Regional range restriction, not national endemism, predicts plant extinction risk: operationalising Conservation Imperatives for under-assessed tropical floras

Running title: Rwanda plant conservation biogeography

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Abstract

Aim: Tropical African flora is potentially threatened, yet species-level conservation priority-setting is rare in under-assessed floras. We tested whether range restriction drives extinction risk and operationalised the Conservation Imperatives at species level.

Location: Rwanda, Albertine Rift biodiversity hotspot, eastern Africa.

Methods: We applied this workflow to 367 IUCN-assessed vascular plant species. The approach combined: (i) Random Forest, partial proportional-odds models, propensity-score matching with Rosenbaum-bounds sensitivity; (ii) a three-tier classification linking formal Protected Area (PA), remnant forest patch and exposed

habitat to distinct actions; (iii) species distribution modelling across three Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5, SSP5-8.5) × two horizons (2041–2060, 2061–2080) with EDGE2 phylogenetic-priority scoring; and (iv) cross-validation against an independent field inventory.

Results: Regional range restriction dominated risk: 68% of 86 Albertine Rift near-endemic species were threatened, against 16% of 266 wider-ranging and 14% of 15 strict Rwandan endemics. The matched effect was robust but modest (OR = 2.74, 95% CI 1.46–5.14; Rosenbaum-bounds Γ ≈ 1.5). Twenty-five of 105 threatened species occupied exposed-habitat tier; only six gained protections from a feasible 2.5 km expansion occurred in the exposed-habitat tier; only six gained protections from a feasible 2.5 km boundary expansion. EDGE2 and threat-based priority were weakly correlated (ρ = 0.162, p = 0.098), indicating partly independent priorities. Projected habitat loss increased monotonically with emissions and time; 41 species (22%) exceeded the IUCN Criterion A2 threshold (≥ 80% loss) under SSP5-8.5 by 2061–2080, and threatened-lineage phylogenetic diversity declined nationally by 22.5%, concentrated in Nyungwe National Park. Cross-validation recovered *Capparis lucens* from a harmonisation artefact and identified further threatened species absent from global datasets, including *Pterygota mildbraedii*.

Main conclusions: Within Rwanda's vascular flora, regional range restriction is the dominant driver of extinction risk and is independent of, and compounded by, projected climate loss. The Conservation Imperatives workflow supports Kunming-Montreal Global Biodiversity Framework (KMGBF) Target 3 reporting in under-assessed floras.

Keywords: Albertine Rift, biogeography, Conservation Imperatives, EDGE2, ensemble species distribution model, KMGBF Target 3, Possibly Extinct, propensity score matching, range restriction, Rwanda

1 Introduction

Tropical African floras carry one of the highest extinction-risk burdens among the world's plants, with about one-third of the tropical African flora now potentially threatened (Stévart et al., 2019). For small, high-endemism countries, a single national protected-area (PA) network is often the de facto safeguard against habitat conversion (Plumptre et al., 2021), yet most lack the species-level analyses to guide its design. Rwanda, in the Albertine Rift biodiversity hotspot, exemplifies this gap: a recent checklist of Nyungwe National Park and Cyamudongo forest records 1,456 vascular plant species, of which 17.7% are Albertine Rift endemics or near-endemics (Fischer et al., 2024). This Albertine Rift system is also biogeographically constrained: even at the Last Glacial Maximum, when alpine habitat was about eight times larger than today, these mountains remained isolated for alpine taxa (Chala et al., 2017), leaving present-day populations with limited corridor-based rescue potential (Damschen et al., 2019; Haddad et al., 2015). Against this deep-time isolation, recent forest-cover change across the wider Kivu Rift has further restructured montane forest configuration (Depicker et al., 2021), and Rwanda's montane forests have become progressively insular, with 8% of cover lost within Nyungwe and Kibira National Park (1986–2015) and 22% in the 5-km buffer (Kayiranga et al., 2016).

Range-restricted species face elevated extinction through demographic stochasticity and reduced spatial buffering, making geographic range size one of the most

consistent cross-taxon predictors of extinction risk (Cardillo et al., 2008; Gaston, 2009). Within vascular plants, this pattern is well supported with range-restricted species decline disproportionately even under moderate habitat loss of ≤50% (Staude et al., 2020). Yet range restriction is scale-dependent: whether elevated risk tracks strict national endemism or the broader regional near-endemism typical of biodiversity hotspots is rarely disentangled, despite divergent implications for where conservation effort is directed. In the Eastern Afromontane hotspot, these risks are amplified by the sky-island structure of high plateaus and isolated peaks, whose tropical-alpine flora is young, disturbed and genetically unsaturated, shaped by repeated range fragmentation rather than stable corridors (Kandziora et al., 2022). Isolation and anthropogenic fragmentation confine species to small, increasingly disconnected, high-endemism patches (Plumptre et al., 2021), and climate change is anticipated to further contract the ranges of high-elevation species via upward shifts in thermal niches (Salah et al., 2025; C. D. Thomas, 2010), concomitantly facilitating the expansion of invasive species (Weldemariam & Dejene, 2021). Recent prioritisation frameworks, including the Conservation Imperatives approach (Dinerstein et al., 2024) and its site-level extensions (Gosling et al., 2026), identify unprotected sites capturing irreplaceable biodiversity but rarely integrate fine-scale predictions of species distributions under this ongoing change. We therefore hypothesise that regional (Albertine Rift) range restriction, rather than strict national endemism, elevates extinction risk independently of the habitat species occupy, and that integrating this signal with spatial-prioritisation outputs identifies critical species that neither approach captures alone.

Prior studies in Rwanda and the Albertine Rift have documented threatened-species distributions, protected-area biodiversity hubs and forest fragmentation from remote sensing and field surveys (Bizuru et al., 2015; Fischer et al., 2024; Kayiranga et al., 2016). Field inventories also verify threatened plants in unprotected remnant forests (Bizuru et al., 2015), but none has been integrated into a species-level Conservation Imperatives framework for an African flora (Dinerstein et al., 2024). Three gaps remain. First, binary protection status classification fails to distinguish species occurring in remnant forests from those restricted to transformed landscapes. Second, global occurrence databases inconsistently capture species documented only in field-survey literature; this coverage gap is documented across under-assessed taxa (Hochkirch et al., 2021) and is exacerbated by ongoing taxonomic description, with new Albertine Rift taxa continuing to emerge (Thomas et al., 2026). Third, IUCN "Possibly Extinct" designations are vulnerable to name-harmonisation artefacts arising from outdated taxonomy, biasing extinction assessments (Abeli et al., 2022; Gippoliti et al., 2024).

To address these gaps, we develop a transferable species-level workflow combining IUCN-assessed flora, global occurrence databases and field-survey inventories with ensemble species distribution models under contrasting climate scenarios. We introduce a three-tier habitat classification (within PAs; outside PAs but within remnant forest; or beyond both) to refine conservation priority and vulnerability assessment. The approach unifies causal inference with spatial prioritisation and provides, to our knowledge, the first operationalisation of the Conservation Imperatives concept at species level for an African plant flora. The design supports the Kunming-Montreal Global Biodiversity Framework (KMGBF), particularly Target 3 (CBD, 2022), and is

intended for transfer to other Albertine Rift countries where comparable inventories remain unintegrated.

The study is structured around a central question: does range restriction, more than the habitats that range-restricted species occupy, increase extinction risk in Rwanda's vascular flora? And if so, does that effect reflect regional (Albertine Rift) range restriction rather than strict national endemism? We address it through five research questions (RQ1-RQ5): (i) the ecological and biogeographic predictors of extinction risk; (ii) whether range restriction is independent of habitat-level predictors; (iii) which threatened species lack both protection and remnant forest cover, and how to prioritise them; (iv) how climate change alters habitat suitability under contrasting emissions; and (v) the status of Data Deficient and Possibly Extinct species and what field-survey cross-validation reveals about database gaps.

2 Methods

2.1 Study area

We conducted this study in Rwanda (26,338 km²), situated in the Albertine Rift of eastern Africa and spanning three World Wide Fund (WWF) terrestrial ecoregions (Olson et al., 2001) from submontane to Afroalpine: the Victoria Basin forest–savanna, Albertine Rift montane forests and Rwenzori–Virunga montane moorlands (988–3,594 m). It includes five formally designated PAs (Akagera, Gishwati–Mukura, Nyungwe, Rugezi Wetland Reserve and Volcanoes) totalling ~233,274 ha, plus 13 remnant forest patches outside the PA network (~2,655 ha; Figure 1). Ecoregion boundaries were obtained from the Regional Centre for Mapping of Resources for Development

(RCMRD) Open Data portal (https://opendata.rcmrd.org/datasets/africa-ecoregions; accessed 17 May 2026).

2.2 Occurrence data and spatial processing

We compiled occurrence data for all 367 IUCN-assessed vascular plant species in Rwanda, including Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), and Data Deficient (DD) (Figure 1; Table S14; Figure S2). We obtained 1,834 georeferenced records (https://www.iucnredlist.org/; accessed 11 April 2025), supplemented with 841 records from the Global Biodiversity Information Facility (GBIF) to improve spatial coverage (https://www.gbif.org/; accessed 17 May 2026). We also retained 1,290 GBIF records from a broader Albertine Rift buffer, used only for species distribution model (SDM) training (Section 2.6, Figure S1) and excluded from policy-scale analyses. After harmonisation we removed within-species duplicates, giving 2,441 unique occurrences (from 2,675).

We calculated the species' Extent of Occurrence (EOO) as the geodesic area of the minimum convex polygon using the geosphere R package (Hijmans, 2026). We estimated the Area of Occupancy (AOO) using a 2 × 2 km grid following IUCN Criterion B guidelines (Akçakaya, 2023). Criterion B lists a taxon as threatened on the basis of a restricted geographic range, namely a small EOO or AOO combined with fragmentation, continuing decline or extreme fluctuation. Because AOO increased with survey effort (Figure S4), SDM-derived ranges were used in the policy analyses.

We digitised remnant forest patches in QGIS from high-resolution satellite imagery based on Bizuru et al. (2015). We derived land-cover and land-use change variables from the Global Land Cover and Land Use Change dataset (2000–2020; Potapov et

al., 2022), with selected classes summarised in Figure S3a. Software, coordinate reference systems and projections are detailed in Appendix S1.

