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Mapping the supply of nature's contributions to people on Mount Kilimanjaro

Netra Bhandari[1,*], Neema Robert Kinabo[2,3,4], Dominic Andreas Martin[5], Andrea Larissa Boesing[2], Margot Neyret[6], Gaëlle Bocksberger[7], Jörg Albrecht[2], Tim Appelhans[8], Ugo Arbieu[9], Joscha N Becker[10], Giovanni Bianco[2,3], Robert Modest Byamungu[11], Alice Classen[12], M Eugenia Degano[2,3], Friederike Gebert[13], Milena Gross[14], Claudia Hemp[7], Victoria Junquera[15], Ralf Kiese[16], Koggani D Koggani[2,3], Armin Komposch[17], Yakov Kuzyakov[18], Dickson Gerald Mauki[2,3,19], Antonia V Mayr[20], Thomas Müller[2], Henry K Njovu[21], Insa Otte[22], Jasmine Pearson[23], Marcell K Peters[12,24], John Sanya[4,14], Matthias Schleuning[2,25], Ingolf Steffan-Dewenter[24], Maximilian G R Vollstaedt[26], Jie Zhang[24], Katrin Böhning-Gaese[27,28], Markus Fischer[15], Andreas Hemp[29], Peter Manning[30] and Dirk Zeuss[1]

1 Department of Geography, Environmental Informatics, Philipps-Universität Marburg, Marburg, Germany
2 Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt am Main, Germany
3 Faculty of Biological Sciences, Goethe University, Frankfurt am Main, Germany
4 College of African Wildlife Management, Mweka, Tanzania
5 Department of Environmental Sciences, Wageningen University, Wageningen, The Netherlands
6 Laboratoire d'Écologie Alpine, UMR 5553, Université Grenoble Alpes, Université Savoie Mont Blanc, CNRS, Grenoble, France
7 Department of Environmental Politics, Helmholtz Centre for Environmental Research—UFZ, Leipzig, Germany
8 Institute of Geography, Friedrich-Alexander-Universität Erlangen-Nürnberg, Erlangen, Germany
9 Université Paris-Saclay, Centre National de la Recherche Scientifique, AgroParisTech, Ecologie Société Evolution, Gif-sur-Yvette, France
10 Institute of Soil Science, CEN Center for Earth System Research and Sustainability, University of Hamburg, Hamburg, Germany
11 Sokoine University of Agriculture, Morogoro, Tanzania
12 Animal Ecology Group (BIOM), University of Bremen, Bremen, Germany
13 Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen, Germany
14 Social-Ecological Systems Institute, Leuphana University Lüneburg, Lüneburg, Germany
15 Institute of Plant Sciences, University of Bern, Bern, Switzerland
16 Karlsruhe Institute of Technology, Campus Alpin, IMKIFU, Garmisch-Partenkirchen, Germany
17 Wirtschafts-, Energie- und Umweltdirektion des Kantons Bern, Amt für Wald und Naturgefahren, Waldabteilung Mittelland, Zollikofen, Switzerland
18 Department of Soil Science of Temperate Ecosystems and Department of Agriculture Soil Science, University of Göttingen, Göttingen, Germany
19 Department of Biology, University of Dodoma, Dodoma, Tanzania
20 Department of Evolutionary Biology and Ecology, Bonn Institute of Organismic Biology (BIOB), Bonn, Germany
21 National Center for Wildlife, Directorate of Protected Areas, Riyadh, Saudi Arabia
22 Department of Remote Sensing, Institut für Geographie und Geologie, Julius-Maximilians-Universität, Würzburg, Germany
23 School of Global, Urban and Social Studies, Royal Melbourne Institute of Technology, Melbourne, Australia
24 Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Würzburg, Germany
25 Department of Biology, Philipps-Universität Marburg, Marburg, Germany
26 Instituto Mediterráneo de Estudios Avanzados (CSIC-UIB), Esporles, Mallorca, Balearic Islands, Spain
27 Helmholtz Centre for Environmental Research—UFZ, Leipzig, Germany
28 University of Leipzig, Leipzig, Germany
29 Department of Plant Systematics, University of Bayreuth, Bayreuth, Germany
30 Centre for Sustainable Area Management and Department of Biological Sciences, University of Bergen, Bergen, Norway
* Author to whom any correspondence should be addressed.

E-mail: netra.bhandari@geo.uni-marburg.de

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Supplementary material for this article is available online

Abstract

Mount Kilimanjaro, with its steep elevational gradient (770–5886 m a.s.l.) and pronounced land-use heterogeneity, supports high biodiversity and diverse nature's contributions to people (NCP), but it is underrepresented in global spatial assessments. We address this gap by mapping NCP supply across 12 ecosystem types on the southern slopes identifying hotspots and coldspots and quantifying synergies and trade-offs among NCP categories. We use 25 context-specific NCP categories that integrate local and scientific knowledge with field measurements and remote-sensing-derived proxies. Combining long-term field data with remote sensing and machine learning, we upscaled plot-scale indicators into standardized supply maps. Total NCP supply is strongly concentrated in mid-elevation ecosystems: the 1100–2200 m band alone accounted for ~59% of total supply compared with ~18% in the lowlands (700–1100 m), and the 1100–2800 m belts together provide ~73%, whereas high-elevation zones (2800–4600 m) contribute <9%. Hotspots clustered in lower montane forest, *Ocotea* forest and homegardens at mid-elevations, while coldspots occur in *Erica* forest and *Helichrysum* vegetation at high elevations and in maize fields and savanna at low elevations. We detected moderate ($r = 0.55$) to strong synergies ($r = 0.83$) among the three NCP groups (material, regulating, non-material). After accounting for climatic co-variation, the correlations among NCP groups weakened ($r = 0.23$–0.44), underscoring the critical role of climate for NCP supply. Our study maps NCP hotspots and coldspots across Mt. Kilimanjaro and provides a decision-support layer for conservation, restoration and agroforestry management, as well as a blueprint for spatially-explicit NCP mapping and analyses.

1. Introduction

Tropical mountain ecosystems provide essential benefits that sustain the well-being of both local populations and downstream communities (Grêt-Regamey and Weibel 2020). As biodiversity hotspots, tropical mountain ecosystems are not only rich in endemic species (Christmann and Menor 2021) they also play a critical role in regulating water cycles, stabilizing climate extremes, buffering natural hazards, as well as providing critical material goods and opportunities of recreation and cultural significance (Martín-López *et al* 2019, Grêt-Regamey and Weibel 2020, Christmann and Menor 2021).

To understand how ecosystems contribute to human well-being, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) developed the nature's contributions to people (NCP) framework (Díaz *et al* 2015, 2018). It encompasses material, regulating, and non-material benefits and disbenefits; ranging from food resources, climate regulation, cultural identity, psychological well-being (Martín-López *et al* 2019), and detrimental contributions such as human—wildlife conflict (Chaplin-Kramer *et al* 2025). Complementing the generalizing perspective that proposes 18 NCP categories, the NCP framework offers a context-specific perspective, which acknowledges that cultural and ecological contexts shape human–nature relationships (Díaz *et al* 2015, 2018). This perspective allows to propose more nuanced, place-based recommendations for conservation, restoration, and sustainable governance (Pascual *et al* 2017, Díaz *et al* 2018) and at the same time, can be linked back to the standardized classification of the generalizing perspective using an interwoven approach (Hill *et al* 2021, Gross *et al* 2025a).

While the NCP framework is increasingly recognized for its utility in describing and assessing nature's benefits to people, tropical mountain ecosystems remain underrepresented in comprehensive assessments that integrate multiple NCP categories (Martinez-Harms *et al* 2025). Existing mountain studies often narrowly focus on climate regulation, soil erosion control, or recreation, neglecting essential regulating NCP (e.g. pollination, water purification) and culturally co-created non-material NCP (e.g. spiritual significance, cultural heritage; Mengist *et al* 2020). Moreover, most assessments rely on local-scale data, which, despite capturing site-specific dynamics, fail to address the spatial complexity of heterogeneous mountain landscapes (Rieb *et al* 2017, Mengist *et al* 2020). This limitation is particularly evident in regions with steep ecological gradients, diverse land-use, and overlapping institutional jurisdictions (Rieb *et al* 2017). Furthermore, logistical and topographic challenges hinder field data collection (Cavender-Bares 2022), leaving many mountain areas and supply of NCP categories unmeasured.

