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Are there enough native tree seed sources to meet forest restoration targets? A spatially explicit assessment in tropical Asia

Riina Jalonen [a,*], Tobias Fremout [b], Rekha R. Warrier [c], Vivi Yuskianti [d], Enrique Tolentino Jr. [e], Cristino Tiburan Jr. [e], Md. Zahidur Rahman Miah [f], Md. Tauhidor Rahaman [g], Peter Wilkie [h], Dede J. Sudrajat [1], Denny [j], Christopher J. Kettle [b]

[a] Bioversity International, c/o WorldFish Headquarters, Jalan Batu Maung, 11960, Bayan Lepas, Penang, Malaysia
[b] Bioversity International, Via di San Domenico 1, 00153, Rome, Italy
[c] ICFRE-Institute of Forest Genetics and Tree Breeding, Indian Council of Forestry Research and Education, 22A, Cowley Brown Road, RS Puram, Coimbatore, Tamil Nadu, 641003, India
[d] National Research and Innovation Agency (BRIN), Research Center for Biota Systems, Jalan Raya Jakarta-Bogor Km 46, Cibinong, Bogor, West Java, 16911, Indonesia
[e] College of Forestry and Natural Resources, University of the Philippines Los Baños, Laguna, 4031, Philippines
[f] Forest Department, Jhum Control Forest Division, Rangamati, 4500, Bangladesh
[g] Forest Department, RIMS Unit, 3rd floor, Bana Bhaban, Plot No- E-8, B-2 Agargaon, Sher-e-Bangla Nagar, Dhaka, 1207, Bangladesh
[h] Royal Botanic Garden Edinburgh, 20A Inverleith Row, Edinburgh, UK
[i] Research Center for Applied Botany, Jl. Raya Jakarta-Bogor Km 46 Cibinong, Bogor, West Java, 16911, Indonesia
[j] Research Center for Ecology, Jl. Raya Jakarta-Bogor Km 46 Cibinong, Bogor, West Java, 16911, Indonesia

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ABSTRACT

Despite growing global investments in ecosystem restoration, seed supply for native tree species remains a major bottleneck, particularly in the Global South where species diversity is high and natural seed sources dwindling due to land use change. This slows down restoration efforts and reduces their biodiversity, climate and socio-economic benefits. We present a spatially explicit methodology for assessing the availability of site-adapted tree seed for restoration, which combines environmental clustering to define seed zones, MaxEnt species distribution models for restoration target species, and data on existing tree seed sources. Species-specific seed source gaps are identified as those zones within species' distribution ranges without any seed sources. Application of the method to 21 native pilot species in Bangladesh, India, Indonesia, and the Philippines revealed that, on average, only 34% of seed zones had designated seed sources, despite the species being widely used in restoration. An analysis of community-managed forests in Mindanao, the Philippines, showed that such forests can potentially fill the identified gaps in seed source availability, but challenges remain in registering and supporting community-managed forests as seed sources. Ninety-seven percent of the seed sources were predicted to remain within the species' suitable habitat under future climates, but the availability of sources in specific seed zones can reduce with climate change projected to shift the seed zone boundaries. The gap analysis methodology enables countries to strategically identify priority areas for seed source development. By addressing critical seed supply constraints, this approach strengthens national capacity to deliver effective, inclusive, and climate-resilient restoration at scale.

1. Introduction

The availability of appropriate tree seeds has emerged as a critical bottleneck (Broadhurst et al., 2016; Jalonen et al., 2018; Höhl et al., 2020) that limits the scale and success of ecosystem restoration as a nature-based solution to the global crises of persistent poverty, environmental degradation, and climate change (Shimamoto et al., 2018; Brancalion et al., 2022; Tuinenburg et al., 2022; Nabuurs et al., 2022). Meeting the national restoration targets has been estimated to require between 3600 and 15,600 metric tons of native tree seed in Brazil

* Corresponding author at: Bioversity International, c/o WorldFish Headquarters, Jalan Batu Maung, 11960, Bayan Lepas, Penang, Malaysia.
E-mail address: R.jalonen@cgiar.org (R. Jalonen).

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(Urzedo et al., 2020); over 150 billion tree seeds and seedlings in India, Indonesia, Malaysia, and the Philippines combined (Bosshard et al., 2021); and anywhere between 2 and 17 trillion seeds of plants globally (Chau et al., 2022). However, seed production systems are reported to exist for less than 2% of the world's known 58,000 tree species, mainly commercially important species (FAO, 2025). Although restoration has been in the global spotlight since the launch of the Bonn challenge in 2011, coordinated investments in building up native seed supply are still lacking, especially across the Global South (Atkinson et al., 2021; Bosshard et al., 2021; Giacomini et al., 2023). This has tangible impacts on restoration delivery and outcomes: in a global survey, over 40% of restoration practitioners reported that they often face delays and cost increases and end up using fewer or different tree species than planned, because suitable seeds and seedlings are not available when needed (Jalonen et al., 2018). Currently, restoration efforts often result in ecosystems that resemble degraded rather than healthy natural ecosystems, in terms of key indicators of population health and ecosystem functionality (Wei et al., 2023).