2.3 Ecological drivers of extinction risk (RQ1)

We modelled the five-level IUCN ordinal response (5=CR to 1=LC) by combining three complementary models to address RQ1 as simultaneously a prediction question (identifying species at risk and key predictors) and an inference question (quantifying the direction and magnitude of drivers). No single model performs both tasks well on small, imbalanced ordinal data with partial separation; agreement across models with different assumptions therefore indicates that the identified drivers are not model-specific artefacts. (i) Random Forest (RF; ranger; 1,000 trees, permutation importance): trained on 80/20 stratified split (train n = 289, test n = 72); SHapley Additive exPlanations (SHAP) values were computed using *fastshap* (200 Monte Carlo replicates). (ii) Cumulative-link model (CLM; ordinal:clm, probit link): fit on n = 361 species (excluding DD); profile-likelihood 95% CI reported. Logit-link sensitivity model confirmed sign agreement for all predictors except one (near zero). (iii) Proportional-odds ordinal logistic regression (MASS::polr): reference model replicating Singini & Baso (2025); proportional-odds assumption assessed with a per-predictor likelihood-ratio test. Predictors violating this assumption were fitted using partial proportional-odds CLM (Peterson & Harrell, 1990).

To address severe class imbalance (4 CR vs. 257 LC), we evaluated class-balanced RFs (binary and four-class) using per-class recall, area under the receiver operating characteristic curve (AUC), and out-of-bag (OOB) error (Supporting Information Section B3). Further details are reported in Supporting Information (Figures S7-S11; Tables S2-S3). Habitat diversity, threat diversity, assessment era and ecological system were excluded for collinearity, methodological artefact, and near-separation,

194 respectively. Invasive pressure was represented as a continuous bias-corrected log
195 density (Section 2.8). Diagnostic plots are in Figures S5 (predictor-selection
196 sequence) and S6 (correlation heatmap of candidate bioclimatic predictors).

197 **2.4 Endemism and range restriction (RQ2)**

198 We re-examined geographic range restriction using a native-range classification from
199 the World Checklist of Vascular Plants (WCVP; Govaerts et al., 2021). From each
200 native species distribution, expressed in the World Geographical Scheme for
201 Recording Plant Distributions (WGSRPD) level-3 'botanical countries' (Brummitt,
202 2001), we assigned one of three ordered classes: i) Rwanda-endemic (native to
203 Rwanda only; n = 15), ii) Albertine Rift near-endemic (native range confined to Rwanda
204 and adjacent Albertine-Rift/montane countries; n = 86), and iii) wider-ranging (n = 266),
205 cross-validated against the IUCN range narrative. We estimated the effect of regional
206 range restriction by propensity score matching (PSM; Rosenbaum & Rubin, 1985) of
207 Albertine Rift near-endemics against wider-ranging species, matching on six habitat
208 types, binarised ecological system, Afrotropical realm and habitat diversity (1:1
209 nearest-neighbour; MatchIt; Ho et al., 2011); Figure S26). After matching, we applied
210 the paired Wilcoxon signed-rank test to IUCN ordinal scores and logistic regression
211 with cluster-robust standard errors (sandwich; Zeileis, 2004), plus Rosenbaum-
212 bounds sensitivity analysis (rbounds; Keele, 2010). Strict Rwandan endemics (n = 15)
213 were too few for matching and are reported descriptively.

214 **2.5 Conservation gap analysis: three-tier framework and Conservation**
215 **Imperatives scoring (RQ3)**

216 We classified the 105 threatened species (CR–NT) into three habitat-protection tiers:
217 i) Tier 1 (at least one occurrence in a formal PA); ii) Tier 2 (no PA overlap but occupied

one of the 13 remnant forest patches >50% of range or one verified occurrence; Table S4); and iii) Tier 3 (neither). We assigned the triple-jeopardy category to species that were simultaneously threatened (CR, EN or VU), geographically restricted (Rwanda-endemic or Albertine Rift near-endemic, as defined in Section 2.4), and lacked active conservation measures, coded from each species' IUCN Red List assessment as the absence of any in-situ (beyond protected-area presence), ex-situ or research action; only 5 of 105 species (4.8%) had such action recorded. We assessed PA-expansion feasibility by buffering the five PAs at 2.5 and 5.0 km and reclassifying coverage (McNemar test; Figure S19). We defined the Conservation Imperatives (CI) priority set by adapting the multidimensional CI priority score (Dinerstein et al., 2024; Gosling et al., 2026) to the species level, combining six conservation-urgency dimensions (Figure S23): threat level, proportion of range outside PAs, irreplaceability, isolation from the nearest PA, 2.5 km PA-expansion urgency, and invasive pressure (habitat-loss urgency was omitted as saturated at 0.97–1.00). Dimensions were normalised to a 0–1 scale and averaged for the top 15 priority species. Ecoregion and district assignments and the Moran's I analysis are detailed in supplement (Figures S12, S13).

2.6 Species distribution modelling and climate projections (RQ4)

Ensemble SDMs were built using biomod2 (Guéguen et al., 2026) following the Overview, Data, Model, Assessment and Prediction (ODMAP) protocol (Zurell et al., 2020; Appendix S1). Species were modelled based on record number: (i) those with ≥10 records (class A) used MAXNET, Generalised Linear Models (GLMs), Generalised Additive Models (GAMs), and Boosted Regression Trees (GBMs); (ii) those with 5–9 records (class B) used MAXNET and Surface Range Envelopes (SREs). Among 367 species, 209 had enough records for modelling (Metrics in Table S7); 185 species met the ensemble inclusion threshold and produced valid projections,

whereas 24 were excluded because their cross-validated true skill statistic (TSS) was below 0.40.

Twelve bioclimatic predictors were retained after iterative variance inflation factor (VIF) selection (Figure S5–S6; Table S1). Background points (n = 5,000) were sampled within Rwanda. Models were trained on the full occurrence dataset (Rwanda IUCN and GBIF records plus the Albertine Rift buffer) and evaluated on the Rwanda occurrences using three-fold cross-validation (70/30 partitions). Only models with TSS ≥ 0.40 were retained in the weighted-mean ensemble.

To assess sensitivity to spatial autocorrelation, the well-sampled class A species were re-evaluated using five-fold spatial-block cross-validation (Table S7b). Future projections were generated under three Shared Socioeconomic Pathways (SSP1-2.6, SSP2-4.5, SSP5-8.5) and two temporal horizons near-term (NT; 2041–2060) and long-term (LT; 2061–2080), using the ensemble mean of two General Circulation Models (GCMs), MIROC6 and MRI-ESM2-0. This factorial of three scenarios crossed with two horizons yields six future projections and is hereafter called the harmonised 3 × 2 design.

Continuous ensemble outputs (range 0–1000) were classified into four suitability classes following Fielding & Bell (1997). Per-species suitability and aggregate richness patterns are shown in Figures S15–S18. Binary suitability thresholds (≥ 500/1000) were aggregated to generate species richness maps by IUCN category, excluding DD species, for both current and projected future climates (Figures S17–S18; Table S9). Projections combined both record class A and class B species that met the TSS threshold; conversely, record class A-only analyses were retained as a sensitivity test (Table S7c). Projected proportional habitat loss was interpreted under IUCN Red List Criterion A2, which lists a taxon on an observed or projected reduction over the longer

of three generations or 10 years, with thresholds of ≥30%, ≥50% and ≥80% for VU, EN and CR, respectively. These thresholds were applied to projected habitat-suitability change as a proxy for the population reduction of Criterion A2, not as a formal A2 listing: species-level generation lengths are unavailable for most of this flora, thus the 2041–2060 and 2061–2080 horizons were adopted as the assessment window.

To quantify evolutionary history at risk under climate change, we combined the *V.PhyloMaker2* phylogeny used in the Evolutionarily Distinct and Globally Endangered (EDGE2) analysis (Section 2.9) with the ensemble projections. For the 51 threatened species that were both modelled and placed in the phylogeny, presence was defined as in the richness analysis (two-GCM ensemble suitability ≥ 500 of 1000, masked to Rwanda) for the current climate and six future scenarios. Per-cell Faith's phylogenetic diversity (Faith, 1992) was calculated with *picante* package (Kembel et al., 2010) and compared with the current baseline. We report per-cell change, change in the national threatened-lineage pool, and species-level extirpations for each scenario. Restricting the analysis to threatened species isolates the evolutionary history most at risk; a whole-flora phylogeny would be dominated by widespread species and hide this signal.

2.7 Data Deficient and Possibly Extinct species (RQ5)

The five DD species and the two species formerly listed Possibly Extinct (*Capparis lucens* Hauman., last collected 1933; *Polystachya erica-lanzae* Eb.Fisch., J.-P.Lebel & Delep., last collected 1992) were examined separately. The IUCN Red List assessed the species under the name *Capparis lucens*, whereas major taxonomic backbones, including Kew’s Plants of the World Online (POWO), GBIF, and iNaturalist, currently recognise *Capparis tomentosa* Lam. as the accepted name and treat *C. lucens* as a synonym.

2.8 Spatial bias correction for invasive density

Raw GBIF invasive plant records were bias corrected using a target group background surface (Phillips et al., 2009), because record density is confounded by survey effort and road accessibility, and the IUCN threat flag is too coarse to distinguish severity. Full model specification and bias diagnostics are given in the Supporting Information (Section A1; Figure S2). Land use intensity was derived from the Global Land Analysis and Discovery (GLAD) 2000–2020 land-cover change raster (Potapov et al., 2022) and grouped into nine transition classes (Figure S3b).

2.9 Evolutionary distinctness and EDGE2 priority scores

To assess the evolutionary heritage at risk among threatened plant species, we reconstructed species-level phylogeny for all 105 threatened vascular plants using V.PhyloMaker2 v0.1.0 (Jin & Qian, 2022). Among the 105 species, 10 were matched directly to the megatree backbone and 95 were placed at their genus-level node (Scenario 3); the calibrated phylogeny with estimated divergence times is shown in Figure S14. EDGE2 scores were computed following Gumbs et al. (2023), combining evolutionary distinctiveness (ED) from phylogenetic branch lengths with extinction probability from IUCN Red List categories. We compared EDGE2 rankings with the threat-weighted Conservation Imperatives priority score (Section 2.5) using Spearman correlation, and tested EDGE2 independence from threat category (Kruskal–Wallis), from PSM-derived endemism status (Wilcoxon) and from spatial priority quantiles (Spearman). Full ranked scores are listed in Table S6, and the underlying phylogeny in Figure 3d. We also quantified the phylogenetic representation of the EDGE2-based priority set (the top-15 EDGE2 and top-15 spatial-priority union) as its Faith's phylogenetic diversity (PD; Faith, 1992), as a proportion of the 105 threatened species'

317 total PD, benchmarked against size-matched greedy PD-maximising, EDGE2-only,
318 spatial-priority-only and random (2,000-draw) selections.

