, generally hosting fewer species than natural forests (Hua et al. 2022; Wang et al. 2022), but more than other human-modified land use types (Brockerhoff et al. 2008). For example, a study in Uganda's Kibale NP, showed that planting native tree species can accelerate biodiversity recovery within a relatively short period (Omeja et al. 2011). In a densely populated landscape like western Rwanda, tree plantations can play an indirect, socially important buffering role by supplying wood and reducing pressure on natural forests. Restoring landscapes with indigenous species instead of exotic plantations could help mitigate anthropogenic pressures on natural forests through community-based forest management, sustainable use zones that allow regulated harvesting, and alternative energy and livelihood options to reduce fuelwood dependence.

FLR-lead restoration efforts have primarily been achieved by the widespread establishment of exotic tree plantations, now comprising more than half of the country's forested area (Ministry of Environment 2019). Our findings suggest that, at least for woody plants and birds, these plantations—especially when disconnected from natural forest patches—function as a 'hard matrix' with limited habitat value and low attractiveness to biodiversity. From the landscape perspective, if this type of restoration practice continues, the landscape matrix may facilitate species invasiveness, eventually leading to biotic homogenization, where diverse native species are replaced by a few widespread, fast-growing exotics, consequently increasing the extinction risk for native species (Crosby 2004; Holl et al. 2022). Such homogenization is already evident in our data, as bird communities in home gardens and forest plantations showed substantial overlap. We thus recommend FLR practice in western Rwanda and other regions of the Albertine Rift to shift from overly simple, short-term, target-based indicators such as tree cover towards strategies that reflect long-term restoration success and ecological functionality, such as the promotion of native vegetation (Raj et al. 2023) and the creation of a mosaic of resources and habitat features that facilitate animal dispersal, foraging, and reproduction (Holl et al. 2022).

## Home gardens could serve as stepping stones for biodiversity

Recent studies showed home gardens in Rwanda are linked to improved conservation of wild plants (Nsengimana et al. 2020), to increased medicinal plant diversity (Rizinjirabake et al. 2024), and to improvements in dietary diversity and thus higher nutritional value of local communities (Issahaku et al. 2023; Dusingizimana et al. 2025). Until to date, little is known about the role of home gardens in supporting connectivity and biodiversity within the landscape matrix. Our study addressed this knowledge gap and showed that home gardens maintain intermediary habitats, following natural forests, in supporting relatively high richness and diversity of woody plants and birds. This is particularly valuable for connectivity since home gardens follow linear features in the landscape, such as along tracks and roads. Thus, our findings suggest that spatially interconnected home gardens may function as a 'soft matrix', positively contributing to biodiversity, even at locations where tree-cover connectivity is low. Unlike tree plantations, home gardens are more heterogenous and offer ecologically valuable habitats, including indigenous trees, shrubs and herbaceous plants arranged in a multistorey system (Hylander and Nemomissa 2009; Galluzzi et al. 2010), thereby attracting a variety of bird species (Engelen et al. 2017; Vargas-Cárdenas et al. 2024). While home gardens offer important benefits, they cannot substitute for natural forests. Our findings indicate that bird communities in home gardens are largely composed of forest visitors and non-forest species predominantly classified as 'Least Concern', suggesting that home gardens cannot replace natural forests in providing essential habitat for forest-dependent specialists. Similar patterns have been reported in the fragmented landscapes of Bangladesh (Bardhan et al. 2012), Guatemala (Haggar et al. 2019), and Ethiopia (Tesfay et al. 2025), where home-garden agroforestry systems function as stepping stones that enhance biodiversity conservation, acting as vital intermediary habitats that bridge and buffer natural forests within the broader landscape.

Agroforestry, including multi-layered home gardens, has been widely recognized as a key restoration element in Rwanda (Ministry of Natural Resources 2014). However, past restoration practices have primarily been based on the 'tree-based approach', which integrates trees with crops to improve soil fertility and water quality (Ministry of Natural Resources 2014; Iiyama et al. 2018). This practice has led to the widespread use of exotic *Grevillea robusta*, which provides little value for native biodiversity (Ruticumugambi et al. 2024). Traditional home gardens have received relatively little attention in conservation and restoration efforts to date. This is due to an ever-increasing mechanisation in agriculture, the use of pesticides, and an increasing number of exotic plants. Such modernization processes make traditional home gardens face great challenges, eventually resulting in a sharp decline in species richness of indigenous plants, insects and birds (Seburanga 2013). Strengthening the conservation of traditional home gardens is therefore critical to sustaining their biodiversity value and ensuring they remain vital components of future restoration landscapes.

## Conclusion

Forest loss, fragmentation, and degradation are major drivers of biodiversity loss in tropical landscapes. While conserving natural forests is paramount, scaling up forest restoration to improve degraded forests and connectivity among remaining patches through raising matrix quality is also vital for biodiversity conservation. Based on our findings, we recommend that restoration efforts prioritize the protection of remaining natural forests, which are irreplaceable for sustaining native biodiversity. Complementary strategies should promote the regeneration of secondary forests dominated by native tree taxa and the expansion of biodiverse agroforestry systems. Traditional home gardens, integrating native plant species and traditional crops, offer a promising social–ecological restoration approach. In western Rwanda, the comparison of two tree-rich land-use systems showed that exotic tree plantations, despite enhancing tree-cover connectivity, provide limited biodiversity benefits, whereas traditional home gardens function as valuable ecological stepping stones. In conclusion, to maximize forest landscape restoration effectiveness in biodiversity-rich regions, we recommend promoting native tree plantations alongside biodiversity-friendly, tree-rich systems such as home gardens.

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**Data availability** All data supporting the findings of this study are provided within the paper and its Supplementary Material and Supplementary Data.

### Declarations

Competing interest The authors have no relevant financial or non-financial interests to disclose.The authors declare no competing interests.

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