The challenges of seed availability are particularly acute in human-dominated landscapes in the Global South. Quality seeds of locally preferred and suitably adapted species are crucial for restoring productive and socio-ecologically resilient landscapes that help address the underlying reasons of degradation, including multi-dimensional poverty (Höhl et al., 2020; Erbaugh et al., 2020). At the same time, decades of deforestation, habitat fragmentation, and unsustainable harvesting of forest products have wiped out many natural seed sources in these landscapes (Gaisberger et al., 2021) and limited reproductive processes (Saavedra et al., 2015; Rocha-Santos et al., 2020), constraining restoration opportunities. Climate change adds to the complexity of finding suitable species and predicting seed availability, as it shifts species ranges (Prober et al., 2015; Manchego et al., 2017; Newbold et al., 2020) and alters flowering and fruiting phenology (Numata et al., 2022; Sullivan et al., 2023).

A promising approach to address seed shortages while ensuring that the benefits of restoration are shared more equitably is to engage indigenous peoples and local communities in tree seed collection, seedling production, and distribution (Urzedo et al., 2022). At least 36% of the world's remaining intact forest landscapes fall within indigenous people's lands (Fa et al., 2020), giving these communities access to high species diversity and genetically diverse populations that produce quality seed, adding value to restoration projects through better survival and growth (Broadhurst et al., 2006; Nutt et al., 2016; Morais et al., 2019). In Brazil alone, fulfilling the national restoration targets is estimated to generate income opportunities of at least US$34 million annually to 13,000 seed collectors in community networks (Urzedo et al., 2020). Seed sources also act as crucial genetic reserves supporting productivity and adaptation (Gaisberger et al., 2021), and mapping, conserving, and monitoring them contributes to the conservation of genetic diversity of wild species, as stipulated in the Kunming-Montreal Global Biodiversity Framework (Convention on Biological Diversity, 2022).

Currently, it is difficult for individual restoration projects to achieve optimal seed sourcing that combines genetic diversity, site suitability and adaptability, because most countries lack sector-wide planning tools, such as registries of seed sources and seed and seedling suppliers (León-Lobos et al., 2020; Jalonen et al., 2023), and seed zones to guide seed transfer (i.e. zones with sufficiently uniform ecological conditions where seed sources show similar phenotypic or genetic characteristics, and in which seeds can be moved around with minimal risk of maladaptation; also called seed transfer zones or regions of provenance; Hufford and Mazer, 2003; OECD, 2024). Addressing these gaps requires targeted investments to build national information systems on tree seed availability, and simple yet robust seed availability indicators to guide decision-making and identify priority interventions. Spatially explicit assessment methods are particularly needed, as they allow evaluating the availability of suitably adapted seed for different environmental contexts (St. Clair et al., 2022) and identifying opportunities to link local seed producers with restoration projects operating in the same seed zones (Lillesø et al., 2018). In Europe, countries collaborate to maintain thousands of genetic conservation units, many of which are also used as seed sources, for over 100 tree species across the continent, and monitor their availability by environmental zones (Lefèvre et al., 2013). Existing seed availability assessments for ecosystem restoration in the Global South (Urzedo et al., 2020; Bosshard et al., 2021; Chau et al., 2022) are country-level, offering invaluable information of the overall gaps but lacking the detail required to develop and operationalize holistic landscape management strategies to address the gaps in the availability of site-adapted tree seed.

The objective of this paper is to test and demonstrate a spatially explicit methodology for assessing the availability of tree seed sources and prioritizing interventions to enable effective forest restoration as a nature-based solution in diverse land use contexts. The proposed methodology establishes a foundation for planning native tree seed supply beyond individual restoration projects, by improving sectoral capacities to evaluate, coordinate and strengthen seed and seedling availability for diverse restoration objectives in a changing environment. Our specific research questions are (1) To what extent are suitably adapted tree seed sources available for restoring resilient tropical forests and landscapes in tropical Asia, under current and changing climates? (2) What role can coordination and collaboration e.g. between land users and jurisdictions play in addressing gaps in native tree seed availability? (3) Is the proposed methodology applicable across diverse ecological and socio-political contexts and does it yield comparable and actionable results? We use ‘seed’ as a generic term to refer to any type of forest reproductive material, including seed, seedlings, and vegetatively propagated material (OECD, 2024). ‘Seed source’ refers here to the area where ‘seed’ originates from and can be either naturally generated or planted. We hypothesize that seed availability gaps are common even for species widely used in restoration efforts. We demonstrate the gap analysis methodology by applying it to 21 native restoration priority species in four South and Southeast Asian countries, Bangladesh, India, Indonesia, and the Philippines, the combined restoration targets of which exceed 47 million hectares. We conclude with a set of technical and policy recommendations for improving tree seed supply as a precondition for the sustainability and effectiveness of restoration projects.