319 **2.10 Cross-validation with independent field-survey records**

320 To assess the completeness of our IUCN-GBIF-based occurrence dataset, we cross-
321 referenced our species list against the field-survey inventory of threatened ecosystems
322 and species (TES) compiled by Bizuru et al. (2015). This follows recommended
323 practice for preliminary conservation assessments (AuBuchon-Elder et al., 2023) and,
324 for the eastern remnant forests, is complemented by a recent multi-taxon baseline
325 survey (CoEB, 2024).

326 We treated the TES report as a cross-validation group and did not include the 38 TES
327 species in the main analyses, because doing so would mix species assessed under
328 the IUCN global protocol with species assessed only under the TES national
329 application. The full name-harmonisation, record-matching and tier-assignment
330 procedure is detailed in the Supporting Information (Table S10).

331 **3 Results**

332 **3.1 Ecological and biogeographic drivers of extinction risk**

333 The threat count differed significantly among IUCN categories (Kruskal–Wallis $H(4) =$
334 63.86, $p < 0.001$, $\epsilon^2 = 0.174$), but not monotonically: NT species showed a multi-threat
335 burden comparable to CR+EN. Mean threat counts were highest in NT (0.95±0.94)
336 and VU (0.82±0.85), followed by CR+EN (0.66±0.64), and lowest in LC. Forest-
337 bamboo habitat showed strong (0.28±0.77) co-occurrence with land conversion, and
338 extraction/logging pressures; this pressure complex becoming increasingly
339 concentrated from LC to the more threatened categories (Figure S6b).

Across modelling approaches, predictor effects were highly consistent. The RF model achieved a test root mean square error (RMSE) of 0.940 (R^2=0.278; OOB R^2=0.224); apparent five-categories accuracy (55.4%) was inflated by LC prevalence. A class-balanced model improved screening performance, raising recall of genuinely threatened species from 28.8% to 83.8% in the binary (Threatened-versus-not) model (AUC ≈ 0.80; Table S2, Figure S7), while retaining the same leading predictors. SHAP decomposition identified regional range restriction (Albertine Rift near-endemic) as the dominant driver, followed by extraction/logging, montane/rocky habitat, land-use intensity and invasive pressure. In contrast, strict Rwandan endemism contributed very little (Figure 2a; Table 1).

Parametric ordinal models confirmed these findings: the probit cumulative-link model identified regional range restriction and invasive pressure as the leading risk-increasing predictors, followed by urban/infrastructure, extraction and overgrazing. Wetland and forest/bamboo habitats showed neutral to protective effects, whereas strict Rwandan endemism was not significant (Figure 2b; Table 1).

A proportional-odds (logit) model returned similar effect directions ($R^2_{Nagelkerke}$ = 0.329; Akaike information criterion (AIC) = 597.9), and was consistent with RF-SHAP and the probit CLM for 12 of 15 predictors (Figure S9). However, the proportional-odds assumption was violated for seven predictors. Allowing category-specific slopes improved model fit substantially (partial proportional-odds: AIC 573.5 vs. 597.9; likelihood-ratio χ^2 = 66.4, df = 21, p = 1.3×10^{-6}).

By using both SHAP and partial proportional-odds thresholds, we identified where drivers operate along the risk gradient. Regional range restriction was the dominant risk-increasing predictor, shifting species from Least Concern into threatened

categories, whereas strict Rwandan endemism showed no such effect (Figure 2a; Figures S9, S10). In contrast, the forest-conversion complex (land conversion, logging/extraction) dominated transitions at higher-risk levels (CR–EN), while NT species reflected contributions from multiple concurrent threats.

3.2 Range restriction and extinction risk

Threat prevalence varied non-monotonically across range classes. Albertine Rift near-endemic species showed markedly higher threat levels (68.2% threatened; Figure 2c), whereas Rwandan endemics were not more threatened than wider-ranging species (14.3% vs. 16.5% threatened; Fisher odds ratio = 0.85, 95% CI 0.09–4.01, p = 1.0), suggesting that only regional range restriction elevated extinction risk (Figure S28). Comparing near-endemics with wider-ranging species, the crude association was strong (odds ratio = 10.80, 95% CI 6.0–19.9, $p = 1.6 \times 10^{-18}$) and the IUCN-ordinal gradient across classes was significant (Kruskal–Wallis H = 85.1, $p = 3.4 \times 10^{-19}$). After propensity-score matching on habitat and ecological system (73 pairs; Figure S26), the effect weakened but remained significant: paired Wilcoxon p = 0.002 (rank-biserial r = 0.36) and matched logistic odds ratio = 2.74 (95% CI 1.46–5.14, p = 0.002). The matched effect lost significance beyond $\Gamma \approx 1.5$ (Figure S27), consistent with partial circularity between small regional range size and IUCN Criterion B listing.

3.3 Conservation priority framework and evolutionary heritage

Among 105 threatened species, 27 (25.7%) had no records within the formal PA network, 77 (73.3%) were forest-dependent and 25 fell into Tier 3 (Figure 3a; Table S16; Table S3). Eighty-four species (80%) fell within 2.5 km of a PA boundary, but the coverage gain from expansion was modest. A 2.5 km buffer included 6 unprotected species (22.2%; McNemar $\chi^2 = 4.17$, p = 0.041) and a 5.0 km buffer 3 more (33.3%;

χ^2 = 7.11, p = 0.0077; Figure 3b; Table S5). Thirty-one species (29.5%) entered the Conservation Imperatives priority set (Figure 3c). The Albertine Rift montane forests ecoregion supported 93 threatened species (82.8% with PA overlap) against 25 species (52.0%) in the Victoria Basin forest-savanna ecoregion (Fisher's exact p = 0.001; Figure S12). District richness correlated with unprotected-species count (Spearman rho = 0.794; Moran's I = 0.0343, p = 0.273; Figure S13).

All 105 threatened species were placed on the phylogenetic backbone (Figure 3d), with mean evolutionary distinctness of 53.9 and the highest EDGE2 score for an *Elaphoglossum* species (5.98). The 20 highest-EDGE2 species, with each score partitioned into evolutionary-heritage and extinction-risk components, are shown in Figure S14b. EDGE2 scores were weakly and non-significantly related to the Conservation Imperatives priority score (Spearman ρ = 0.162, p = 0.098), and independent of IUCN category (Kruskal–Wallis χ^2 = 0.12, p = 0.94) and of priority-species list (Wilcoxon W = 1,259, p = 0.43) (Figure 3e; Tables S6, S6b, S6c). This suggests that evolutionary heritage and threat-based priority partly identified different species. To integrate both dimensions, the priority species were re-ranked by an EDGE2 × spatial-priority composite, which promoted evolutionarily distinct lineages that spatial scoring alone under-ranked (Table S6c). The union of the top-15 EDGE2 and top-15 spatial-priority species (29 species) captured 55.1% of the 105 threatened species' phylogenetic diversity, above random selections (44.1%) but below a PD-maximising set (65.6%), with EDGE2 alone at 59.7%; these PD values are approximate given the largely genus-level phylogeny.

Across all 365 assessed species, 73.7% had an occurrence within 2.5 km of a protected area, exceeding the global Conservation Imperatives benchmark (51.53%; Gosling et al*.,* 2026), and feasibility declined from 100% in Tier 1 to 21.6% in Tier 2

and 15.2% in Tier 3 (Figures S19, S20). Active conservation was recorded for only 5 of 105 threatened species (4.8%), and 48 of 49 threatened range-restricted species (98.0%) faced concurrent threat, restriction and no active conservation (Figures S21, S29); range restriction lowered the odds of any conservation response (OR = 0.14, 95% CI 0.05–0.35, $p < 0.001$).

3.4 Climate vulnerability across emission scenarios and time horizons

Across the 185 retained species, projected habitat change formed a graded emissions response that deepened over time (Figure 4a). Loss increased monotonically from SSP1-2.6 through SSP2-4.5 to SSP5-8.5 and from the near- to the long-term horizon, with the threatened categories shifting furthest towards contraction. The number of species projected to lose at least 80% of suitable area by 2061–2080 rose from 13 (7.0%) under SSP1-2.6 to 41 (22.2%) under SSP5-8.5 (Figure S22). Range-restricted species fared far worse than wide-ranging ones (median −33.9% vs. +55.8% under SSP5-8.5 long-term; Wilcoxon $p = 1.3 \times 10^{-4}$).

Pairwise pathway contrasts showed that mitigation, not warming alone, governs many outcomes (Figure 4b). Sixty-two species (33.5%) were projected to contract under both the optimistic and the severe pathway and 27 (14.6%) gained habitat under SSP1-2.6 but lost it under SSP5-8.5. This pathway sensitivity was greatest in the most threatened species (median divergence −21.2% for CR+EN vs. +3.9% for LC; Kruskal–Wallis $p = 1.5 \times 10^{-5}$). The relative share of each IUCN category in predicted habitat remained broadly stable even as the total pool contracted (Figure S18; Table S9).

Projected loss concentrated where threatened species were already richest (Figure 4c; Figures S17, S18). The steepest decline in CR+EN richness fell on the lower Congo–Nile Divide in Nyungwe NP (up to −47 species in a single cell; Table S8), and per-cell richness change correlated negatively with current threatened-species density (Spearman $\rho = -0.156$, $p = 1.85 \times 10^{-8}$), indicating that current threat and projected loss coincided. Whole-flora richness maps for every scenario are given in Figure S15. The five focal species spanned the full range of responses (Table S15; ensemble maps in Figure S16): from near-complete loss regardless of pathway (*Ocotea michelsonii*, ≈ −100%) and contraction crossing the IUCN Criterion A2 Critically Endangered threshold by 2061–2080 under SSP5-8.5 (*Polystachya fallax*, *Psychotria palustris*) to strongly mitigation-dependent expansion (*Impatiens erecticornis*). The apparent expansion of *Capparis lucens* is interpreted cautiously given weak discrimination (AUC = 0.766). Annual precipitation (bio12) and annual mean temperature (bio1) were the dominant predictors of suitability (Figure S24), defining the flora's cool, moist montane climatic space. Because that space warmed progressively under higher emissions and longer horizons while precipitation changed little (Figure S24b), the projected contraction was driven mainly by warming rather than by rainfall change.