Here, we use the term NCP supply to refer to the biophysical capacity of ecosystems to provide NCP, irrespective of whether these contributions are currently realized or demanded. Spatially explicit, comprehensive NCP assessments for tropical mountain ecosystems are currently limited. Traditional land-cover proxy methods, which assign uniform values to ecosystem types, fail to adequately capture the ecological and socio-cultural complexity of NCP supply by ignoring variation driven by ecological processes and human interactions (Egoh *et al* 2008, Eigenbrod *et al* 2010, Maes *et al* 2012, Sharp *et al* 2014, Rieb *et al* 2017). Effective NCP mapping requires moving beyond these coarse ecosystem classifications toward nuanced, process-oriented frameworks integrating remote sensing indicators of ecosystem function (e.g. biomass, vegetation indices), species-specific functional traits, and landscape configuration metrics (Pereira *et al* 2025). Such frameworks require multidisciplinary collaboration for accurate, real-world NCP assessments (Pereira *et al* 2025).

Integrating plot-scale data with remote sensing and predictive modeling enables high-resolution, area-wide predictions of NCP supply (Scowen *et al* 2021, Senf 2022). Machine learning algorithms are particularly well suited for this task, as they can efficiently handle large, heterogeneous, non-linear datasets (Meyer and Pebesma 2021, Scowen *et al* 2021, Almeida *et al* 2024). In data-scarce, diverse tropical mountains, integrative modeling efficiently predicts NCP supply, bridging critical knowledge gaps, supporting cross-scale governance, and guiding sustainable land-use planning even when causal ecological relationships are unclear (Pettorelli *et al* 2014, Willcock *et al* 2018, Senf 2022).

Beyond mapping individual NCP supply, identifying spatial hotspots and coldspots of NCP supply is critical for guiding conservation and land-use planning (Mitchell *et al* 2021). Hotspots are commonly defined as areas with a high supply of multiple NCP per unit area, while coldspots represent areas with a low supply of few or all NCP, often indicating zones of ecological degradation or low multifunctionality (Egoh *et al* 2008, García-Nieto *et al* 2013, Geneletti *et al* 2018). In this study, we define hotspots as areas exhibiting *high total potential supply* of NCP, and coldspots as areas with *low total potential supply* of NCP. The term potential supply refers to the ecosystem's capacity to provide NCP based on its biophysical characteristics, independent of actual use or demand by different social actors.

While trade-offs and synergies between NCP across landscapes have been described often, the cause of these remain poorly understood (Bennett *et al* 2009, Spake *et al* 2017). However, assessing the cause of NCP synergies and trade-offs is challenging as the underlying drivers are often correlated, e.g. both climate and land-use strongly influence ecosystem functions and biodiversity, which ultimately underpin NCP supply (Peters *et al* 2019). Given the strong climatic gradients in tropical mountains, it is thus essential to disentangle the effects of climate for better understanding the underlying causes of NCP relationships.

Mount Kilimanjaro (Kilimanjaro from hereupon) in northern Tanzania presents a compelling system to map landscape-scale NCP supply, identify hot and coldspots and synergies-tradeoffs. As one of Africa's most ecologically and culturally diverse mountains, it illustrates how tropical mountain ecosystems are increasingly threatened by land-use change, agricultural intensification, invasive species, and climate change, which together degrade biodiversity and the NCP they provide (Martín-López *et al* 2019, Peters *et al* 2019, Christmann and Menor 2021, Said *et al* 2021). Moreover, in its mid-elevation belt, Kilimanjaro hosts a unique traditional agroforestry system, the Chagga homegarden system, which essentially is a multilayered forest-like mosaic that supplies multiple benefits to Chagga people, but is increasingly threatened by land division (*Kihamba* tradition), socio-economic change and expanding settlements (Hemp 2006a, Soini 2005, Ichinose *et al* 2020).

Existing NCP research in mountains shows a pronounced geographical and conceptual bias toward temperate, Global North ranges, while work in the Andes, Himalaya and East African 'water towers' such as Mt. Kenya tends to focus on single land-use systems or themes and is only loosely coupled to long-term ecological data (Nature Kenya 2019, Murillo-López *et al* 2022, Kockelkoren *et al* 2023, Johansson *et al* 2025, Moreira *et al* 2025, Sood *et al* 2025). Against this backdrop, Kilimanjaro provides an exceptional model system for NCP research. It concentrates an almost continuous ecological gradient from semi-arid savannas through densely populated agroforestry and montane cloud forest to afro-alpine and glaciated zones. Long-term ecological and social research (Peters *et al* 2019, Albrecht *et al* 2021, Masao *et al* 2022, Hemp and Hemp 2024, Sanya *et al* 2025, Gross *et al* 2025b, 2025c) has created an outstanding infrastructure of plots, socio-ecological data and IPBES-aligned studies on material, regulating and non-material NCP and human well-being, including works that differentiates NCP demands and values across farmers, conservationists, tour guides and tourists (Pearson *et al* 2024, Degano *et al* 2025, Sanya *et al* 2025, Gross *et al* 2025c).

In this study, we deliver the first integrated assessment of NCP on Kilimanjaro by mapping the potential supply of 25 *positive* NCP categories. We use 57 NCP indicators and 44 optical remote-sensing layers to: (1) identify hotspots and coldspots of NCP supply, (2) analyze synergies and trade-offs among material, regulating, and non-material NCP, and (3) assess how NCP synergies and trade-offs change once effects of climate are removed via residual analysis. Our approach provides high-resolution spatial insights and opens new possibilities for landscape-scale assessments in tropical mountain ecosystems for conservation, planning, and decision-making contexts.

2. Materials and methods

2.1. Study area

The study area is located on the southern slopes of Mount Kilimanjaro (2°45'–3°25'S, 37°00'–37°43'E; figure 1(a)). Kilimanjaro is the world's