2. Materials and methods

2.1. Overview of the proposed methodology

The proposed methodology to assess gaps in the availability of tree seed sources consists of dividing a country (or part of a country) in generalized seed zones, based on environmental variation (climate and soil variables) and climate change scenarios (Fremout et al., 2021), and comparing those with the modelled distributions of target species and existing seed sources (the details are described in the following sections). In this way, the methodology allows identifying zones that lack any designated seed sources (i.e. the seed source gaps) to enable effective restoration (Fig. 1). It can also identify potential areas for additional seed sources such as community forests, national parks or protected area buffer zones, each requiring different governance mechanisms and implementation strategies to fill in seed source gaps. While seed zones are often developed separately for individual species to reflect patterns of local adaptation, in this study they are used as generalized ecological management units. This multi-species seed zone framework enables comparison of seed source availability across species and provides a practical tool for sector-wide planning in contexts where species-specific seed zones are not yet available or are difficult to operationalize due to high species diversity or capacity constraints (Hufford and Mazer, 2003; Boshier et al., 2015).

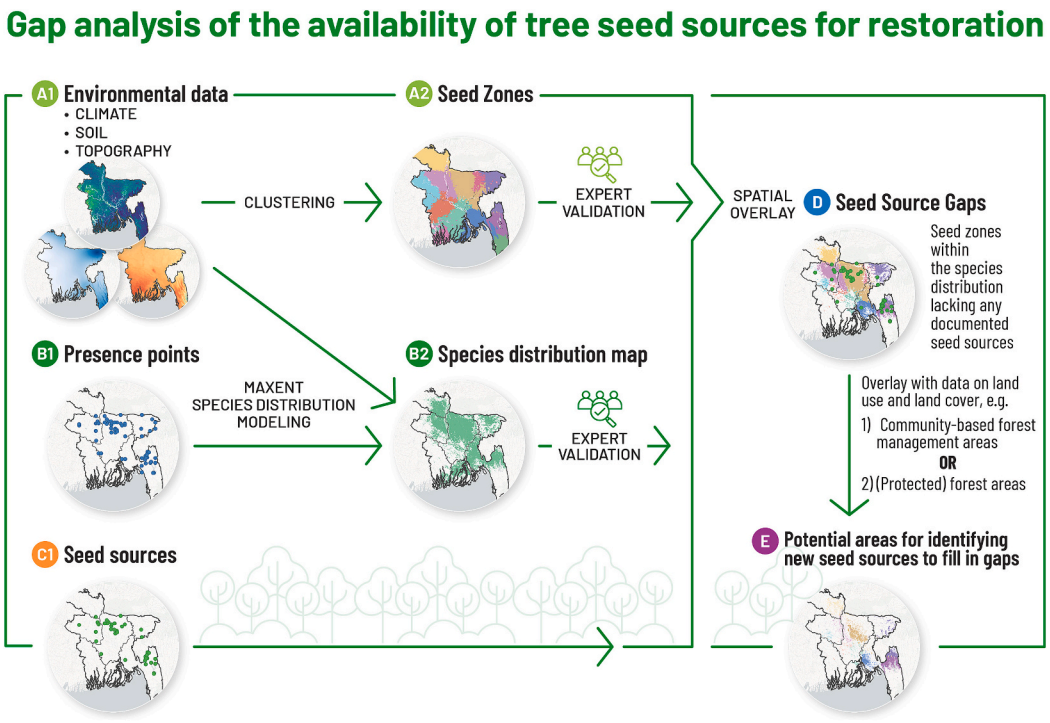

Fig. 1. Overview of the methodology to assess gaps in the availability of tree seed sources. See text for details on methodology (Sections 2.4–2.6) and data sources (Appendix A).

2.2. *Context of tree seed systems in the study countries*

The study countries, India, Bangladesh, Indonesia, and the Philippines, represent a range of environmental, social, and political contexts that affect the demand and supply of tree seed for restoration. The countries have combined land restoration targets exceeding 47 million hectares (Table 1) and a vast rural population of, in total, nearly 1.2 billion. Our analysis was country-wide in Bangladesh, for the four southernmost states in India (Andhra Pradesh, Kerala, Karnataka, and Tamil Nadu), the island of Java in Indonesia, and the island of Mindanao in the Philippines, reflecting the local partnerships required to access official data on tree seed sources. Bangladesh and Mindanao are dominated by humid evergreen tropical forests, while South India and Java experience stronger rainfall seasonality and include large areas of semi-evergreen, moist and dry deciduous forests. The study areas in Bangladesh (148,460 km^2), Java (138,793 km^2), and Mindanao (97,530 km^2) were of similar extent, while the study area in India (523,671 km^2) was larger than the other countries combined.

Table 1
Overview of governance mechanisms related to tree seed supply for restoration in the study countries, based on literature and document review and authors' expert knowledge (see Section 2.2 for details).