Combining the threatened-species phylogeny (Section 3.3) with projections showed a redistribution of evolutionary history rather than uniform loss: local phylogenetic diversity increased across much of Rwanda as broad-ranging species expanded, whereas the national pool of threatened lineages contracted.

Among the 51 threatened species that were both modelled and phylogenetically placed, 17 (33%) lost all suitable habitat under SSP5-8.5 by 2061–2080, reducing national phylogenetic diversity by 22.5% (Figure S25; Table S11). This loss increased

with emissions, from 2.6–5.5% under SSP1-2.6 to 22.5% under SSP5-8.5, and was concentrated in Nyungwe NP, where the highest concentration of threatened evolutionary history is currently observed and cool-adapted lineages lack upslope analogues.

Among the 20 best-modelled threatened species, 14 followed national-extirpation trajectories under SSP5-8.5 by 2061–2080, with complete loss of moderate-to-high suitability (Table S13). The most evolutionarily distinct lost lineages included *Beilschmiedia michelsonii* Robyns & R.Wilczek (EN, ED = 109.46), *Polygala engleri* Chodat (VU, ED = 105.31), alongside other distinct species such as *Ocotea michelsonii* (Robyns & R.Wilczek) Trofimov (VU), and *Vepris renieri* (G.C.C.Gilbert) Mziray (EN) (Table S12).

3.5 Data Deficient species, the *Capparis lucens* rediscovery and the IUCN Red List gap

Among the five DD species, the median Rwanda record count was 2 (interquartile range 1–2), consistent with the designation following from insufficient survey; these species clustered along the western montane axis, close to but largely outside the formal PA network (Figure 5a). *Capparis lucens,* previously last recorded in 1933, was recovered through GBIF and iNaturalist name-harmonisation (20 records, 1933–2026, including 5 post-2020), giving a complete range polygon for the first time. The recomputed suitable area covered about 3,356 km², of which only 6.6% lay within the formal PA network (Figure 5b). The second Possibly Extinct species (*Polystachya erica-lanzae*, last recorded 1992) returned no recent records. Cross-validation against field survey identified 30 of 38 documented threatened species (7 CR, 19 EN, 4 VU) that were absent from both our IUCN-assessed list and our georeferenced occurrence dataset, including the CR *Blighia unijugata* Baker, *Pterygota mildbraedii* Engl. and

Nymphaea thermarum Eb.Fisch. (Figure 5c; Table S10). These field-survey-only records concentrated in the same Tier 2 remnant-forest patches identified by our framework (Karama, Ibanda-Makera, Mashoza, Mukura), a further set of data-deficient threatened species beyond the five formally classified as such.

4 Discussion

4.1 Ecological and biogeographic drivers of extinction risk

We identified continuous invasive pressure and regional range restriction as the signatures of extinction risk across three independent models, supporting island-biogeographic predictions in which range size carries a demographic signal beyond habitat condition (MacArthur & Wilson, 2001); the range signal, however, was carried by Albertine Rift near-endemics rather than by strict Rwandan endemics, which were no more threatened than wider-ranging species. Invasive pressure dominated the cumulative-link estimate, and regional range restriction remained a leading contributor once measured on a reproducible native-range. The continuous bias-corrected invasion metric out-performed the binary IUCN threat flag, suggesting text-derived categories under-capture the severity gradient; invasion pressure was similarly concentrated in the most threatened categories of another sub-Saharan African hotspot (Singini & Baso, 2025), consistent with the projected expansion of invasive *Senna* under regional warming (Weldemariam & Dejene, 2021). At the western protected-area cluster, field survey of Nyungwe NP records naturalised invasive neophytes, including *Acacia mearnsii*, already expanding into natural vegetation (Fischer et al., 2024). Near Threatened species, whose threat exposure rivals higher-risk categories, need targeted monitoring as a leading indicator for the next Red List cycle.

4.2 Geographic range restriction and extinction risk assessment

Range restriction is associated with extinction risk in this flora, but the effect is regional rather than national and more modest than a single binary flag implied: strict Rwandan endemics, most confined to the well-protected Nyungwe and Gishwati forests, are not disproportionately threatened, and the signal is carried by Albertine Rift near-endemics (matched odds ratio ≈ 2.74). This regional, modest effect aligns with trait-based analyses of tropical angiosperms in which range explains only a small share of extinction variance (Sodhi et al., 2008), and with experimental evidence that extinction-promoting traits act synergistically, so any single trait predicts risk unreliably (Davies et al., 2004). A dose-response test reinforces this: broadening the native-range criterion outward from Rwanda raised the odds of being threatened monotonically, from strict Rwandan endemics (no elevated risk) to Albertine Rift near-endemics, the reverse of what national endemism would predict. The pattern is consistent with metapopulation theory (Hanski, 1998) and the documented need for naturally rare plants to receive disproportionate protected-area coverage (Vellak et al., 2009). This gradient extends island-biogeographic theory to a sky-island system in which Albertine Rift mountain blocks function as habitat islands (Plumptre et al., 2021). These Afroalpine sky-island floras are young, unsaturated and repeatedly reshaped by Pleistocene climate oscillations and rare long-distance dispersal rather than equilibrium connectivity, leaving many lineages with low genetic diversity and heightened sensitivity to warming (Brochmann et al., 2022; Kandziora et al., 2022). A structural limitation is that the range-restriction exposure is partly circular with IUCN Criterion B, therefore the matched estimate should be read as associational rather than a clean causal effect.

4.3 Conservation priority and evolutionary heritage

To operationalise the three-tier framework, we applied a distinct policy instrument to each category: i) within-PA enforcement (Tier 1); ii) a fragile informal remnant forest habitat (Tier 2); and iii) external exposed-habitat measures (Tier 3), the latter addressing niches or historical local extinction events not captured by the current PA network.

The spatial implication is policy-relevant but limited: PA boundary expansion is necessary but not sufficient, as only a modest fraction (<15%) of unprotected species falls within a feasible buffer of an existing PA. The western PA cluster (Nyungwe NP and Gishwati–Mukura NP) carries the highest concentration of feasibly recoverable species and aligns with the biodiversity hubs identified by Gatwaza & Wang (2021). The protection deficit reflects a mismatch between conservation action and threat severity rather than spatial coincidence; few threatened species currently receive active intervention. Because many threatened species persist in collapsing, unprotected ecosystems, KMGBF Target 3 reporting should distinguish formal protected-area coverage from total threatened-species protection.

Combining evolutionary distinctness (EDGE2) scores reveals a partially independent priority set. EDGE2 and the threat-weighted Conservation Imperatives ranking identified different species, consistent with the divergence between threat-based and phylogenetic prioritisation reported by Gumbs et al. (2023). EDGE2 was developed for tetrapods; its recent application to vascular plants (Zhang et al., 2024) supports its use here, although uncertainties remain regarding genus-level placement and data deficiency (Section 4.7). This decoupling parallels the spatial decoupling of taxon richness, phylogenetic diversity and threat status in other plant radiations (Pirie et al., 2024), suggesting broader generality. To reduce potential prioritisation bias, we used the union of the two top-15 sets for both metrics as our operational species pool: i) to

maximise evolutionary irreplaceability coverage and ii) to ensure spatial feasibility in our recommendations to the Rwanda Environment Management Authority (REMA).

The priority union performs above chance but is not phylogenetically optimal. The threat-ranked species it adds are largely redundant with the EDGE2 set, contributing spatial urgency, not evolutionary heritage. This is consistent with evidence that rare and threatened species do not disproportionately contribute to phylogenetic diversity (Veldhuisen et al., 2025). However, several studies report phylogenetically nonrandom extinction eroding disproportionately more evolutionary history than random loss, including an East African montane flora (Eiserhardt et al., 2015; Molina-Venegas et al., 2020; Vamosi & Wilson, 2008). Similarly, a continental analysis of the African plant Tree of Life reports that threatened species, though not individually more distinct, are clustered, with their extinction implying disproportionate erosion of evolutionary history (Tiawoun et al., 2025 [Preprint]). A criterion targeting phylogenetic-diversity complementarity (Rosindell et al., 2024) would recover the residual representation, at the cost of the spatial urgency the threat axis provides.

4.4 Climate vulnerability across emission scenarios and time horizons

The harmonised 3 × 2 design resolves three patterns that two-scenario contrasts cannot. First, projected habitat change for the threatened categories is monotonic in emissions, a graded response to mitigation, not a step change under worst-case conditions. Second, loss increases consistently from the near- to the long-term horizon, and mid-century projections systematically understate end-century risk. These monotonic, mitigation-sensitive patterns match ensemble projections for other African montane and tropical floras (Ayebare et al., 2018; Ortega et al., 2024; Vidal

Junior et al., 2025). Third, the near-complete loss projected for *Ocotea michelsonii* matches the upslope-refugium dynamics documented for giant *Lobelia* in East Africa (Salah et al., 2025). Isotherm-shift modelling for the Ethiopian highlands similarly projects a 55% decline in mean area per species under the A2 scenario (Kreyling et al., 2010). Conversely, *Impatiens erecticornis* gains substantial range under mitigation alone, a candidate for assisted-colonisation planning under SSP1-2.6 (Casazza et al., 2021).

Ecophysiological evidence shows that montane trees along a Rwandan elevation gradient already sit near their photosynthetic heat-tolerance limits and acclimate only weakly to warming (Manzi et al., 2024, 2025), and undergo stand-level thermophilisation concentrated in slow-growing late-successional taxa (Mujawamariya et al., 2023; Ntirugulirwa et al., 2023), consistent with the upslope contraction the model's project. The largest projected richness losses fall on the lower Congo–Nile Divide in Nyungwe NP and coincide with the current concentration of threatened-species records, with present threat and future climate vulnerability are not independent for this flora. The projected contraction is driven by warming, not rainfall, reflecting near-constant precipitation in these scenarios; where warming is compounded by drying, montane plants can instead track moisture downslope, a discordant temperature-precipitation response that threatens montane biodiversity (McCain & Colwell, 2011) and is documented for the upland flora of Mount Kenya (Fu et al., 2026). This attribution should not be generalised to futures with substantial high-elevation rainfall decline.

