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Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	QGIS v3.40.3 was used for site selection, spatial data preparation, and mapping. Google Earth Pro v7.3.6.10201 was used to inspect high-resolution satellite imagery and historical imagery during site selection and neighbourhood-age classification. Google Earth Engine Code Editor / JavaScript API, accessed 2022–2025, was used to load, process and filter land-cover layers, delineate vegetation patch polygons using the hand-drawing tool, mask selected land-cover classes and export spatial data. Custom Google Earth Engine scripts used for masking classes and exporting polygons are available at: https://code.earthengine.google.com/f39bf4d3daab84fd0f70777b60d8b947. The code that support the findings of this study is available via Figshare at https://doi.org/10.6084/m9.figshare.29125403.
Data analysis	Data processing and analyses were conducted in Python and R/RStudio. Python packages included GeoPandas v0.8.1, Shapely v2.1.2, rasterio v1.4 and SciPy v1.0/NumPy for spatial data processing, morphometric calculations and correlation matrices. Statistical analyses were conducted in R v4.4.0 using RStudio v2024.12.1. R packages included tidyverse v2.0.0 for data wrangling, vegan v2.7-5 for community analyses, MASS v7.3-65 for negative-binomial GLMs, AICcmodavg v2.3-4 and MuMIn v1.48.11 for AICc-based model selection and model averaging, emmeans v2.0.0 for estimated marginal means, pscl v1.5.9 for zero-inflated model diagnostics, mgcv v1.9-3 for spatial GAMs, sp/spdep v2.3.4 for spatial autocorrelation, car v3.1-5 for variance-inflation diagnostics, iNEXT v3.0.1 (estimateD function) for coverage-based richness estimation, and ggplot2 + corrplot v0.95 for visualization. ChatGPT (OpenAI) was used to support limited parts of the coding, and all outputs were subsequently reviewed, tested, and verified by the authors. A detailed description of software and workflows is provided in the Methods section of the main manuscript and the Supplementary Materials.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The data required to reproduce the findings presented in this study are available via Figshare at https://doi.org/10.6084/m9.figshare.29125403. These include all spatial, predictor and analysis datasets, as well as an anonymized vegetation dataset and a vegetation-data snippet sufficient to reproduce the reported analyses. The complete raw vegetation inventory, including the full species list, scanned field/herbarium images and associated herbarium specimen documentation, is not publicly released at this stage because it is intended for a future standalone botanical publication led by the Malagasy co-authors. The complete raw vegetation inventory can be made available by the corresponding author upon reasonable request, for example for restoration initiatives, conservation planning or research collaborations. Publicly available data are released under a CC BY 4.0 licence.

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	n/a
Reporting on race, ethnicity, or other socially relevant groupings	n/a
Population characteristics	n/a
Recruitment	n/a
Ethics oversight	n/a

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Observational vegetation inventory of natural woody plant regeneration across a 40 × 40 km area in and around Antananarivo, Madagascar, recording 25,261 non-adult woody plant individuals from 206 species. Experimental units were vegetation patches (n = 329), each sampled once with 1–6 transects (10 × 4 m) treated as subsamples and averaged to one patch-level value. Primary outcomes were patch-level native and exotic species richness. At the landscape scale, richness was compared among categories using coverage-based rarefaction (95% sample coverage). Explanatory factors of variation in species richness were 12 predictors of urban form and configuration, socio-economic and cultural context, and environmental heterogeneity. We argue that assessing local and landscape-scale variation in natural regeneration as a function of different predictor variables allows to assess resilience and capacity of species and communities to naturally maintain and recover biodiversity in heavily disturbed urban landscapes. This is key knowledge for conservation initiatives in such heavily human-modified urban areas.
Research sample	Naturally regenerating woody plants (trees and shrubs), surveyed in vegetation patches across the Antananarivo urban to peri-urban landscape. All woody individuals taller than 5 cm were recorded; analyses used non-adult individuals with DBH ≤ 5 cm. Planted individuals were excluded. In unmanaged or abandoned sites, natural regeneration was usually evident from irregular growth form and heterogeneous size and age patterns, while planted vegetation growth was more uniform and usually limited to a few species. Species identifications were verified with the University of Antananarivo herbarium and global databases. The sample is intended to represent spontaneous recruitment of native and exotic woody flora across urbanization gradients in the study area.
Sampling strategy	For sample site selection, we used a high-resolution land-cover map of Antananarivo to classify all Fokontany (n = 856, the smallest administrative unit in Madagascar, approximately equivalent to neighbourhoods or villages) within a 40 × 40 km study area into four classes along an urban-rural gradient. We then randomly selected Fokontany from each class and inventoried 1–7 vegetation patches within each selected Fokontany (mean 2.0 ± 0.1), starting, where possible, with the largest one. If no accessible vegetation patches