	Bangladesh	India	Indonesia	Philippines
National land restoration target[a]	0.75 Mha	26 Mha	14 Mha	7.1 Mha
Regulations mandating restoration	–	Yes	Yes	Yes
Participatory forest management mechanisms	Yes	Yes	Yes	Yes
Regulations on tree seed quality and origin for restoration	–	–	Yes	Yes
Defined seed zones	–	–	(Yes)[b]	–
Mechanisms to register seed sources on private land	–	–	Yes	Yes
Government restoration programmes engaging community organizations in seed or seedling supply	–	–	Yes	Yes

[a] Combined from National Forestry Policies, Nationally Determined Contributions, Land Degradation Neutrality targets. The targets are for 2030, except for in the Philippines where it is set to 2028. Source: FAO (2024).

[b] Seed zone map exists but resembles a forest type map (Ministry of Forestry, 2012).

Main governance mechanisms related to land restoration, tree seed systems (the institutional frameworks and processes involved in supplying appropriate seed for tree planting and restoration), and local community participation in seed supply are summarized in Table 1. All four countries have formal mechanisms allowing community participation in forest management (e.g., community forestry, Joint Forest Management, and Social Forestry schemes), granting communities access to natural seed sources, although implementation success varies (Bhattacharya et al., 2010; Nath et al., 2016; Pulhin et al., 2024; Rakatama and Pandit, 2020). Regulatory frameworks linking restoration programmes to tree seed sourcing differ across countries and are generally more advanced in Indonesia and the Philippines than in Bangladesh and India. All countries except Bangladesh have legally binding regulations mandating restoration or rehabilitation when economic activities such as mining or infrastructure development result in deforestation [e.g., the National Compensatory Afforestation Fund (2016) of India, Forestry Act No. 41 (1999) of Indonesia, and the Philippine Mining Act (1995)], which helps create stable demand for tree seed. Indonesia and the Philippines also have established mechanisms through which local communities provide seeds or seedlings to public restoration programmes (Bosshard et al., 2021; Gregorio et al., 2016; Valette et al., 2020).

Despite these governance mechanisms, tree seed systems remain relatively weak compared to the scale of national restoration ambitions. A comparative study of tree seed systems in India, Indonesia, and the Philippines revealed a mismatch between the demand and supply of native species, a lack of quality assurance mechanisms, and a lack of capacities to consider the impacts of climate change in restoration design (Bosshard et al., 2021). As of 2025, three of the four countries –

Bangladesh, India and the Philippines – had not established seed zones to guide seed transfer. In Indonesia, the Forestry Administration has issued a seed zone map (Indonesian: *Peta Zona Benih*; Ministry of Forestry, 2012) for national use since 2012. However, it is based on broad forest ecosystem types, some of which extend over a thousand kilometers, and is not easily understood or accessible, providing only limited practical guidance on seed transfer to ensure local adaptation.

Forestry departments in all four countries have identified and established tree seed sources or seed stands on government land, but without seed zones, the availability of suitable seed sources for diverse environmental conditions cannot be systematically assessed. In Indonesia, key requirements for seed source certification include a minimum of 25 mother trees with good phenotypes, healthy trees, and easy access to the site (National Standardization Agency, 2020). As of 2025, it is mandatory to use seed from certified seed sources when planting 11 species groups (Ministry of Forestry, 2013; Ministry of Environment and Forestry, 2017), and not all species, due to the limited availability of certified seed sources. The certified seed source database is managed nationally by the Directorate of Greening and Forest Tree Seeds, Ministry of Forestry, however, it is not fully accessible to the public and the system is still partly paper-based (Directorate of Forest Tree Seeds, 2022). In the Philippines, government restoration programmes are required to only use quality seedlings from accredited suppliers, but reliable seed source maps for native tree species are lacking. Both Indonesia and the Philippines have mechanisms to recognize and register seed sources on private land (DENR, 2010; Ministry of Environment and Forestry, 2010, 2020) enabling income generation from maintenance and management of seed source forests. In India and Bangladesh, there are no national quality control mechanisms to record and monitor seed sources, seed origin or quality in forest restoration; in India, several efforts to establish such mechanisms have been made since as early as 1979 but have not received adequate legal backing (Bosshard et al., 2021).