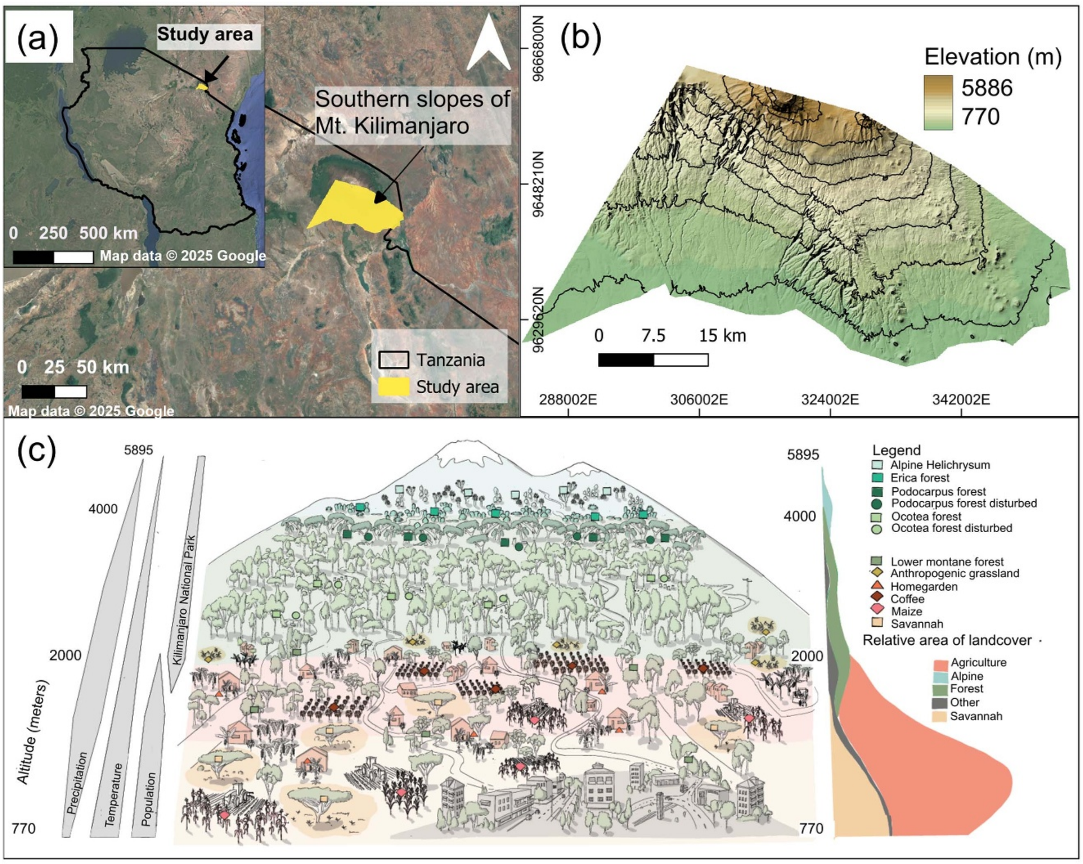

Figure 1. Study area. (a) Study area location embedded in the Kilimanjaro region in northern Tanzania, (b) elevational gradient of the southern slopes and (c) a representation of the 12 ecosystems along altitudinal, precipitation and temperature gradients. The areas above 1800 m are enclosed within the Kilimanjaro National Park and the areas below are inhabited. The colored shapes in (c) indicate the 60 plots used for data collection on indicators of NCP supply for upscaling. Design credit for panel - Jelke Meyer.

tallest free-standing mountain and a biodiversity hotspot. Its vast elevational gradient (700–5895 m a.s.l., figure 1(b)) creates unique climatic and vegetation zones (figure 1(c)), with bimodal rainfall (Hemp 2006a, Appelhans *et al* 2016) and temperatures decreasing with altitude (25 °C at foothills to −8 °C at the summit). The elevational gradient spans diverse ecosystems, from savannah to alpine zones (figure 1(c)). Between 1200 and 1700 m a.s.l, fertile soils and favorable climate support dense populations (up to 1500 people km^{-2}) engaged predominantly in smallholder agriculture and tree-based farming systems (Mtallo and Rubagumya 2015). Tourism, focused on high-elevation trekking routes (∼50 000 visitors per year), further contributes to the region's economy (Kilungu *et al* 2019, TANAPA 2023), but engages little with the rich cultural landscapes of the lower zones (Anderson 2015).

2.2. Data collection

We spatially upscaled NCP supply using a four-step process. First, we compiled context-specific NCP indicators for Kilimanjaro. Second, we assembled spatial predictor variables from remote sensing data (e.g. vegetation indices, topography, climate, land cover). Third, we employed machine learning models to upscale indicators from plot to landscape scale using these predictors. Fourth, for unsuitable indicators, we utilized alternative approaches like geostatistical interpolation and downscaling. Each step is detailed in subsequent sections and an overview of the workflow is shown in figure 3.

2.2.1. Indicator selection and classification

We first based our study on 25 context-specific NCP categories spanning across regulating, material, and non-material NCP groups (figure 2) that were identified through 130 interviews and an analysis of 1255 Twitter posts with different social actors in Kilimanjaro (Pearson *et al* 2024, Degano *et al* 2025, Sanya *et al* 2025, Gross *et al* 2025b). We relied on these works for the identification of context-specific NCP in Kilimanjaro, as perceived by different actors, but did not consider the social actors' preferences for these NCP, i.e. we did not assign explicit numerical weights to different actor groups for the NCP. For these 25 NCP categories, we then curated and synthesized 57 indicators of NCP supply

	NCP category	Indicator(s)	Unit
Regulating NCP	Habitat creation and maintenance	Tree microhabitat diversity	Shannon Wiener diversity index
		Terrestrial microhabitat index	Index
		Vertical structural heterogeneity	Shannon Wiener diversity index
	Pollination	Visitation rate birds	Visits / second
		Bee species richness	Total number of species per plot
	Dispersal of seeds	Bird-fruit interactions	Total number of fruits consumed
	Regulation of air quality	Leaf Area Index (LAI)	Index
		Relative humidity	%
	Regulation of climate	Aboveground carbon stock	Mg C/ha
		Belowground carbon stock	Mg C/ha
		CH4 gas flux (inverted)	mg C/m^2/h
		CO2 gas flux (inverted)	mg C/m^2/h
		N2O gas flux (inverted)	mg C/m^2/h
		Canopy cover	%
	Regulation of freshwater quantity	Mean annual precipitation	mm
		Topographic wetness index	Index
	Regulation of freshwater quality	Nitrate leaching (inverted)	Concentration (N-NO3μg/gm)
		Normalized Difference Built-up Index (inverted)	Index
		Bare soil index (inverted)	Index
	Regulation of soil fertility and protection of soils	Slope (inverted)	Degrees
		Total plant cover	Sum of % cover per plot
		Nitrate leaching (inverted)	Concentration (N-NO3- μg/gm)
		Ammonium leaching (inverted)	Concentration (N-NH4+ μg/gm)
		Soil quality index	Index
		Litter decomposition rate	Percent of decomposition per year
		Glucosidase	μmol/g/hr
		Phosphatase	μmol/g/hr
		Urease	μmol/g/hr
		Cellobiohydrolase	μmol/g/hr
	Regulation of hazards and extreme events	Total plant cover	Sum of % cover
		Fire resistance index	Index
	Regulation of detrimental species	Herbivorous insect abundance (inverted)	Number of individuals
		Predatory insect species richness	Number of species
		Insectivorous bird abundance	Number of individuals
Material NCP	Food	Crop calories for coffee, banana, maize and beans	Joules per hectare
		Crop market value for coffee, banana, maize-beans	Dollar equivalent per hectare
		Number of plant species that can be used for food	Number of species
	Feed	Fodder species cover	Sum of percentage cover
	Energy	Biomass of charcoal suitable trees	Tonnes per hectare
		Total deadwood biomass	Tonnes per hectare
	Building materials	Timber value	Dollar equivalent per hectare
	Materials for domestic use	Abundance of non-tree construction plants and trees used for poles	Number of individuals
	Medicine	Medicinal plants richness	Number of species
Non-material NCP	Learning	Biodiversity of observable taxa	Index
		Bioacoustic index	Index
	Aesthetic enjoyment	Aesthetic plant cover	%
		Proportion visible area in the viewshed	%
	Recreation	Slope	Degrees
		Universal thermal climate index (optimum at 17.5 °C)	Index
	Therapeutic and restorative benefits	Leaf Area Index	Index
		Proportion visible area in the viewshed	%
	New and unique experiences	Biodiversity of observable taxa	Multidiversity Index
	Connectedness with nature	Bioacoustic index	Index
	Cultural heritage and identity	Abundance of culturally important mammals	Number of individuals
		Percentage cover of culturally important plant species	Sum of % cover
	Social cohesion and bonding	Average of non-material NCP indicators	Index
	Intergenerational benefits	Biodiversity of above and belowground taxa	Index

Figure 2. Overview of the 25 context-specific nature's contributions to people (NCP) categories spanning across regulating, material, and non-material NCP groups, and their indicators used in this study. Adapted from Gross *et al* (2025a). CC BY 4.0. and Sanya *et al* (2025). CC BY 4.0. Supplementary material A contains justifications of these indicators. Design credit for icons - Jelke Meyer.

(e.g. tree microhabitat diversity, bee species richness; figure 2) (Sanya *et al* 2025, Gross *et al* 2025a), using ecological relevance, data quality and spatial coverage as key criteria. We drew on available field, remote-sensing and ancillary data spanning 2010–2023 (Peters *et al* 2019, supplementary material A), ensuring that all selected indicators were measurable and regionally relevant.