	were present, we selected another Fokontany. Sampling was conducted in 40 m² transects (n = 604) with a minimum of one transect per patch and more added based on patch size and, sometimes, time constraints (n = 1–6). Each transect was further divided into ten 2 × 2 m squares for easier species recording. Coverage-based species richness estimation indicates that the sampling intensity is sufficient for this type of analysis, with estimated richness reaching >95% sample coverage across the landscape.
Data collection	In each transect, we recorded all woody plants taller than 5 cm (trees and shrubs), excluding obviously planted individuals, and measured diameter at breast height (DBH) for individuals taller than 1.3 m. Some sampling locations contained several vegetation patches, which we numbered accordingly. We classified species as native (naturally occurring in Madagascar) or exotic. In total, 29,341 woody individuals were recorded across 329 vegetation patches. To focus on natural regeneration, we retained only individuals with DBH ≤ 5 cm for analysis (n = 25,261) -- a threshold suggested in other studies to separate non-adults from adults. We estimate that >95% of these non-adult individuals were spontaneous recruits, either from seed or from vegetative resprouting of cut stems. We applied this size filter in addition to field-based classification of spontaneous regrowth versus planted individuals to reduce potential misclassification. All data were recorded on paper in the field and later transcribed into shared Excel files by our research team.
Timing and spatial scale	Time: Between June 2022 and January 2024. Spatial scale: Approximately 40 × 40 km study area around Antananarivo. Patch sizes ranged from 65 m2 to >100,000 m2. Transects were 10 × 4 m (40 m2), subdivided into 10 subquadrats of 2 × 2 m.
Data exclusions	To focus on natural regeneration, we excluded individuals with DBH > 5 cm from analysis. Obviously planted individuals were excluded during field recording. For native and exotic richness analyses, individuals not confidently assignable to native or exotic status were excluded. For landscape-scale comparisons involving Aggregation Index and Nearest Neighbour Index, patches without sufficient building data were excluded from those specific categorical analyses only.
Reproducibility	All analyses are fully reproducible with the deposited data, code and metadata files (Figshare https://doi.org/10.6084/m9.figshare.29125403). No experiments were conducted.
Randomization	Sampling was randomized within the stratified design: Fokontany were randomly selected within four urban to rural classes. Within selected Fokontany, vegetation patches were selected based on accessibility and field constraints, starting, where possible, with the largest patch. No experiments were conducted. For data analysis, coverage-based species richness estimates used bootstrap re-sampling with a fixed random seed; other analyses did not require randomization as they were deterministic.
Blinding	not applicable

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Fieldwork took place in urban, peri-urban and immediate rural surroundings of Antananarivo. Access varied by site and was sometimes limited by factors such as land ownership, physical barriers, steep slopes, safety considerations, travel time and road access. Permissions were obtained at commune and Fokontany levels and, where applicable, from local landowners.
Location	Antananarivo, Madagascar (18.9185° S, 47.5211° E), including the urban centre and peri-urban and immediate rural surroundings. Elevation in the broader study area ranges from ca. 1,200 to 1,600 m a.s.l.
Access & import/export	Before sampling, we obtained a project-level research permit letter issued by Future Cities Laboratory Global, Singapore-ETH Centre (https://fcl.ethz.ch/research/food-and-territories/resilient-blue-green-infrastructures.html), signed by the national representative in Antananarivo and addressed to district, commune, Fokontany and landowners, authorizing the listed researchers to request site access. For each Fokontany visited, we obtained a local research permit from the Chef de Fokontany; these authorizations were stamped and dated and used to approach landowners. We entered sites only with landowner consent and often involved landowners in fieldwork activities. No plant material was exported internationally; collected identification material remained in Madagascar and was transported to the University of Antananarivo herbarium. Copies of the signed research permits and the project letter can be provided to editors and reviewers on request.
Disturbance	Non-destructive vegetation inventory. Only material needed for identification, including photos, seeds, fruits and flowers, was collected in accordance with local landowners. Collected material was labelled and transported the same day to the University of Antananarivo herbarium.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☐	☒ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Dual use research of concern

Policy information about dual use research of concern

Hazards

Could the accidental, deliberate or reckless misuse of agents or technologies generated in the work, or the application of information presented in the manuscript, pose a threat to:

No	Yes
☒	☐ Public health
☒	☐ National security
☒	☐ Crops and/or livestock
☒	☐ Ecosystems
☒	☐ Any other significant area

Experiments of concern

Does the work involve any of these experiments of concern:

No	Yes
☒	☐ Demonstrate how to render a vaccine ineffective
☒	☐ Confer resistance to therapeutically useful antibiotics or antiviral agents
☒	☐ Enhance the virulence of a pathogen or render a nonpathogen virulent
☒	☐ Increase transmissibility of a pathogen
☒	☐ Alter the host range of a pathogen
☒	☐ Enable evasion of diagnostic/detection modalities
☒	☐ Enable the weaponization of a biological agent or toxin
☒	☐ Any other potentially harmful combination of experiments and agents

Plants

Seed stocks	No seed stocks were established. We collected minimal plant material strictly for taxonomic identification, including photos and, where useful, seeds, fruits or flowers, in accordance with local landowners. No live plants were removed for propagation, and no plant material was imported or exported internationally. Collected identification material was labelled and transported to the University of Antananarivo herbarium.
Novel plant genotypes	N/A
Authentication	Plant species were identified and validated using the University of Antananarivo herbarium and the authors' taxonomic expertise, together with global repositories including Plants of the World Online, GBIF and Tropicos. Species were classified as native or exotic based on these repositories and reference literature. Overall, 99% of recorded plant individuals were identified and validated.