2.3. Species selection

The purpose of the pilot species was to (1) demonstrate the applicability of the proposed methodology to diverse species in different countries and contexts, (2) assess if gaps in seed source availability are common for species widely used in restoration; if yes, this would suggest that gaps were likely common also for other, less widely used species, and (3) illustrate how the results from species-specific analyses can be aggregated to provide an overview of seed source availability for restoration and inform priorities for action. Other than that, the specific identity of the pilot species was not central to the study, and so the criteria for species selection were relatively generic: (i) native species already used or prioritized in restoration projects and programmes; (ii) socio-economic importance, including food or other non-timber forest products and species providing important ecosystem services; (iii) at least some threatened species in each country, including species listed in the Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES); (iv) data availability to perform species distribution modelling (generally at least 30 presence locations representative of the species range, Wisz et al., 2008). Species phenology, seed biology, or propagation methods were not considered during selection, because seed sources are needed for restoration for all species independent of their biological characteristics. Five or six pilot species were selected in each country (in total 21 from an initial list of 44 species). Both initial and final species lists were based on consultations with key partners and agencies: the Bangladesh Forest Department; Bangladesh Forest Research Institute; Institute of Forest Genetics and Tree Breeding, India (which in turn consulted state forest departments); Directorate of Greening and Forest Tree Seeds in the Ministry of Forestry, Indonesia; National Research and Innovation Agency, Indonesia; College of Forestry and Natural Resources, University of the Philippines; and Mindanao Forest Tree Seed Centre, the Philippines. Majority of the initially selected species in Bangladesh and the Philippines had to be changed due to a lack of presence points for species distribution modelling. For Indonesia, the species were selected from the list of the 11 species groups for which sourcing seed from registered seed sources is mandatory (Ministry of Forestry, 2013; Ministry of Environment and Forestry, 2017). Characteristics of the selected pilot species and their use in land restoration are provided in Appendix A, Table A3. The species' conservation status was retrieved from the IUCN Red List of Threatened Species (2025).

2.4. Species distribution modelling

We estimated the distribution of suitable habitat of the selected species using species distribution models (also called habitat suitability models or environmental/ecological niche models) and the maximum entropy (MaxEnt) algorithm (Phillips and Dudík, 2008). Often used interchangeably with habitat suitability models and environmental/ecological niche models, we opted for the term 'species distribution models', as this study focuses on the spatial distribution of the species and its overlay with the seed zone maps and seed source locations, rather than on species-environment relationships. MaxEnt is one of the most commonly used and performant algorithms, performing similarly well as ensemble models or even better, especially if the ensembles consist of non-tuned models (Kaky et al., 2020; Valavi et al., 2022, 2023).

Presence locations used for estimating the distribution ranges of the selected species were sourced from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and other published and unpublished sources available at the co-authors' organizations (national research institutions, forestry departments and academia, see Appendix A for details on presence locations and background points). Unpublished presence locations were used because they came from authoritative sources and helped to improve the models, through more and better distributed presence points available as input.

We selected 25 climatic, edaphic and terrain variables as possible predictors for modelling, consisting of 11 (out of a total of 19) bioclimatic variables of the WorldClim v2 database (Fick and Hijmans, 2017), 9 continuous soil variables from the SoilGrids v1 database (Hengl et al., 2017; rather than the v2 database because the latter had many gaps in some of the target regions), and 5 terrain variables based on the MERIT digital elevation model (Hengl, 2018), all at a resolution of 30 arcsec (ca. 0.9 km at the equator) (for details on the methodology and data sources, see Appendix A and Table A.1). No further variable selection was carried out, as MaxEnt models can handle multicollinearity (Feng et al., 2019). To project the distribution models to future (years 2041–2060), we used the same bioclimatic variables as predicted by five general circulation models (GCMs): ACCESS-CM2, GISS-E2–1-G, INM-CM5–0, MIROC6 and MPI-ESM1–2-HR, under the emission scenarios SSP2.45 and SSP3.70 (i.e. an intermediate and a more pessimistic scenario), also at a resolution of 30 arcsec. These five GCMs were chosen based on their performance to predict current climatic conditions and their independence (as different GCMs are often not independent from each other due to shared code), following Brunner et al. (2020), subject to availability in the WorldClim database.

To avoid overfitting and to ensure transferability of the MaxEnt distribution models, we used the ENMeval package (Muscarella et al., 2014; Kass et al., 2021) to adjust model complexity. The ENMeval package allows tuning of the two hyperparameters of MaxEnt models: the feature classes used and the value of the regularization multiplier. We tested the 'LQ', 'H', 'LQH' and 'LQHP' combinations of feature classes (L: linear features, Q: quadratic features, H: hinge features, P: product features) and values of 1,3 and 5 of the regularization multiplier (i.e. twelve combinations of parameter settings were tested for each species). Models with only linear features or models including threshold ('T') features were not included as they were not deemed ecologically realistic. Threshold features (i.e. an abrupt change in suitability above or under a threshold value of an environmental variable) are not used by

default anymore in Maxent, both in the Java-based software as in the R package maxnet, as hinge ('H') features seem to be more effective in modelling similar responses (Phillips et al., 2017).

To select the most suitable hyperparameter settings, the MaxEnt models were cross-validated using spatial blocks, using the blockCV package for R (Valavi et al., 2019), as randomly partitioning data into training and testing data is inappropriate for spatial data (Roberts et al., 2017). Dividing the data into training and testing data using spatial blocks allows testing the models in regions where no training data were used, avoiding inflated model accuracy estimates and optimizing model transferability, which is crucial when projecting species distributions to future climates (Wenger and Olden, 2012; Muscarella et al., 2014). Presence and background points were partitioned using 8 folds, each fold consisting of one or more 100 km-wide squared blocks. This means that each of the models was run eight times during cross-validation, each time setting apart one of the eight folds for testing.