The climate-versus-habitat lever is sequential: PA boundary protection dominates near-term, but by 2061–2080 mitigation determines whether multiple threatened

species retain any modelled climatic envelope, because area-based protection alone cannot accommodate climate-driven range shifts (Krosby et al., 2010). Critically, the regional range restriction that elevates present extinction risk (Section 4.2) also concentrates future climate loss, and Rwanda's range-restricted species face a compounding double jeopardy rather than two separate threats (Manes et al., 2021). Because these losses fall on the lineages concentrating the flora's evolutionary distinctness, the national pool of threatened phylogenetic diversity contracts even as broad-ranged species expand locally, with roughly a third of modelled threatened lineages projected to disappear under high emissions by 2061–2080. That 14 of the 20 best-modelled threatened species lose all suitable habitat nationally suggests end-century extirpation is a broad property of the threatened flora, not just a few focal species.

4.5 Conservation implications

The three-tier framework provides, to our knowledge, the first species-level, causal operationalisation of the Conservation Imperatives concept (Dinerstein et al., 2024) for an African plant flora, matching three policy instruments to the three tiers. For the buffer-feasible group around Nyungwe NP and Gishwati–Mukura NP, a 2.5 km PA boundary expansion is justified (Gosling et al., 2026); a resourced land-registry and legal review of these two western PAs should be REMA's first KMGBF Target 3 action. Other Effective Conservation Measures (OECMs) and community agreements suit unprotected species beyond the buffer-feasible distance, with Bugesera, Kirehe and Karongi the highest-priority districts and the Victoria Basin forest-savanna ecoregion the principal context. Because much of this buffer-infeasible group persists in farmed mosaics, agroforestry could seve as a *circa situm* reservoir for native and endemic

trees, complementing OECMs—provided native species are favoured, given that Rwandan agroforestry reports among the lowest native-species proportions in the tropics (William et al., 2026). Ex situ propagation and targeted research are needed for the Tier 3, Data Deficient and field-survey-only groups (the last from cross-validation against Bizuru et al., 2015), with EDGE2 ranking guiding ex situ priority. Regional range restriction further predicts conservation neglect, not only elevated risk; Rwanda's most imperilled range-restricted species are those least likely to receive action, the triple jeopardy the framework is built to break. This gap is central to the 30 × 30 debate: meeting the area target need not secure species, because placement and management quality, not extent, determine whether protection conserves (Geldmann, 2026; Wan et al., 2026). At the ecosystem scale, Rwanda's first Spatial Biodiversity Assessment independently classifies most ecosystem types as threatened under the IUCN Red List of Ecosystems (SANBI et al., 2022); our species-level workflow resolves the threatened taxa its ecosystem-type surrogate omits.

For other Albertine Rift countries (Burundi, eastern Democratic Republic of the Congo (DRC), Uganda) the framework is directly applicable, sharing the same hotspot endemism (Plumptre et al., 2021), comparable PA configurations and overlapping ecoregions. The implied KMGBF Target 3 pathway comprises four sequential components: i) PA boundary review at the two western PAs; ii) OECM designation in the three priority districts and the Victoria Basin forest-savanna ecoregion; iii) ex situ propagation and population monitoring for the Tier 3 and field-survey-only groups; and iv) routine GBIF–POWO name-harmonisation audits for all current Possibly Extinct designations.

4.6 Implications for the IUCN Red List and KMGBF reporting

The absence from the IUCN Red List of several highly threatened species found by national field surveys shows it is not yet a complete record of Rwanda's threatened plants. This matches reported gaps in global plant coverage (Nic Lughadha et al., 2020). Several species (e.g. *Blighia unijugata*, *Nymphaea thermarum*) are nationally assessed as CR under IUCN Criterion B yet lack global assessment. This pattern likely extends beyond Rwanda, implying KMGBF Target 3 reporting should not treat the Red List as a closed list. Conversely, global status can understate national concern: *Diospyros abyssinica*, globally Least Concern, is represented in Rwanda by fewer than 20 individuals at one site, with no in-country ex situ collection (Thomas et al., 2026). Field-survey-only and DD species cluster in unprotected remnant forests, indicating structural under-assessment rather than intermediate risk, in line with evidence that DD species are likely to be threatened (Borgelt et al., 2022) and should be prioritised for reassessment (Cazalis et al., 2023).

The *Capparis lucens* case reveals a database limitation. Its Possibly Extinct status arose from a taxonomic mismatch between IUCN and POWO despite existing records under a synonym.

4.7 Limitations and future directions

Across districts, occurrence coverage is uneven, and grid AOO is strongly correlated with record count, partly reflecting survey effort (Robertson et al., 2010); we therefore avoided AOO for inference and used SDM-based ranges consistently. IUCN Criterion B subcriteria could not be evaluated because population-trend data were unavailable. The SDM ensemble assumes climatic pseudo-equilibrium (Guisan & Thuiller, 2005) and, without explicit dispersal scenarios, cannot resolve the spatial disequilibrium

created by fragmentation, particularly where the matrix between current and projected suitable area is hostile or unresolved (Sandel et al., 2025). Consequently, projected range shifts should be read as a potential climate envelope, not realised distributions; because realised range change depends on dispersal capacity, dispersal-limited projections yield smaller gains than the full climatic envelope (Thuiller et al., 2019). A dispersal-buffer envelope approach (Thuiller et al., 2019) is a practical remedy, but was out of scope because the Albertine Rift lacks validated dispersal-trait estimates for the assessed flora, itself an open data gap (Zurell et al., 2016). Future work should prioritise (i) collecting population-trend data and (ii) adding dispersal-limited range-shift projections to better constrain predicted expansion within modified landscapes.

5 Conclusion

Across the complete set of IUCN-assessed Rwandan vascular plants, regional (Albertine Rift) range restriction, rather than national endemism, is the dominant biogeographic driver of extinction risk. The policy instruments needed to act on it align with a three-tier protection classification, from within-PA enforcement to remnant forest-patch protection and ex situ or community-managed measures for species that boundary expansion alone cannot reach. Range size therefore carries a demographic signal beyond habitat condition, in line with island-biogeographic theory extended to an Afroalpine sky-island system where the Albertine Rift mountain blocks function as habitat islands (Plumptre et al., 2021), and whose flora is young, disturbed, unsaturated and repeatedly reshaped by Pleistocene fragmentation rather than equilibrium connectivity (Kandziora et al., 2022).

Ensemble projections show that climate change compounds rather than parallels the present threat structure: under SSP5-8.5 by 2061–2080 forty-one species (22% of the modelled set) cross the IUCN Criterion A2 threshold (≥80% suitable-area loss), and

the spatial gradient of future loss coincides with current threatened-species richness, making mitigation a prerequisite for, not an alternative to, area-based protection. The methodological contribution is twofold: i) operationalising the Conservation Imperatives concept at species level with causal inference to provide a defensible mechanistic basis for prioritisation; and ii) cross-validating global occurrence data against an independent national field-survey inventory to reveal a structural gap between the IUCN Red List and the threatened plants known to occur in Rwanda. The workflow offers a transferable template for species-level Target 3 implementation in any under-assessed flora, beginning with the remaining Albertine Rift countries.

Author Contributions

Author conceptualised the study, analysed data, and led the writing of the manuscript.

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Conflict of Interest

The authors declare no conflict of interest.

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Data Availability Statement

Processed species-level tables (the master assessment table with IUCN categories, range metrics [EOO, AOO], SDM-class assignments, spatial-conservation metrics, protection tiers, EDGE2 scores and projected range changes), all model outputs, a full variable dictionary (data_dictionary.csv) defining every predictor and its coding, and the complete analysis code, including the master reproducibility workflow (Appendix S2) and the ODMAP protocol (Appendix S1), are archived at Zenodo under a Creative Commons Attribution 4.0 International licence (https://doi.org/10.5281/zenodo.21680809). Underlying georeferenced occurrence records are from the IUCN Red List (https://www.iucnredlist.org; Version 2024-2, accessed 11 April 2025) and the Global Biodiversity Information Facility (GBIF), including research-grade iNaturalist records served through GBIF; the exact GBIF downloads are citable at https://doi.org/10.15468/dl.76q3qx (occurrence supplementation, GBIF.org, 13 June 2026) and https://doi.org/10.15468/dl.38cuct (invasive-species records for the Figure S1 sampling-bias correction). Native-range classifications are from the World Checklist of Vascular Plants (WCVP; Govaerts et al., 2021), accessed via Plants of the World Online (https://powo.science.kew.org; bulk data at http://sftp.kew.org/pub/data-repositories/WCVP/). Bioclimatic layers are from WorldClim v2.1 (Fick & Hijmans, 2017,

https://www.worldclim.org) and the CMIP6 general circulation models MIROC6 and MRI-ESM2-0 (CHELSA-CMIP6, https://chelsa-climate.org); land-cover change is from the GLAD Global Land Cover and Land Use Change 2000–2020 product (Potapov et al., 2022); protected-area and administrative boundaries are from GADM and national sources. All third-party datasets are freely downloadable without special agreement.

Tables

Table 1. Ecological and biogeographic drivers of extinction risk in the IUCN-assessed Rwandan plant flora (RQ1). All 15 model predictors are listed, ordered by Random-Forest SHAP importance, each with its cumulative-link (probit) model coefficient.

Predictor	Mean |SHAP|	CLM probit estimate	95% CI	P(dir)
Range restriction (Albertine near-endemic)	0.261	1.13	0.82, 1.45	1.000
Extraction/logging threat	0.072	0.64	0.22, 1.05	0.999
Montane/rocky habitat	0.069	0.39	0.04, 0.72	0.987
Land-use intensity (GLAD)	0.065	−0.67	−1.51, 0.17	0.941
Invasive pressure (continuous)	0.065	2.09	0.27, 3.93	0.988
Urban/infrastructure threat	0.047	0.88	0.38, 1.37	1.000
Epiphytic habit	0.041	0.21	−0.25, 0.66	0.817
Forest/bamboo habitat	0.034	−0.12	−0.46, 0.21	0.764
Overgrazing threat	0.033	0.59	0.03, 1.15	0.982
Land conversion threat	0.030	0.08	−0.36, 0.52	0.646

Grassland habitat	0.029	0.10	−0.28, 0.46	0.694
Wetland habitat	0.014	−0.64	−1.34, 0.00	0.970
Fire threat	0.009	−0.31	−1.06, 0.39	0.799
Range restriction (Rwanda-endemic)	0.004	0.17	−0.71, 0.96	0.653
Aquatic habitat	0.002	−0.08	−1.11, 0.81	0.563

Note. Predictors are ordered by Random-Forest SHAP importance. Mean |SHAP| is the mean absolute SHapley value from the five-level IUCN ordinal Random-Forest model (n = 361); the CLM probit estimate and 95% CI are from the cumulative-link (probit) model; P(dir) is the posterior/bootstrap probability that the effect direction is as signed. Positive coefficients raise extinction risk. SHAP, mean absolute SHapley value from the Random-Forest model of the five-level IUCN ordinal outcome (n = 359). CLM, cumulative-link probit model (n = 361; Data Deficient excluded). 95% CI, profile-likelihood confidence interval. P(dir), probability of direction (proportion of the coefficient's posterior mass on the sign shown). Positive estimates raise extinction risk. Range restriction follows the World Checklist of Vascular Plants native-range classification (Section 2.4): the Albertine near-endemic and Rwanda-endemic contrasts are each relative to wider-ranging species.