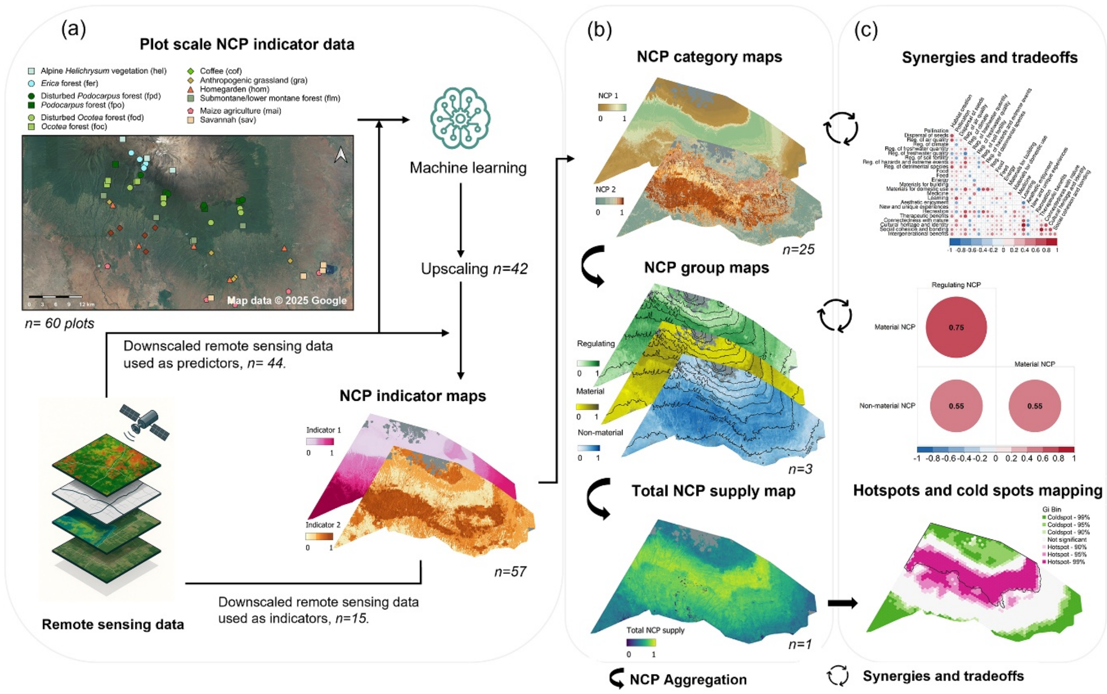

Figure 3. Overview of the workflow used to assess and map the supply and spatial distribution of nature's contributions to people (NCP) on the southern slopes of Mt. Kilimanjaro. (a) We collected field data for 42 NCP indicators across 60 ecological plots and combined them with 44 downscaled remote sensing predictors to upscale plot-scale values across the landscape. We also used an additional 15 remote sensing variables directly as NCP indicators, resulting in a total of 57 mapped indicators. (b) We aggregated the mapped NCP indicators into 25 NCP categories and further grouped them into regulating, material, and non-material NCP groups and created a composite map of total NCP supply by summing values across all three NCP groups. (c) Using these aggregated layers, we assessed pairwise relationships to identify synergies and trade-offs among individual NCP categories (top panel (c)) and NCP groups (middle panel (c)) and mapped significant hotspots and coldspots of total NCP supply (bottom panel (c)).

2.2.2. Plot scale data collection and processing

We used a stratified sampling design based on 60 permanent plots covering 12 ecosystem types (five plots per type) across the main vegetation zones and land-use types on the southern slopes of Kilimanjaro (figure 1(c); supplementary material A) (Hemp *et al* 2017). Plots were located in core areas of each habitat type along elevational and east–west gradients and spaced ⩾300 m apart to capture within-type heterogeneity while limiting spatial autocorrelation. Plot-scale field data from these 60 plots were available for 42 NCP indicators (figure 3(a)).

2.2.3. Data collection of NCP predictors

To enable spatial upscaling of the NCP indicators we compiled 44 ecologically relevant predictor variables derived from optical remote sensing datasets. These included climatic variables (e.g. mean annual temperature, mean annual precipitation), soil properties (sand, silt, clay, soil pH, soil organic carbon, cation exchange capacity), topographic metrics (elevation, slope, aspect, topographic wetness index, solar radiation), vegetation and land-cover metrics normalized difference vegetation index; enhanced vegetation index; leaf area index, canopy height model, forest cover, tree cover, plant species richness), and management/landscape configuration indicators (land-use intensity, biomass removal index, BRI; distance to forest, road density, Shannon diversity of land-cover types). The BRI quantifies direct human impact on a plot based on plant biomass removed through mowing, cattle grazing, fire events, logging, and firewood collection (Peters *et al* 2019). A full list and data sources are provided in table S1 and supplementary material A. We harmonized all datasets to match the spatial extent and resolution of our study area.

2.3. Upscaling NCP supply

We applied an upscaling framework using two machine learning models, Random Forest and XGBoost, to generate landscape-scale maps for 42 NCP indicators. Random forest is a tree-based ensemble method that handles non-linear relationships and multicollinearity, is robust to noise, and provides measures of predictor importance (Breiman 2001), whereas XGBoost is a gradient-boosting algorithm optimized for computational efficiency and predictive accuracy, with strong performance on structured environmental data and the ability to capture complex predictor interactions (Chen and Guestrin 2016, Scowen *et al* 2021). By combining a bagging approach (random forest) with a boosting approach (XGBoost), we were able to compare predictions from two conceptually different algorithms and assess the robustness of model performance to the choice of learning method, reducing our dependence on any single modeling approach. We modeled each indicator across 60 plots using ecologically relevant predictors, excluding highly correlated variables ($|r| > 0.85$; final predictors listed in table S2). We randomly split the data into 80% training and 20% testing sets and used leave-location-out spatial cross-validation (CAST package in R; Meyer *et al* 2024) with folds defined by ecosystem type. For random forest, the number of variables tried at each split (mtry) was tuned via caret's internal grid search, whereas for XGBoost we defined a tuning grid and varied maximum tree depth, learning rate (eta) and gamma, while fixing the number of boosting iterations (nrounds), minimum child weight, and the row- and column-subsample fractions at values chosen from preliminary trials. Model performance was evaluated using the coefficient of determination (R^2), root mean squared error (RMSE) and mean absolute error (MAE) under spatial cross-validation. For each indicator, we compared random forest and XGBoost and selected the algorithm with higher R^2 and lower RMSE for mapping; the full range of spatial cross-validated performance across indicators is reported in table S3, and indicators with low R^2 are interpreted as weakly predictable. We then applied the selected models to the 10 m predictor rasters, inverted selected indicators where necessary so higher values consistently indicate greater NCP supply, and rescaled all predictions to 0–1 using averaged min-max, optimum value, and index scaling methods (supplementary material A). As our empirical framework integrates heterogeneous data sources (field measurements, remote-sensing products and secondary climatic and soil layers), all of which are affected by measurement and preprocessing uncertainty, model outputs may be sensitive to plausible errors in key predictors. We therefore conducted a perturbation-based sensitivity analysis to assess how such uncertainties influence model performance, and the direction of key predictor–response relationships (supplementary material A and table S4).

For 15 indicators, we used tailored mapping approaches based on data characteristics. These included downscaling remote sensing products (e.g. LAI from 250 m to 10 m), kriging precipitation data with environmental covariates, clipping existing indices, deriving viewshed visibility (i.e. the analysis of which parts of a landscape are visible from a given observation point; Germino *et al* 2001), and interpolating sparse species data.

2.4. Aggregation of supply maps

To map the spatial distribution of NCP supply, we first summed the 57 standardized indicator maps for each of the 25 NCP categories using equal weights and then scaled the results from 0 to 1 (figure 3(b)). For food NCP, we used a weighted approach: crop yield calories and market value received 90% weighting, while edible plant diversity received 10%, reflecting the importance of production quantity versus diversity (Remans *et al* 2011). Greenhouse gas fluxes were converted to their carbon dioxide equivalent. In the second step, we aggregated the 25 NCP categories into the three NCP groups: regulating, material, and non-material contributions using equal weights and in the third step we aggregated the three NCP groups and scaled again between 0 and 1 to obtain the total NCP supply. Equal weighting minimizes subjective value judgments and avoids amplifying the influence of inter-correlated indicators, which could otherwise lead to double-counting some processes while underrepresenting others. In this way, we treat each indicator and NCP category as an equally valid and complementary dimension of NCP supply (Burgass *et al* 2017).