For each species, the cross-validation procedure was used to evaluate the hyperparameter settings based on tendency to overfitting and predictive accuracy. First, the four models with the highest Area Under the receiver operating characteristic Curve (AUC) value were selected. Among these, we then selected the model where the difference between the AUC of the training data and the AUC of the testing data (AUC_{diff}, a measure for overfitting, see for example Low et al., 2021) was smallest. This model was then used to predict habitat suitability, which was converted to presence-absence using a threshold corresponding to 10% omission of presence points. The distribution models were also projected to future climatic conditions using the GCMs and emission scenarios mentioned above. The average importance of the environmental variables in predicting the distributions of the species in the study regions are shown in Appendix A, Table A.2.

We found that the models had difficulties in estimating habitat suitability in mangrove and swamp forests (none of the selected species were mangrove or swamp forest species), presumably because of limitations of the SoilGrids data (Hengl et al., 2017), and/or a lack of a layer expressing water table depth. We therefore used the Dinerstein et al. (2017)'s ecoregions map to remove mangrove areas from the predicted distributions. In Java, we similarly removed mangrove and swamp forests using the abovementioned forest type map of the Indonesian government (Ministry of Forestry, 2012).

2.5. Seed zones

To guide seed sourcing decisions in the target countries and to assess seed source gaps (i.e. seed zones without identified seed sources), we constructed seed zones following the methodology proposed by Fremout et al. (2021). This method, further detailed in the next paragraph, was applied to the entire target region in case of Bangladesh, India (the four southern states) and the Philippines (Mindanao). In Indonesia (Java), where the government has adopted a forest type map to guide seed sourcing efforts (Ministry of Forestry, 2012), we chose to align our seed zone map with existing government policies by subdividing each of the forest types into one or more seed zones, using the same methodology as outlined below.

We created seed zones with the CLARA (Clustering Large Applications) algorithm, implemented using the 'cluster' package for R (Mächler et al., 2019). This algorithm is an extension for large datasets of the partitioning-around-medoids (PAM) algorithm, a more robust alternative to the k-means algorithm (Kaufman and Rousseeuw, 1990). As input variables, we used the same predictor variables as those used in the distribution modelling, excluding the topographic variables (as these are more local-scale, while local adaptation of tree species is mostly in response to larger scale patterns (Boshier et al., 2015), along with geographical location (i.e. longitude and latitude). Both environmental data and geographical location were included because genetic differentiation between tree species populations is often related to both environmental differences and isolation-by-distance (Orsini et al., 2013; Sexton et al., 2014; Fremout et al., 2021). We first submitted the environmental variables to a principal component analysis to remove multicollinearity, and selected the first n principal components with an eigenvalue higher than one, i.e. the Kaiser criterion (Kaiser, 1960). Longitude and latitude were rescaled to have a variance equal to the average variance of the selected principal components. To determine the number of clusters (i.e. number of seed zones), we used the number of ecoregions (Dinerstein et al., 2017) within the target region as a proxy for the amount of environmental variation (and thereby also a proxy for genetic differentiation of tree species populations) and multiplied this number of ecoregions by three to obtain the number of seed zones, in consultation with experts from the same organizations who participated in the selection of the pilot species (Section 2.2). Significant population differentiation in tree species often occurs at scales finer than broad ecoregion boundaries (Boshier et al., 2015), and similar stratification of ecoregions into multiple seed has been applied in other countries: for example, the UK which consists of four ecoregions is divided into 24 seed zones (Forestry Commission, 2019), and Cambodia which consists of six terrestrial ecoregions (excluding mangroves and freshwater ecoregions) divided into ten gene-ecological zones (Forestry Administration, 2003). Our approach resulted in 33 zones for the four southern states of India, 12 zones for Bangladesh, and 9 zones for Mindanao (Philippines). In Java, each forest type was divided into a number of seed zones equal to the number of ecoregions (Dinerstein et al., 2017) with which it overlaps (if only one ecoregion, the forest type was converted to a single seed zone). This resulted in a total of 16 zones, which is equivalent to four times the number of ecoregions on the Java Island (Dinerstein et al., 2017), and lends support to the idea that each ecoregion can be subdivided into a few seed zones. To facilitate the practical use of the seed zone maps, we also made a version in which seed zones were fixed to the third-level administrative divisions of the target regions ('subdistricts' in India, Bangladesh, and Java, 'barangays' in Mindanao), assigning each of these divisions to the seed zone that covers the highest number of grid cells in that division.