Figure Legends

Figure 1. Study system of the IUCN-assessed vascular plant flora of Rwanda (Albertine Rift, eastern Africa). **(a)** Rwanda within the Albertine Rift (inset), showing surface elevation, the five national protected areas and 2,441 deduplicated occurrence records (367 species) coloured by IUCN Red List category: CR, Critically Endangered;

EN, Endangered; VU, Vulnerable; NT, Near Threatened; LC, Least Concern; DD, Data Deficient; PE, Possibly Extinct. **(b)** The three terrestrial ecoregions of Rwanda (Albertine Rift montane forests, Rwenzori–Virunga montane moorlands, Victoria Basin forest–savanna) with the five protected areas and 13 remnant forest patches. Equal-area projection (Lambert Azimuthal Equal Area); scale bars in km.

Figure 2. Ecological drivers of extinction risk (RQ1) and the effect of regional (Albertine Rift) range restriction (RQ2) in Rwanda's plant flora. **(a)** Random-Forest SHAP beeswarm; **(b)** cumulative-link (probit) coefficients with 95% confidence intervals; **(c)** proportion of threatened species across WCVP native-range classes (Rwanda-endemic / Albertine Rift near-endemic / wider-ranging); **(d)** IUCN ordinal risk and category composition in the matched comparison. Range-restriction predictors: Albertine Rift near-endemic (native range confined to Rwanda and adjacent Albertine-Rift/montane countries); Rwanda-endemic range (endemic to Rwanda only). SMD, standardised mean difference (dashed line = 0.1 balance threshold).

Figure 3. Conservation priority (RQ3) and evolutionary heritage (EDGE2) of Rwanda's 105 threatened plant species. Panels a and b show proportions; absolute counts are given here. IUCN Red List categories: CR, Critically Endangered; EN, Endangered; VU, Vulnerable; NT, Near Threatened (CR+EN pooled in a–c). Protection tiers: Tier 1, in a protected area; Tier 2, remnant-forest; Tier 3, fully exposed. **(a)** Protection-tier composition by IUCN category — CR+EN*n*= 35 (Tier 1/2/3 = 23/2/10), VU*n*= 50 (39/0/11), NT*n* = 20 (16/0/4). (b) Conservation-action gap by IUCN category (PA only, protected-area presence only; Research; Ex situ; Ex+res., ex situ + research) — active conservation reaches only 5 of 105 species, all CR+EN. **(c)** Protection Deficit Index

versus irreplaceability score (colour, IUCN category; shape, protection tier T1/T2/T3; Spearman ρ = 0.032, p = 0.748). **(d)** Circular phylogeny (V.PhyloMaker2 backbone); tip colour, IUCN category; outer ring, evolutionary distinctiveness (ED, Fair Proportion); Dashed lines at medians define four conservation-archetype quadrants: Upper-right (high EDGE, high spatial priority), Upper-left (high EDGE, low spatial priority), Lower-right (low EDGE, high spatial priority), Lower-left (lower-urgency). **(e)** EDGE2 score versus spatial conservation-priority score (colour, IUCN category; point size, proportion of range outside protected areas. Panels d and e share one IUCN category legend; category colours follow the official IUCN Red List scheme.

Figure 4. Climate vulnerability of Rwanda's plant flora under three emission scenarios and two time horizons (185 modelled species; two-GCM ensemble: MIROC6, MRI-ESM2-0). IUCN Red List categories are abbreviated: CR+EN, Critically Endangered and Endangered pooled; VU, Vulnerable; NT, Near Threatened; LC, Least Concern. **(a)** Projected change in suitable habitat area (%) relative to current conditions, by IUCN category, emission scenario (columns: SSP1-2.6, SSP2-4.5, SSP5-8.5) and time horizon (rows: 2041–2060, 2061–2080). Boxes show medians and interquartile ranges, whiskers 1.5 × IQR, points outliers; the dashed line marks no change. **(b)** Scenario-divergence scatterplots in a 3 (pairwise emission-scenario contrasts: low–mid, mid–high, low–high) × 2 (time horizon) grid. Columns: SSP1-2.6 vs SSP2-4.5, SSP2-4.5 vs SSP5-8.5, SSP1-2.6 vs SSP5-8.5; rows: near-term (2041–2060) and long-term (2061–2080). Each point is one species; x and y show projected percentage change in suitable habitat area under the lower and higher scenario of each contrast, respectively, relative to current conditions. The solid 1:1 line marks equal sensitivity; points below it lose proportionally more under higher emissions. Dashed lines at zero

divide each panel into four zones: upper-right (gain under both), lower-left (loss under both; “double jeopardy”), upper-left (gain only under the higher scenario), and the blue-shaded lower-right ($x > 0$, $y < 0$; mitigation-dependent species). Open circles indicate range-restricted species (Rwanda endemics or Albertine Rift near-endemics). Point colour denotes IUCN category; point shape denotes SDM class (A, ≥ 10 records; B, 5–9 records). **(c)** Net change in projected richness of threatened (CR+EN+VU) species per ~0.04° grid cell relative to current conditions; columns are emission scenarios and rows are time horizons (left-hand labels). Red indicates projected loss and blue gain on a shared diverging colour scale. Protected-area outlines in grey; national boundary in black.

Figure 5. Data deficiency, rediscovery and IUCN Red List gaps in the Rwandan flora (RQ5). **(a)** Occurrence records of the five Data-Deficient species in the assessed flora (n = 8 records). **(b)** Records of *Capparis lucens*, represented by 20 records in total: a single historical collection (1933; grey circle, ≤ 1950), 14 mid-century herbarium specimens (1957–1958) and 5 post-2020 field observations (the latter two shown as orange triangles); the dashed orange polygon is the resulting minimum convex extent of occurrence. **(c)** Cross-validation against the independent Threatened and Endemic Species field survey of Bizuru et al. (2015): 38 threatened species mapped to 78 species site records, coloured by IUCN Red List category and shaped by data source, distinguishing species already represented in our combined IUCN and GBIF dataset (circles: 8 species, 14 records) from those documented only by the field survey (triangles: 30 species, 64 records). IUCN Red List categories: CR, Critically Endangered; EN, Endangered; VU, Vulnerable. Coordinates are in decimal degrees

(WGS84). In all panels the national boundary is shown in black, protected areas in green and remnant natural forest patches in orange