2.5. Spatial clustering of NCP supply

We analyzed spatial clustering patterns of total NCP supply by aggregating data into 1×1 km hexagonal bins (figure 3(c)). Using Getis–Ord Gi* statistics in ArcGIS Pro (version 3.4.0), we identified significant hotspots (clusters of high NCP supply, indicated by high positive *z*-scores) and coldspots (clusters of low NCP supply, indicated by low negative *z*-scores). Non-significant scores suggested spatial randomness (supplementary material A). We preferred the Getis–Ord Gi* statistic because it is a local indicator of spatial association that directly identifies statistically significant clusters of high and low NCP values in continuous data, while accounting for spatial neighborhood structure. Unlike global statistics (e.g. Moran's I) or partitioning algorithms (e.g. *k*-means), Gi* does not require predefining the number or location of clusters and is therefore well suited to mapping emergent hotspot and coldspot patterns of NCP supply (Li *et al* 2017).

2.6. Synergies, trade-offs, and climate controls

We calculated pairwise synergies and trade-offs among NCP indicators and NCP groups (figure 3(c)) using Spearman correlation analysis, where positive correlations indicate synergies and negative correlations indicate trade-offs. Since climate is a key driver of mountain ecosystem dynamics (Peters *et al* 2019), we controlled for climatic effects by modeling each of the 25 NCP indicators using:

$$\mathrm{NCP} \sim \mathrm{MAT} + \mathrm{MAT}^2 + \mathrm{MAP},$$

where MAT is mean annual temperature, MAT^2 captures nonlinear relationships (such as unimodal responses along elevation gradients), and MAP is mean annual precipitation. This approach accounts for climate's role in shaping ecosystem functions, which often peak at mid-elevations on Kilimanjaro, supported by the very strong negative correlation between elevation and MAT ($r = -0.98$; Peters *et al* 2019). We re-scaled residuals (representing climate-independent NCP variation) between 0 and 1 and aggregated by NCP groups to evaluate NCP supply independently of climatic gradients.

3. Results and discussion

We mapped the supply of 25 NCP categories using 57 indicators across Kilimanjaro's southern slopes, revealing spatial hotspots, coldspots, synergies, and trade-offs. Previous research on the southern slopes of Kilimanjaro has primarily focused on plot- or field-scale observations, limiting landscape-scale insights.

3.1. Spatial distributions of NCP

Total NCP supply closely mirrored the three aggregated NCP groups (material, regulating, non-material), revealing a clear unimodal elevational pattern (figures 4(a)–(d)). Mean standardized total NCP supply was highest at mid-elevations (1100–2800 m a.s.l.; mean ≈ 0.60, figure S2), and substantially lower in foothills (700–1100 m; mean ≈ 0.32) and high-elevation zones (3200–4600 m; mean ≈ 0.23). Our machine learning models effectively mapped these patterns, with spatial cross-validated R^2 ranging from 0.24 for terrestrial microhabitats to 0.94 for below-ground carbon stock).

While individual NCP indicators showed substantial fine-scale heterogeneity (supplementary material A, figure S3), aggregating them into material, non-material and regulating groups revealed consistent hotspots in the mid-elevation belt (∼1100–2800 m a.s.l.), particularly in homegardens, coffee plantations and lower montane forests, both within and outside Kilimanjaro National Park (KINAPA) (figures 4(a)–(c)). Regulating NCP generally peaked in this forest–agroforestry mosaic, with habitat creation, seed dispersal and freshwater quality regulation concentrated from low to mid elevations, while pollination was highest in the low-mid agricultural belt and hazard regulation in upper *Erica* vegetation. Material NCP showed complementary patterns: food supply was concentrated in the lowland subsistence agriculture zone, whereas energy, building materials and domestic materials peaked in the mid-elevation forest belt. Non-material NCP were generally medium to high across the landscape, with learning, social cohesion and cultural heritage strongest in lower and mid elevations, and aesthetic enjoyment and therapeutic benefits peaking in high-elevation and mid- to high-elevation zones, respectively.

The supply of individual NCP categories also aligns with farmer perceptions of 'critical NCP' reported by Sanya *et al* (2025). Upland farmers (1500–1800 m a.s.l., near the KINAPA border) perceived freshwater quality as important but relatively secure compared to mid- and lowland farmers, matching our maps that show high freshwater quality regulation in this belt and lower supply below it. Mid- and lowland farmers favored energy and building-material NCP, which correspond to mid-elevation hotspots of energy and building-material supply in our results. For non-material NCP, farmer preferences for learning, cultural heritage and social cohesion (Sanya *et al* 2025) are also reflected in the spatial distribution of these categories in our supply maps.

Low total NCP supply at the elevational extremes (foothills dominated by maize and savannah and high-elevation *Helichrysum* vegetation, bare rock and snow) underscores both the multifunctionality of mid-elevation landscapes and the potential for targeted restoration or management interventions in low-NCP supply areas. These elevational trends are consistent with unimodal patterns reported for biodiversity and ecosystem functions on Kilimanjaro (e.g. Pabst *et al* 2013, Becker *et al* 2015, Ensslin *et al* 2015, Rutten *et al* 2015, Mollel *et al* 2017, Peters *et al* 2019) and with global evidence that NCP supply tends to decrease towards foothills in many mountain systems (Grêt-Regamey and Weibel 2020).

3.2. Spatial hotspots and coldspots in NCP supply

The spatial distribution of NCP supply across the Kilimanjaro landscape revealed distinct clusters of hotspots and coldspots (figure 5(a)). Local Getis–Ord Gi* analysis identified a statistically significant ($p < 0.001$) concentration of NCP hotspots at mid-elevations (approximately 1500–3000 m a.s.l), particularly within areas dominated by homegardens, lower montane, and *Ocotea* forests (figure 5(b)). Other contributing ecosystems include maize and coffee plantations, *Podocarpus* and *Erica* forests, and grasslands highlighting the ecological richness and multifunctionality of these mosaic landscapes. These findings align with previous research (Peters *et al* 2019) emphasizing higher NCP supply, especially regulating and non-material contributions, in mid-elevation zones, underscoring the vital role of agroforestry and forest ecosystems.

We propose that these NCP hotspots are associated with both environmental conditions (Peters *et al* 2019) and socio-cultural and institutional history of Kilimanjaro. The establishment and management of the KINAPA and the Half Mile Forest Strip (HMFS, an 8800 ha of social buffer zone and catchment forest) have significantly influenced local access to forest-related NCP and perceptions of ecosystem stewardship (Newmark 1991, Durrant 2004, Sébastien 2010, Sanya *et al* 2025). The HMFS, originally managed by the Chagga Council and later integrated into KINAPA, transitioned from community-based resource management to stricter institutional control (Newmark 1991, William 2003, Durrant 2004, Sébastien 2010, Sanya *et al* 2025). Recent enforcement, like the 2021 firewood collection ban, reduced resource extraction, supporting forest recovery and contributing to emergence