To assess how the seed zones may change under future climate conditions, the predicted future environmental conditions of every grid cell were projected to the same principal components as those used for the clustering of the current seed zones. Next, each grid cell was assigned to the closest cluster medoid, using the 'cl_predict' function of the 'clue' package for R (Hornik, 2019). In this way, the current seed zones were projected under future climate conditions as predicted by each of the selected GCMs under the emission scenarios mentioned above. Future seed zones were made for all target countries or regions except for Java (Indonesia), as we used the abovementioned forest type map of the Indonesian government as basis for the seed zone map, and we did not have a way to predict how different forest types may shift under climate change.

2.6. Seed source gap analysis

Seed zones can be used to guide seed sourcing decisions for restoration initiatives, or they can serve as 'management units' or 'evolutionary significant units' that should be subject of gene conservation efforts (Potter and Hargrove, 2012; Azpilicueta et al., 2013; Soliani et al., 2017). For both purposes, there should be at least one protected seed source in each of the seed zones, but ideally more to reduce risks from land use change or other threats. Hence, in the seed source gap analysis, we overlaid each of the species distribution maps with the seed zone map of the target region and the seed sources of that species. This allowed us to determine the number of seed sources in each seed zone and identify seed zones lacking any seed sources, thereby highlighting the seed source gaps. All seed sources included in this analysis were defined by national authorities as either *seed sources* (trees in any area where seed is collected) or *stands* (delineated populations of trees possessing sufficient uniformity, e.g., plus trees), according to the OECD (2024) definition.

Table 2
Availability of known seed sources by seed zone within species' modelled ranges in study countries. Forest cover (last column) is based on the GLAD-GLC land cover map (Potapov et al., 2022).

Species	Conservation status[a]	Country	Target area	Total number of seed sources	Seed zones within sp. distribution	Seed zones with designated seed sources		Seed zones with documented species occurrence (in forest)	
						Number	%	Number	%
Aglaia chittagonga	VU			36	11	7	64	7	64
Aglaia spectabilis	LC			37	12	9	75	7	58
Artocarpus chama	NE			34	8	6	75	6	75
Schima wallichii	LC			29	10	4	40	4	40
Stereospermum colais	LC	Bangladesh	Country-wide	37	5	3	60	3	60
Aquilaria malaccensis	CR			25	13	1	8	1	8
Falcataria falcata	LC			26	18	5	28	7	39
Magnolia sumatrana	LC			0	19	0	0	5	26
Neolamarckia cadamba	NE			3	22	0	0	4	18
Pinus merkusii	VU	Indonesia	Java	24	22	3	14	11	50
Agathis dammara	VU			6	9	1	11	8	89
Cinnamomum mercadoi	LC			0	8	0	0	8	100
Eucalyptus deglupta	VU			0	9	0	0	8	89
Pterocarpus indicus	EN			0	8	4	50	8	100
Pentacme paucinervis	LC	Philippines	Mindanao	24	9	0	0	8	89
Dalbergia latifolia	VU			228	28	14	50	12	43
Pterocarpus marsupium	NT			49	33	11	33	10	30
Tectona grandis	EN			149	33	8	24	23	70
Terminalia bellirica	LC			35	33	16	48	13	40
Terminalia chebula	LC			55	33	20	61	17	51
Xylia xylocarpa	LC	India	Andhra Pradesh, Kerala, Karnataka, Tamil Nadu	38	33	17	51	11	33

[a] Conservation status on the IUCN Red List of Threatened Species: CR = Critically Endangered, EN = Endangered, VU=Vulnerable, NT = Near Threatened, LC = Least Concern, NE = Not Evaluated (2025).