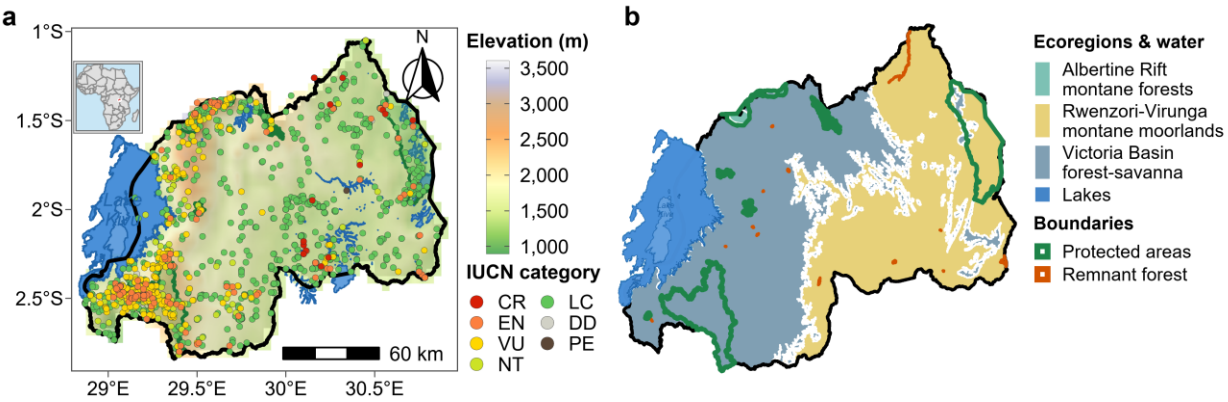

Figure 1

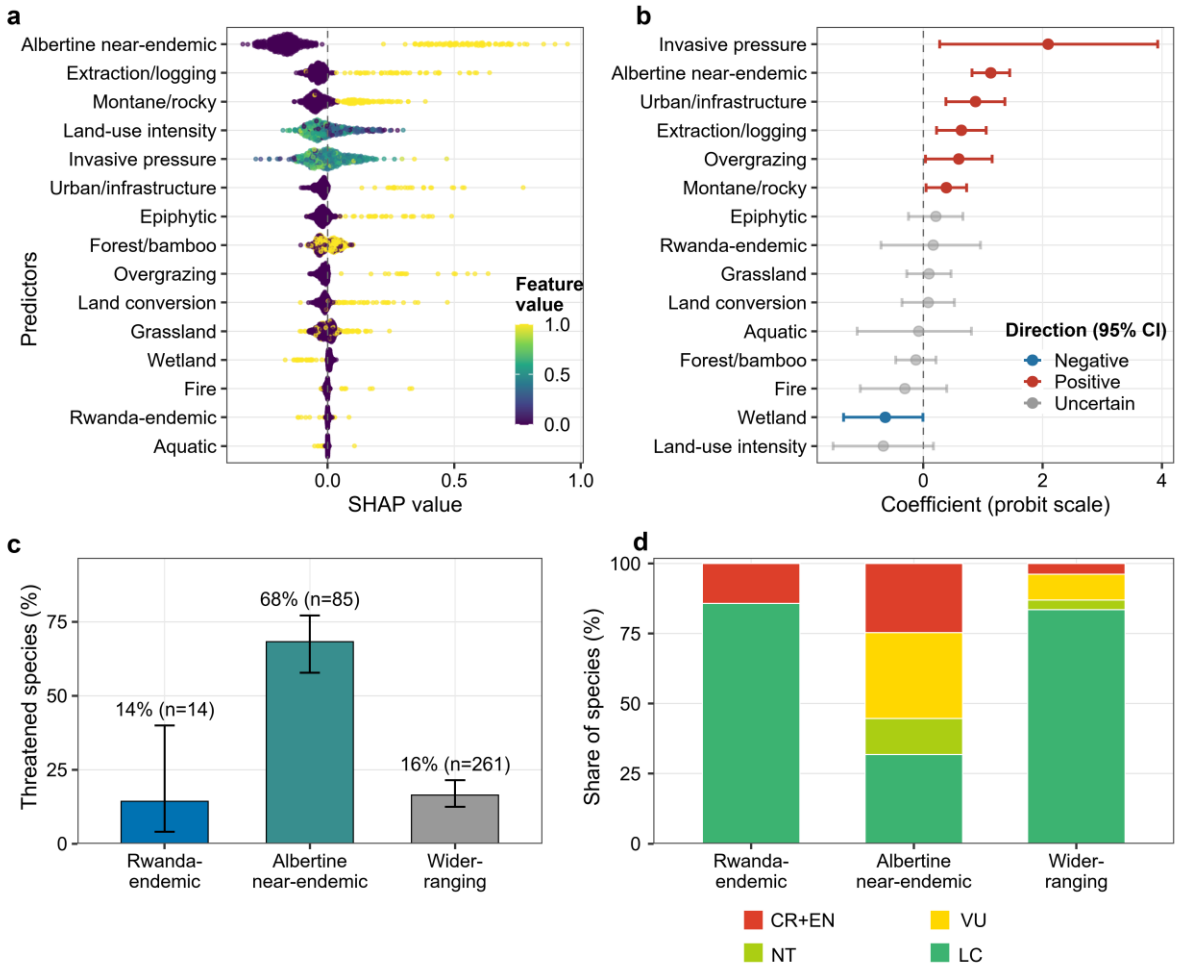

Figure 2

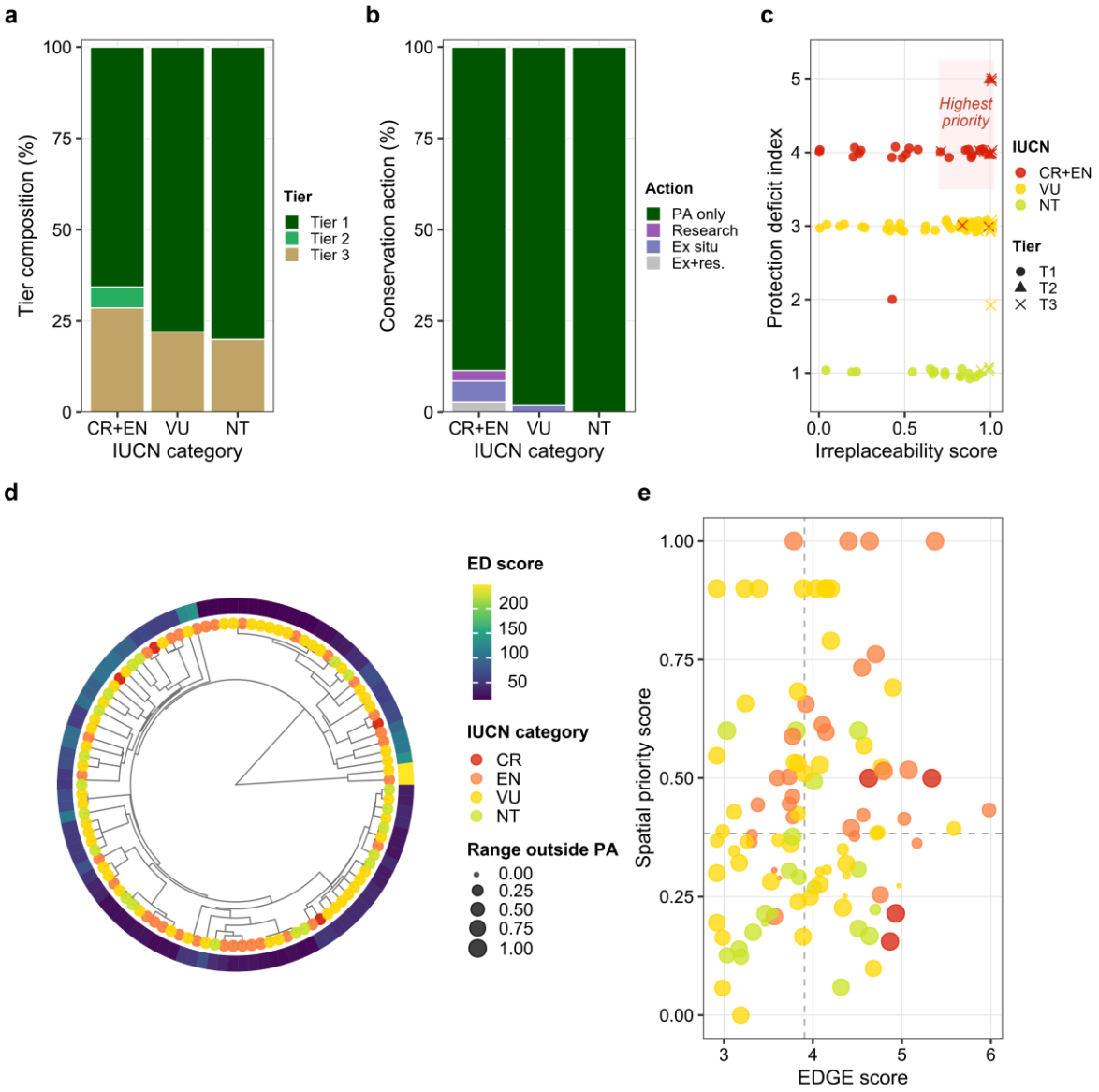
a
Tier composition (%)
100
75
50
25
0
CR+EN
VU
NT
IUCN category
Tier
Tier 1
Tier 2
Tier 3
b
Conservation action (%)
100
75
50
25
0
CR+EN
VU
NT
IUCN category
Action
PA only
Research
Ex situ
Ex+res.
c
Protection deficit index
5
4
3
2
1
Highest priority
0.0
0.5
1.0
Irreplaceability score
IUCN
CR+EN
VU
NT
Tier
T1
T2
T3
d
ED score
200
150
100
50
IUCN category
CR
EN
VU
NT
Range outside PA
0.00
0.25
0.50
0.75
1.00
e
Spatial priority score
1.00
0.75
0.50
0.25
0.00
3
4
5
6
EDGE score

Figure 3

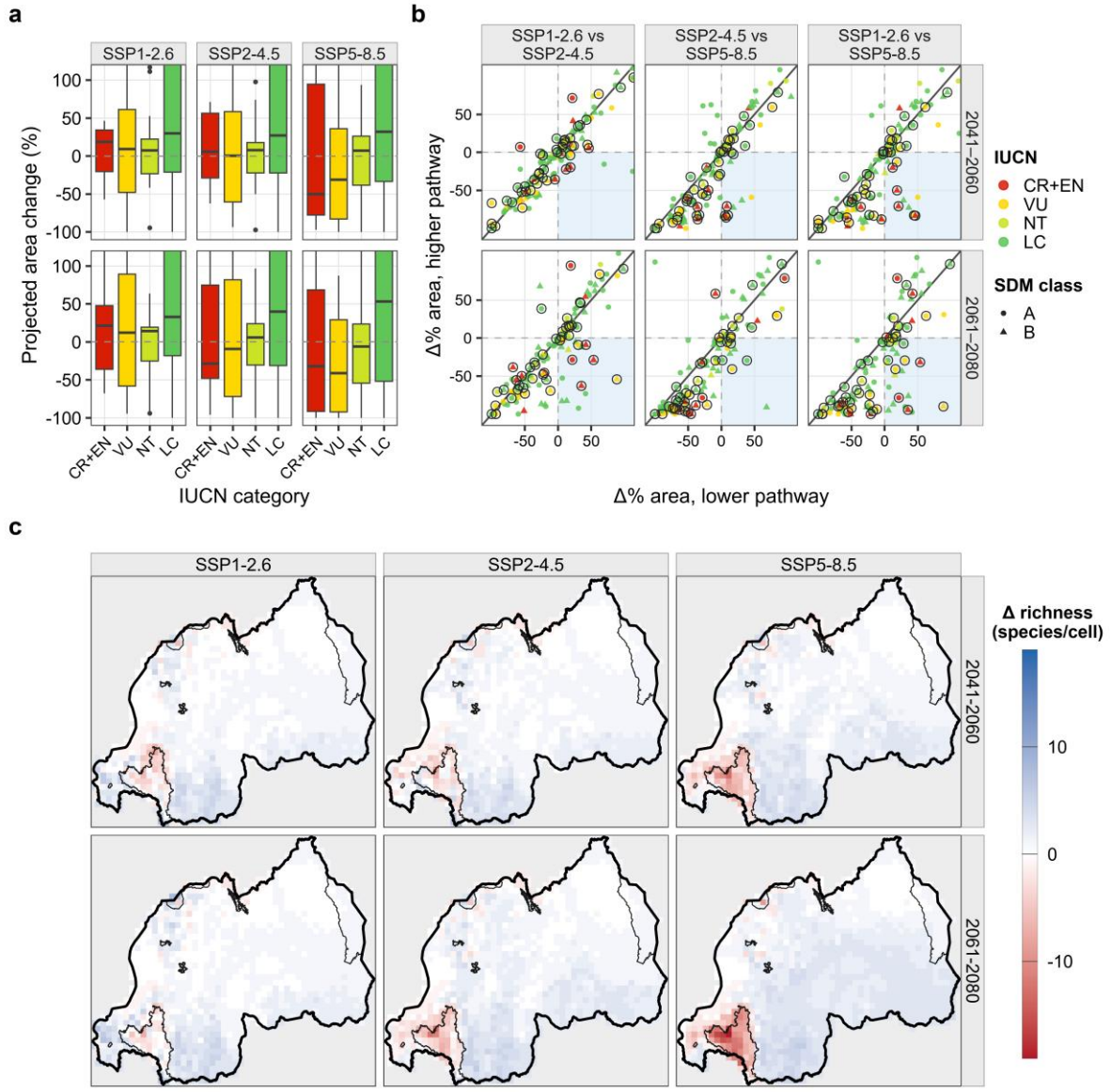
a
SSP1-2.6
SSP2-4.5
SSP5-8.5
Projected area change (%)
100
50
0
-50
-100
CR+EN
VU
NT
LC
IUCN category
b
SSP1-2.6 vs SSP2-4.5
SSP2-4.5 vs SSP5-8.5
SSP1-2.6 vs SSP5-8.5
2041–2060
2061–2080
Δ% area, higher pathway
Δ% area, lower pathway
IUCN
CR+EN
VU
NT
LC
SDM class
A
B
c
SSP1-2.6
SSP2-4.5
SSP5-8.5
2041-2060
2061-2080
Δ richness (species/cell)
10
0
-10