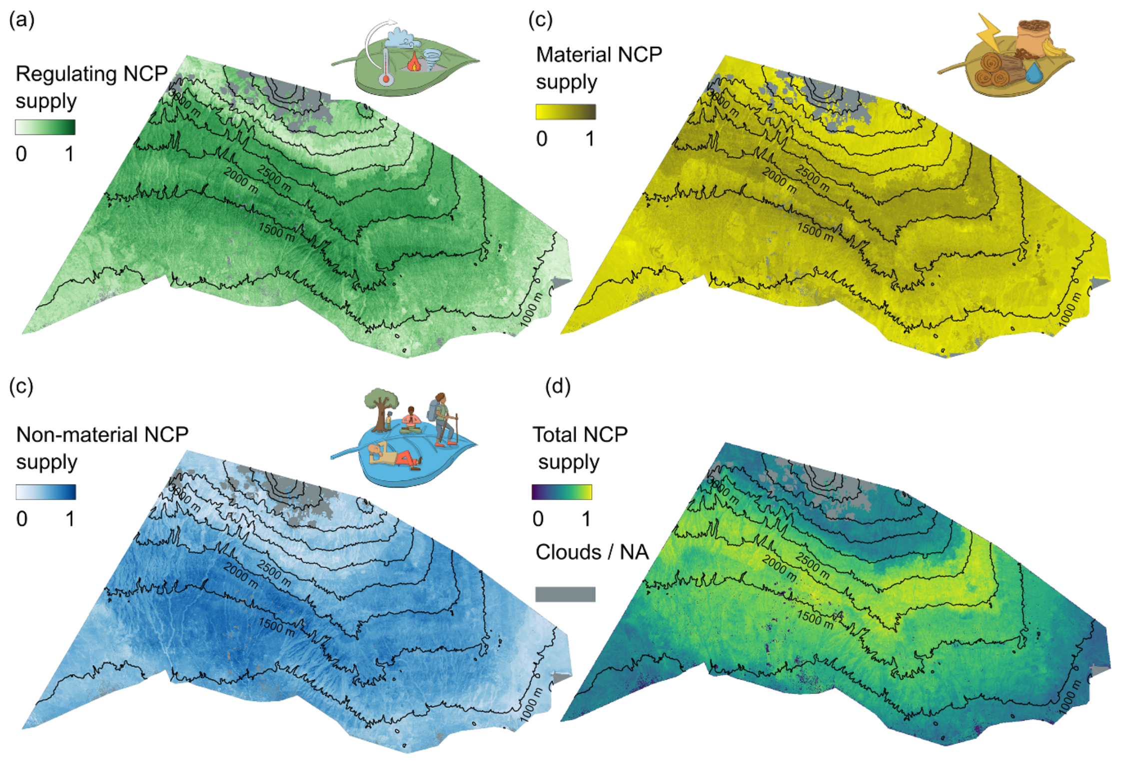

Figure 4. Spatial distribution of nature's contributions to people (NCP) supply across the southern slopes of Kilimanjaro: (a) material, (b) non-material, (c) regulating, and (d) total NCP. Design credit for icons - Jelke Meyer.

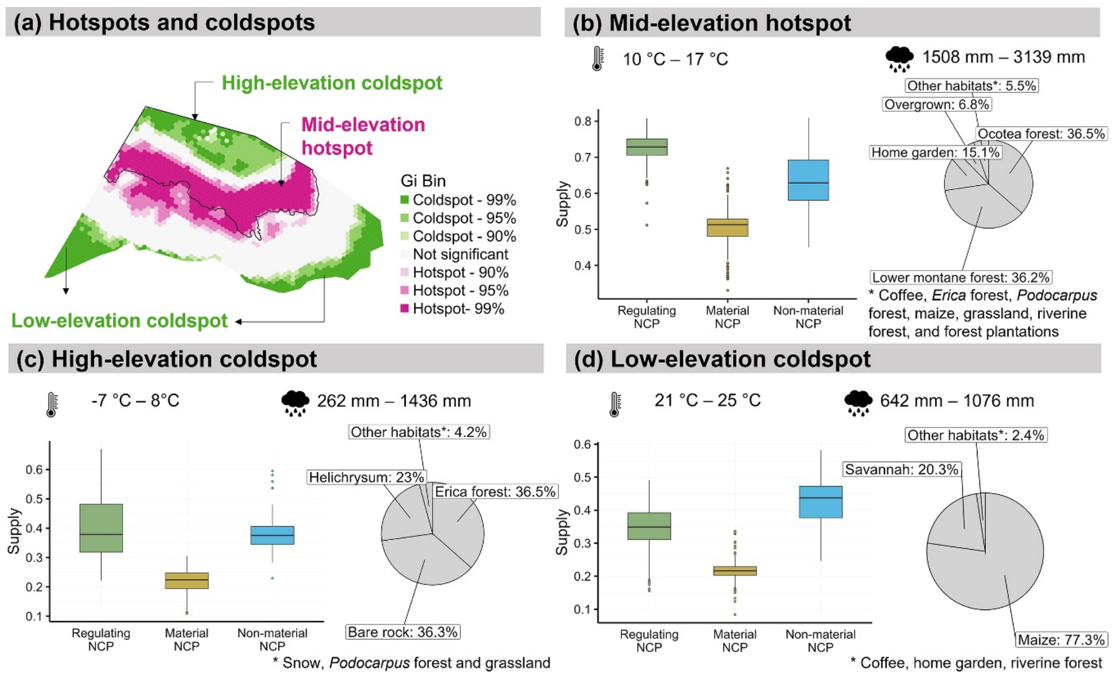

Figure 5. Spatial hotspot and coldspot for the total supply of nature's contributions to people (NCP) across our study area. (a) Spatial distribution of Getis–Ord Gi* *z*-scores (confidence values of 90%, 95% and 99%) for total NCP supply across the Kilimanjaro landscape, highlighting areas of statistically significant hotspots (red), coldspots (blue), and non-significant clustering (white). Panels (b)–(d) show 99% confidence in high-value (b) and low-value (c) and (d) NCP supply clusters. Inset pie charts depict dominant land-cover proportions. Boxplots show comparative distributions of material, non-material and regulating NCP. The mean annual temperature and precipitation values on top of panels b, c, and d highlight the climatic differences between the identified NCP hotspots and coldspots.

and persistence of the mid-elevation hotspot (personal communication with KINAPA chief officer for ecology).

While previous NCP hotspot studies often focused on formally protected areas, emphasizing biodiversity and recreation (Bagstad *et al* 2017, Móstiga *et al* 2023, Moreira *et al* 2024), our findings demonstrate that tropical mountain ecosystems outside protected zones, such as Kilimanjaro's biodiverse agroforestry systems (Hemp 2006a, 2006b), provide significant NCP. This aligns with the findings of Buschke and Capitani (2025), who reported NCP values three to six times higher outside protected areas, highlighting the crucial, often underrecognized, role of these landscapes in supporting human well-being. In this context, agroforestry systems outside protected areas can complement conservation strategies by functioning as multifunctional buffer zones and ecological corridors that sustain habitat connectivity, carbon storage and other regulating and non-material NCP while supporting agricultural production and rural livelihoods (Garrity *et al* 2010, Mbow *et al* 2014, Sanya *et al* 2025).

Conversely, coldspots (areas of low NCP supply) were located in high elevation zones (figure 4(c)) and the lowland foothills (figure 5(d)). In the high elevation coldspot (figure 5(c)), both regulating and non-material NCP were higher than material NCP and the underlying land cover consisted of *Erica* forest and bushland (36%), *Helichrysum* vegetation (23%), and bare rock (36%). The presence of natural geological features like bare rock, snow, glacial ice and alpine landscapes, emphasizes that geological contributions of nature (also known as 'geoservices', Fox *et al* 2022), should be integrated into NCP assessments (Degano *et al* 2025) as they provide significant non-material benefits not captured by traditional biophysical indicators focused on biological processes. Given that conservation policies have largely focused on biodiversity, recognizing and safeguarding geodiversity and geoservices implies that these apparent biophysical 'coldspots' are better suited for strict geoheritage protection and carefully managed tourism (van Ree *et al* 2024).

The low elevation coldspot similarly consisted of higher supply of non-material NCP followed by regulating and material NCP (figure 5(d)). Maize plantations cover 77% of these areas, with savannah restricted to 20%. Transitional elevation bands show no significant clustering, indicating average supplies across all NCP groups. These low-elevation coldspots dominated by maize monocultures highlight priority areas for restoration, for example through agroforestry enrichment, crop diversification and savannah restoration to enhance regulating and non-material NCP.

The spatial pattern of coldspots highlights important limitations in current NCP assessment approaches. Our findings contrast with Degano *et al* (2025), who, using social media analysis of tourist perceptions, found a 'U' shaped pattern where non-material NCP, like a sense of achievement from unique experiences, were strongly perceived at both high and low elevations. For high elevations, the mismatch between low biophysical supply indicators and high perceived benefits can be explained by the dominance of geoservices over biophysical NCP. Tourists derive significant non-material benefits from abiotic factors like glacial ice, volcanic rock formations, and sunrises at summit of Kilimanjaro, which our indicators do not capture.