Figure 4

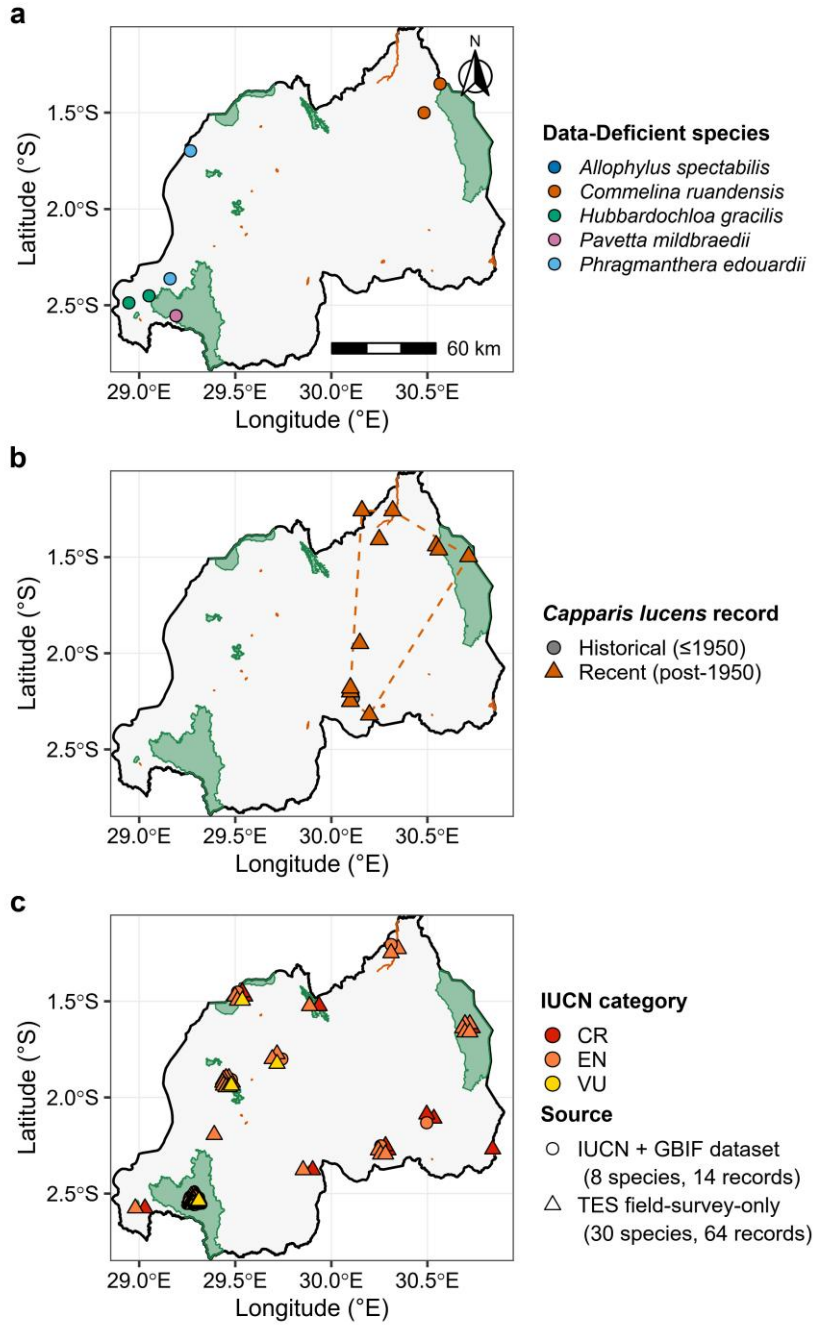

Figure 5

Supporting Information

Additional supporting information can be found online in the Supporting Information section for this article.

Table S1. Climate-predictor selection for species distribution modelling: all 20 candidate variables (19 WorldClim v2.1 bioclimatic variables and elevation) with VIF and selection outcome.

Table S2. Class-balanced versus standard Random Forest performance across the binary, three-class and four-class framings (mean over 40 stratified 80/20 resamples): overall.

Table S3. Tier 3 conservation-vacuum species (n = 25) — complete list with IUCN category, nearest PA name, distance to PA (km).

Table S4. Tier 2 (remnant-forest refuge) threatened species (n = 2).

Table S5. McNemar tests of PA-expansion coverage gain (S0→S1 χ^2 = 4.17 p = 0.041; S0→S2 χ^2 = 7.11 p = 0.0077).

Table S6. EDGE2 species-level scores (n = 105 threatened species) — evolutionary distinctness, GE, EDGE2, V.PhyloMaker2 backbone placement.

Table S6b. Evolutionary-heritage-gap species (n = 17).

Table S6c. Conservation Imperatives Table T5 priority species (n = 31) re-ranked by the EDGE2 × spatial-priority composite (EDGE2 = ln(1+ED) +.

Table S7. Per-species SDM performance (n = 209 modelled species) — AUC, TSS, number of records, Class A/B, ensemble algorithms.

Table S7b. Class A spatial-block cross-validation sensitivity analysis.

Table S7c. Class A versus pooled projection sensitivity across the harmonised 3 × 2 climate design.

Table S8. Worst-cell species turnover under SSP5-8.5 2061–2080 at 29.2292 °E, 2.4792 °S (the cell with the greatest projected richness loss, −47.

Table S9. Per-scenario IUCN-category composition of predicted habitat.

Table S10. Bizuru et al. (2015) TES report cross-validation species.

Table S11. Projected phylogenetic diversity of threatened species across the harmonised 3 × 2 climate design in Rwanda.

Table S12. Threatened plant lineages projected to lose all suitable habitat in Rwanda under SSP5-8.5 by 2061–2080.

Table S13. The 20 focal threatened plant species (the sole Critically Endangered species, *Capparis lucens*, plus the 19 highest-AUC Endangered/Vulnerable/Near-Threatened species that.

Table S14. Composition of the IUCN-assessed Rwandan plant flora (n = 367) by IUCN Red List category and species-distribution-model (SDM) sampling-adequacy tier.

Table S15. Ensemble species-distribution-model statistics and projected range change for five focal threatened plant species under the harmonised 3 × 2 climate.

Table S16. Three-tier habitat-protection framework for the 105 threatened (NT–CR) Rwandan plant species (RQ3): species counts per protection tier and IUCN Red.

Figure S1. Geographic distribution of GBIF supplementary records.

Figure S2. GBIF spatial bias diagnostics for the invasive density surface.

Figure S3a. Spatial layers overview map: Rwanda national boundary (GADM level-0), five protected areas (Akagera, Gishwati–Mukura, Nyungwe, Rugezi, Volcanoes), 13 remnant forest.

Figure S3b. GLAD land-cover change raster for Rwanda 2000–2020, reclassified into twelve transition categories: terra firma / vegetation, stable wetland, open water.

Figure S4. Sampling-effort diagnostics.

Figure S5. Iterative VIF selection of bioclimatic predictors.

Figure S6. Correlation heatmap (Spearman) of the 19 candidate WorldClim v2.1 bioclimatic variables plus elevation at Rwanda occurrence points (N = 3,930).

Figure S6b. Prevalence of each habitat and threat within each IUCN Red List category (n = 367).

Figure S7. Class-balanced versus standard Random Forest screening performance.

Figure S8. Random Forest permutation importance and its dependence on outcome framing.

Figure S9. Proportional-odds diagnostics and partial proportional-odds model.

Figure S10. Category-resolved SHAP. Mean signed SHAP for every predictor within each IUCN category (warm = raises predicted risk for species.

Figure S11. SHAP recomputed on the class-balanced binary Random Forest (contribution to the predicted probability of being threatened), confirming that the driver.

Figure S12. Ecoregion breakdown for Rwanda's 105 threatened plant species (records restricted to Rwanda; species occurring in more than one WWF ecoregion.

Figure S13. District-level choropleths of Rwanda (30 districts, GADM level-2): (a) threatened species richness; (b) unprotected species count; (c) mean conservation priority.

Figure S14. Calibrated phylogeny of the 105 threatened plant species, Rwanda, with estimated divergence times (Ma = million years before present; tips.

Figure S14b. The 20 threatened plant species with the highest EDGE2 scores, Rwanda.

Figure S15. Projected plant species richness in Rwanda under current conditions and the full set of CMIP6 scenarios, arranged as a current.

Figure S16. Ensemble habitat suitability for the five focal threatened species under the harmonised 3 × 2 design (three Shared Socioeconomic Pathways.

Figure S17. Threatened-species (CR+EN+VU) predicted richness under current climate (reference panel) and the harmonised 3 × 2 design (three SSPs × two.

Figure S18. IUCN-category composition of total predicted species-cell presence per scenario.

Figure S19. Protected-area buffer-expansion scenarios for the 105 threatened Rwanda plants.

Figure S20. Protected-area-expansion feasibility by protection tier, benchmarked against the global Conservation Imperatives mean (Gosling et al.).

Figure S21. Threat-pathway alluvial diagram for the 105 range-restricted threatened and near-threatened species.

Figure S22. Emissions-pathway sensitivity of climate vulnerability across the 185 modelled species (divergence = ΔSSP5-8.5 − ΔSSP1-2.6).

Figure S23. Multidimensional conservation-priority radar (policy brief) for the highest-priority Rwanda plant species.

Figure S24. Ensemble SDM predictor importance for Class A species (mean TSS-permutation importance across the four-algorithm ensemble).

Figure S24b. Rwandan plant occurrences in climate space under current and future scenarios.

Figure S25. Projected change in the phylogenetic diversity of threatened plants under the harmonised 3 × 2 climate design in Rwanda.

Figure S26. Propensity-score-matching covariate balance for the corrected RQ2 analysis.

Figure S27. Rosenbaum-bounds sensitivity for the matched near-endemic.

Figure S28. Dose-response of the threat association as the native-range definition is broadened outward from Rwanda.

Figure S29. Conservation Imperatives triple-jeopardy cascade for the 105 threatened Rwandan plant species.

Appendix S1. ODMAP protocol for the species distribution models (model overview, data, predictors and settings).

Appendix S2. Master reproducibility document (master_analysis_reproducible.Rmd) containing the complete analysis code.