At low elevations coldspot, biophysical supply is low, yet Degano *et al* (2025) report high perceived non-material benefits from cultural tourism. However, this reflects the experiences of a specific social group (tourists) rather than local communities. As previously discussed, farmers perceived non-material NCP supply differently (Sanya *et al* 2025) with higher values in lower regions compared to tourist preferences for higher elevations. This suggests that perceived NCP supply varies significantly across different social actors and land-use contexts, emphasizing the need for more inclusive NCP assessment approaches that consider diverse perspectives and the full spectrum of nature's contributions, including both biological and geological services.

3.3. Synergies and trade-offs between NCP

The analysis of synergies and trade-offs among NCP supply revealed clear patterns of association both within and across NCP categories (figures 6(a) and (b)). Overall, positive correlations dominated between NCP groups, showing moderate to strong relationships across the landscape. The highest correlation was observed between regulating and material NCP ($r = 0.83$), followed by regulating and non-material NCP ($r = 0.56$), and material and non-material NCP ($r = 0.55$). Pairwise analysis of individual NCP categories largely showed positive associations among regulating, material, and non-material NCP (figure 6(b)).

Within regulating NCP, strong synergies ($r = 0.5-0.7$) were found for habitat creation, seed dispersal, air quality regulation, hazard/extreme event regulation, and regulation of detrimental species. Conversely, pollination and freshwater quality regulation showed strong trade-offs with multiple other contributions ($r = -0.5$ to -0.7). Freshwater quantity and soil fertility regulation showed weak correlations. Within the material NCP, the energy and materials for domestic use NCP showed strong synergies with most NCP. Moderate positive correlations were observed between food and feed NCP.

For non-material NCP, we observed strong to moderate synergies among therapeutic and restorative benefits, connectedness with nature, cultural heritage, and social cohesion and bonding. In contrast,

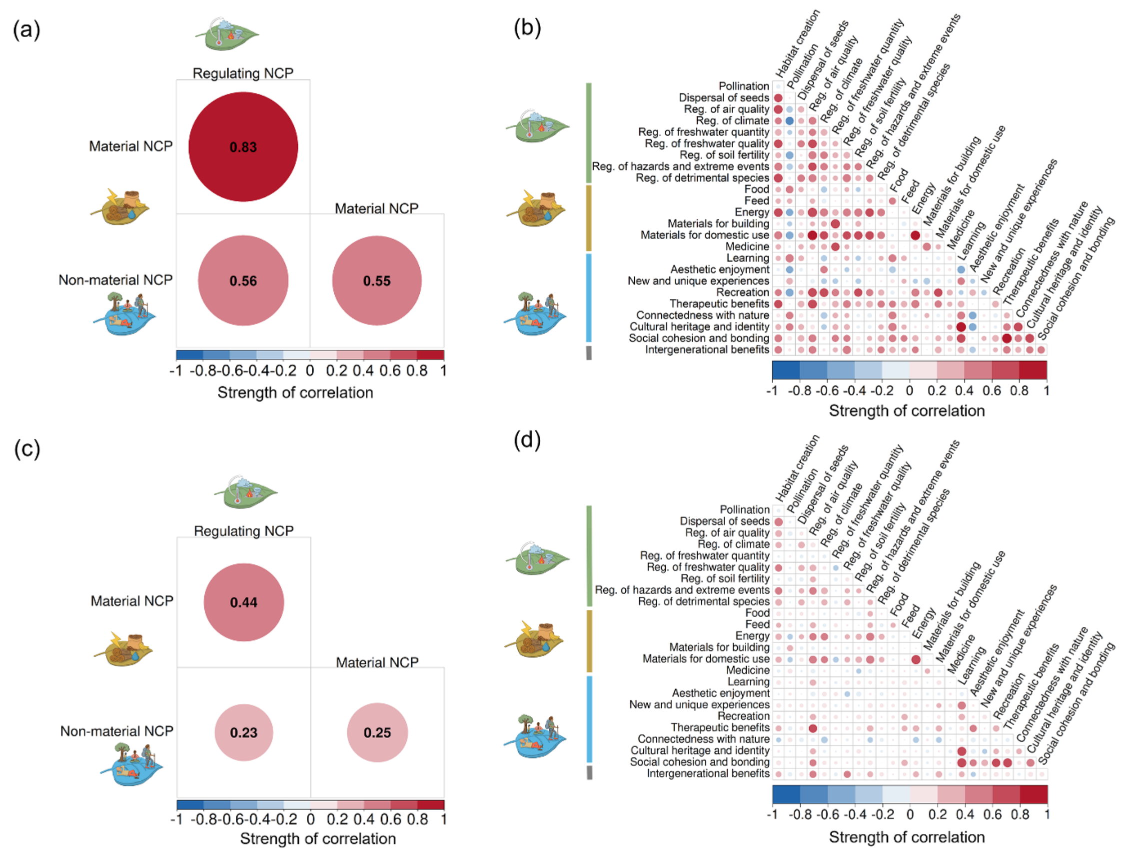

Figure 6. Synergies and trade-offs between nature's contributions to people (NCP) supply. Panel (a) shows the synergies and trade-offs between aggregated supply of the three NCP groups: material, non-material and regulating supply with their respective coefficient of correlation represented by the circles. Panel (b) shows the pairwise correlation strength and direction of NCP categories. Panel (c) and panel (d) indicate the synergies and trade-offs calculated from the residuals of the supply of NCP when controlled for climate. Design credit for icons - Jelke Meyer.

aesthetic enjoyment and new and unique experiences generally showed weak to moderate negative correlations with other non-material NCP, while learning was positively correlated (moderate to strong).

The predominantly positive correlations among multiple NCP categories and groups suggest that current management practices in the Kilimanjaro landscape are largely effective at simultaneously supplying multiple NCP, presenting significant win-win opportunities. For example, the strong synergies between regulating and material NCP in tree-rich agroforestry and homegarden systems suggest that these areas are priority zones for sustainable intensification, where food and energy production can be increased without sacrificing climate and habitat regulation (Hemp 2006b). Conversely, trade-offs involving pollination and freshwater quality regulation imply that further expansion of high-input monocultures and encroachment into riparian areas should be avoided, and that maintaining semi-natural habitats, riparian buffers and diversified cropping is critical to safeguard these regulating NCP. Additionally, it is critical to recognize that our study assessed potential NCP supply rather than actual utilization; realizing the supply of certain material NCP such as building materials would inevitably create further trade-offs, highlighting the need for careful governance and planning to sustainably balance NCP supply and demand (Neyret *et al* 2024). Specifically, we suggest overlaying NCP supply maps with information on population distribution, land tenure and accessibility (e.g. roads, markets, water points) to identify where high NCP supply coincides with high local dependence or limited access, thereby guiding priority areas for conservation, restoration and equitable management of trade-offs.

3.4. Controlling for climate

The NCP hotspots and coldspots identified above were strongly associated with climatic gradients, characterized by high rainfall and distinct temperature regimes. To assess the extent to which these associations were driven by climate, we statistically controlled for climatic effects allowing us to isolate other influential drivers, such as land-use intensity, topographic heterogeneity, landscape configuration, and management regimes, which operate independently of climate. Changes in land-use intensity, for instance, have been identified as key drivers influencing biodiversity and consequently NCP supply in the lowlands of Kilimanjaro (Peters *et al* 2019, Hemp *et al* 2025). After controlling for climate, the previously moderate-to-strong synergies observed among NCP groups (figure 6(c)) and most NCP categories (figure 6(d)) weakened but remained generally positive. Notably, certain non-material NCP categories, including recreation, learning, social cohesion, and bonding, retained strong correlations within the non-material group, indicating that multiple non-material NCP are jointly supplied within climatic belts. Additionally, controlling for climate substantially reduced the strength of multiple negative correlations (figures 6(c) and (d)). For example, trade-offs between other NCP and pollination were weaker and even non-significant, suggesting that climate primarily drove their perceived negative interaction, rather than an intrinsic ecological conflict between the NCP themselves.

3.5. Limitations and further directions

Our study on NCP supply in the Kilimanjaro region, while comprehensive, faced several limitations. First, we were unable to fully assess temporal dynamics of NCP supply because the underlying datasets were not temporally aligned. Field measurements, social data, remote-sensing products, and climatic layers were collected over different years and time periods, but were combined into a single cross-sectional representation of 'current' NCP supply. This temporal mismatch means that short-term changes in land use, management, or climate are not explicitly captured, and we implicitly assume that ecosystem conditions remained relatively stable over the period of data acquisition. Second, mapping hazard regulation NCP was constrained by a lack of high-resolution, process-based indicators. As a result, some hazard-related NCP were represented by relatively coarse measures, which may not fully reflect fine-scale spatial patterns of regulation. Third, our use of machine learning models, while powerful for handling large, heterogeneous datasets, inherently lacks explicit causal interpretation. We mitigated this by preselecting predictors based on ecological knowledge, aligning our findings with established theory. Future improvements in model performance could benefit from additional field data or ensemble modeling to better capture these spatial dependencies. Finally, although we quantified uncertainties for individual NCP indicators, we did not implement a systematic framework to propagate these uncertainties through subsequent aggregation steps. In the context of NCP, such a framework would track uncertainty from indicators to NCP categories and further to total NCP supply and hotspot/coldspot classifications by (i) assigning an uncertainty distribution to each indicator (e.g. from measurement error, sampling variance, or prediction intervals), and (ii) propagating these distributions through the rescaling and aggregation rules to obtain probability distributions for total NCP supply and hotspot status at each location. This would enable mapping not only expected NCP supply but also confidence intervals and the probability that a given area is a hotspot or coldspot, making the robustness of spatial patterns more explicit for decision-making. Developing and applying such uncertainty propagation frameworks across the hierarchical structure of NCP indicators and categories is an important direction for future work.

4. Conclusions

Our study provides one of the first comprehensive, high-resolution maps of NCP supply across Mount Kilimanjaro's diverse, tropical mountain ecosystem. These spatially explicit maps offer a crucial foundation for future ecological and socio-ecological research. We urge further investigation into non-climatic drivers of NCP supply, integrating land-use dynamics and governance shifts to project future changes. Our findings also highlight spatial mismatches between NCP supply and demand, with implications for all social actors including local communities. This adaptable approach can inform targeted conservation and planning in other regions globally.

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Data availability statement

The maps, code and data that support this finding are openly available at https://doi.org/10.5281/zenodo.17869262.

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Conflict of interest

The authors declare no conflict of interest.

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Author contributions

Netra Bhandari 0000-0002-1996-0752
Conceptualization (equal), Data curation (lead), Formal analysis (lead), Investigation (lead), Methodology (equal), Resources (equal), Software (equal), Validation (equal), Visualization (lead), Writing – original draft (lead), Writing – review & editing (lead)

Neema Robert Kinabo 0000-0002-5062-3172
Data curation (supporting), Formal analysis (supporting), Investigation (supporting), Methodology (supporting), Resources (supporting), Validation (supporting), Writing – original draft (supporting), Writing – review & editing (supporting)

Dominic Andreas Martin 0000-0001-7197-2278
Conceptualization (lead), Data curation (supporting), Formal analysis (supporting), Methodology (supporting), Software (supporting), Supervision (supporting), Validation (supporting), Visualization (equal), Writing – original draft (supporting), Writing – review & editing (supporting)

Andrea Larissa Boesing 0000-0002-7467-4281
Conceptualization (supporting), Formal analysis (supporting), Methodology (supporting), Software (supporting), Supervision (supporting), Validation (supporting), Visualization (supporting), Writing – review & editing (supporting)

Margot Neyret 0000-0001-9435-1634
Conceptualization (supporting), Writing – review & editing (supporting)

Gaëlle Bocksberger 0000-0002-3399-0405
Data curation (supporting), Writing – review & editing (supporting)

Jörg Albrecht 0000-0002-9708-9413
Formal analysis (supporting), Writing – review & editing (supporting)

Tim Appelhans 0000-0002-9824-2707
Formal analysis (supporting), Funding acquisition (supporting), Investigation (supporting), Resources (supporting)

Ugo Arbieu 0000-0002-0655-8756
Funding acquisition (supporting), Writing – review & editing (supporting)

Joscha N Becker 0000-0002-3210-3632
Formal analysis (supporting), Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Giovanni Bianco 0000-0002-4595-8824
Formal analysis (supporting), Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Robert Modest Byamungu 0000-0001-5011-1970
Funding acquisition (supporting), Writing – review & editing (supporting)

Alice Classen 0000-0002-7813-8806
Formal analysis (supporting), Investigation (supporting), Resources (supporting)

M Eugenia Degano 0009-0009-9748-8586
Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Friederike Gebert 0000-0001-7433-8336
Formal analysis (supporting), Investigation (supporting), Resources (supporting)

Milena Gross 0000-0003-3148-627X
Data curation (supporting), Writing – review & editing (supporting)

Claudia Hemp 0000-0001-9170-7113
Funding acquisition (supporting), Investigation (supporting), Project administration (supporting), Resources (supporting)

Victoria Junquera 0000-0003-0402-3659
Methodology (supporting), Writing – review & editing (supporting)

Ralf Kiese 0000-0002-2814-4888
Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Koggani D Koggani
Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Armin Komposch 0009-0004-2184-4330
Investigation (supporting), Writing – review & editing (supporting)

Yakov Kuzyakov
Investigation (supporting), Writing – review & editing (supporting)

Dickson Gerald Mauki 0000-0001-7765-0026
Formal analysis (supporting), Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Antonia V Mayr 0000-0001-6581-7490
Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Thomas Müller 0000-0001-9305-7716
Funding acquisition (supporting), Project administration (supporting), Writing – review & editing (supporting)

Henry K Njovu 0000-0002-7240-3058
Data curation (supporting), Resources (supporting), Validation (supporting), Writing – review & editing (supporting)

Insa Otte 0000-0001-9704-9668
Formal analysis (supporting), Funding acquisition (supporting), Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Jasmine Pearson 0000-0001-6341-1382
Writing – review & editing (supporting)

Marcell K Peters 0000-0002-1262-0827
Formal analysis (supporting), Investigation (supporting), Writing – review & editing (supporting)

John Sanya 0000-0002-2986-9813
Writing – review & editing (supporting)

Matthias Schleuning 0000-0001-9426-045X
Data curation (supporting), Funding acquisition (supporting), Project administration (supporting), Supervision (supporting), Writing – review & editing (supporting)

Ingolf Steffan-Dewenter 0000-0003-1359-3944
Formal analysis (supporting), Funding acquisition (supporting), Project administration (supporting), Resources (supporting)

Maximilian G R Vollstaedt 0000-0001-6209-5955
Formal analysis (supporting), Investigation (supporting), Resources (supporting), Writing – review & editing (supporting)

Jie Zhang
Data curation (supporting), Formal analysis (supporting), Investigation (supporting), Resources (supporting)

Katrin Böhning-Gaese 0000-0003-0477-5586
Conceptualization (supporting), Funding acquisition (lead), Project administration (lead), Writing – review & editing (supporting)

Markus Fischer
Conceptualization (supporting), Funding acquisition (lead), Project administration (lead)

Andreas Hemp 0000-0002-5369-2122
Conceptualization (supporting), Funding acquisition (supporting), Project administration (lead), Supervision (supporting), Validation (supporting), Writing – review & editing (supporting)

Peter Manning 0000-0002-7940-2023
Conceptualization (supporting), Funding acquisition (supporting), Investigation (supporting), Methodology (supporting), Project administration (supporting), Supervision (supporting), Validation (supporting), Writing – review & editing (supporting)

Dirk Zeuss 0000-0001-6457-2866
Conceptualization (equal), Funding acquisition (supporting), Methodology (equal), Project administration (lead), Software (supporting), Supervision (lead), Validation (supporting), Writing – review & editing (supporting)

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