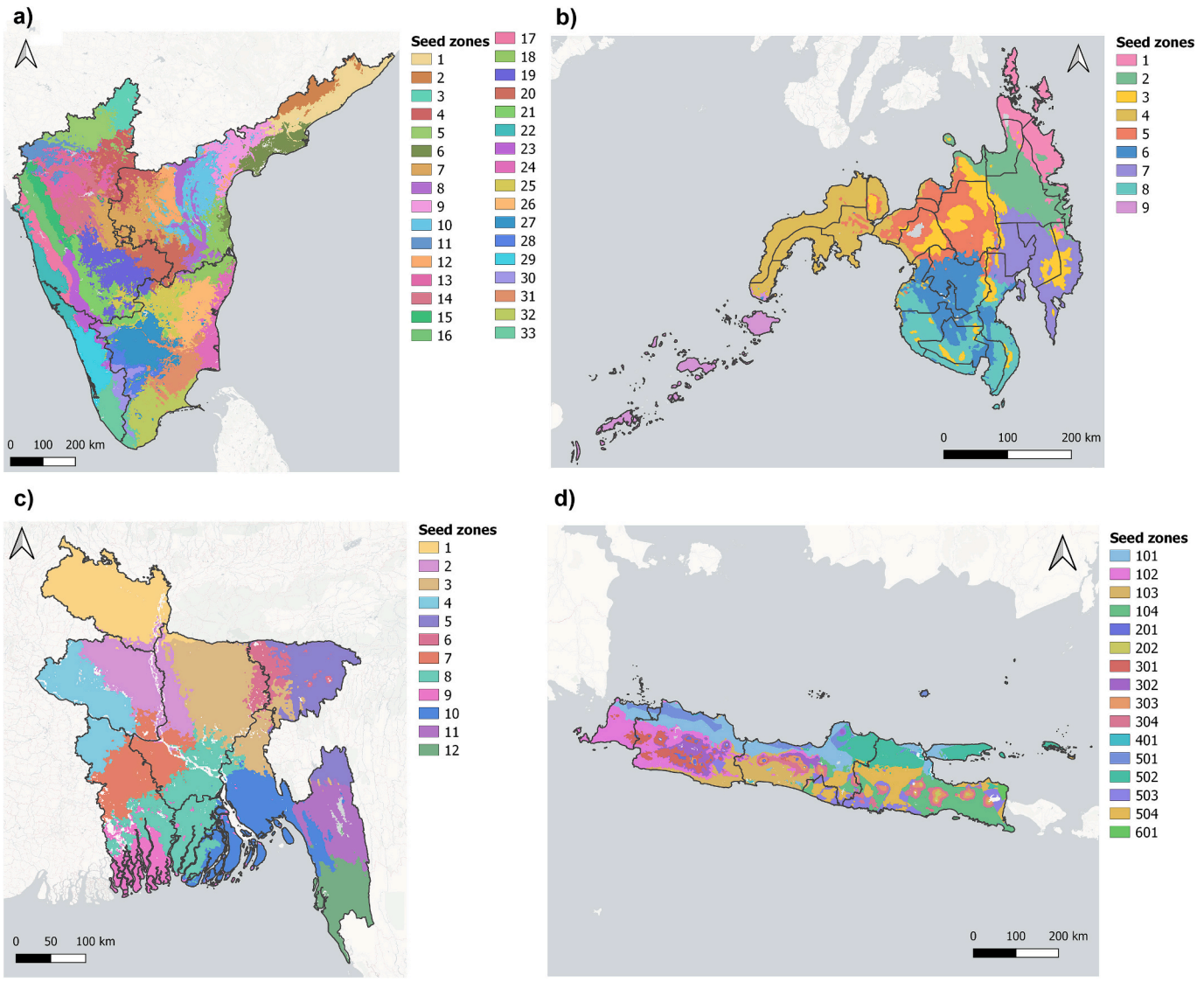

Fig. 2. Seed zone maps of the four target regions: (a) four southern states of India, (b) Mindanao (Philippines), (c) Bangladesh and (d) Java. The shown borders indicate the boundaries of the first-level administrative divisions ('states' in India, 'provinces' in Mindanao and Java, 'divisions' in Bangladesh). Note that the numbering of the seed zones in Java starts at 101 rather than 1 because the seed zone map was constructed differently as the others; the first of the three digits in the number of the seed zones refers to the forest type that was subdivided into seed zones.

This seed source gap analysis was carried out in two ways. First, for each species, we simply identified the seed zones (within the distribution range of that species) without any seed sources. As some existing seed sources may only consist of small forest patches or even isolated trees, which are less likely to have the necessary genetic diversity, we also evaluated which of these seed sources are located outside of forest areas, using the GLAD-GLC land cover map (Potapov et al., 2022), resampled to a resolution of 30 arcsec. Next, recognizing that some countries do not have registries of designated seed sources, we included an alternative way of implementing the seed source gap analysis, in which we use coordinates of the target tree species located inside of forest (using the same land cover map) as proxies for seed sources.

To narrow down the areas where new seed sources could be established, especially in those seed zones without existing seed sources, the seed zone map can be overlaid with a land cover map (to exclude non-forest areas), and maps of community forests or protected areas. To illustrate this for the case of Mindanao, we overlaid the seed zone map of Mindanao with the abovementioned land cover map (Potapov et al., 2022) and a map showing areas of community-based forest management (CBFM). These areas can then be used to prioritize the establishment of new seed sources. Note that all shown map lines delineate study areas and do not necessarily depict accepted national boundaries.

3. Results

The pilot species are described in Table 2. All species have economic value, mostly as timber, medicine, or food, and include some of the world's most valuable tree species such as teak (*Tectona grandis*) and agarwood (*Aquilaria malaccensis*) as well as emblematic species such as Narra (*Pterocarpus indicus*), the national tree of the Philippines. Nine of the species are threatened and two are listed in the CITES Appendix II (*Aquilaria malaccensis* and *Dalbergia latifolia*, Table 2). Species' predicted distributions were most influenced by precipitation of the driest quarter, topography, and temperature seasonality and variability (Table A.2, Appendix A).

The seed zones for each country are shown in Fig. 2. The number of seed sources per species (Table B.1, Appendix B) was relatively high (average 38, range 0–228), but they were generally heavily clustered in a few seed zones, resulting in wide gaps in the availability of seed sources by seed zone for all countries and almost all species (Table 2;

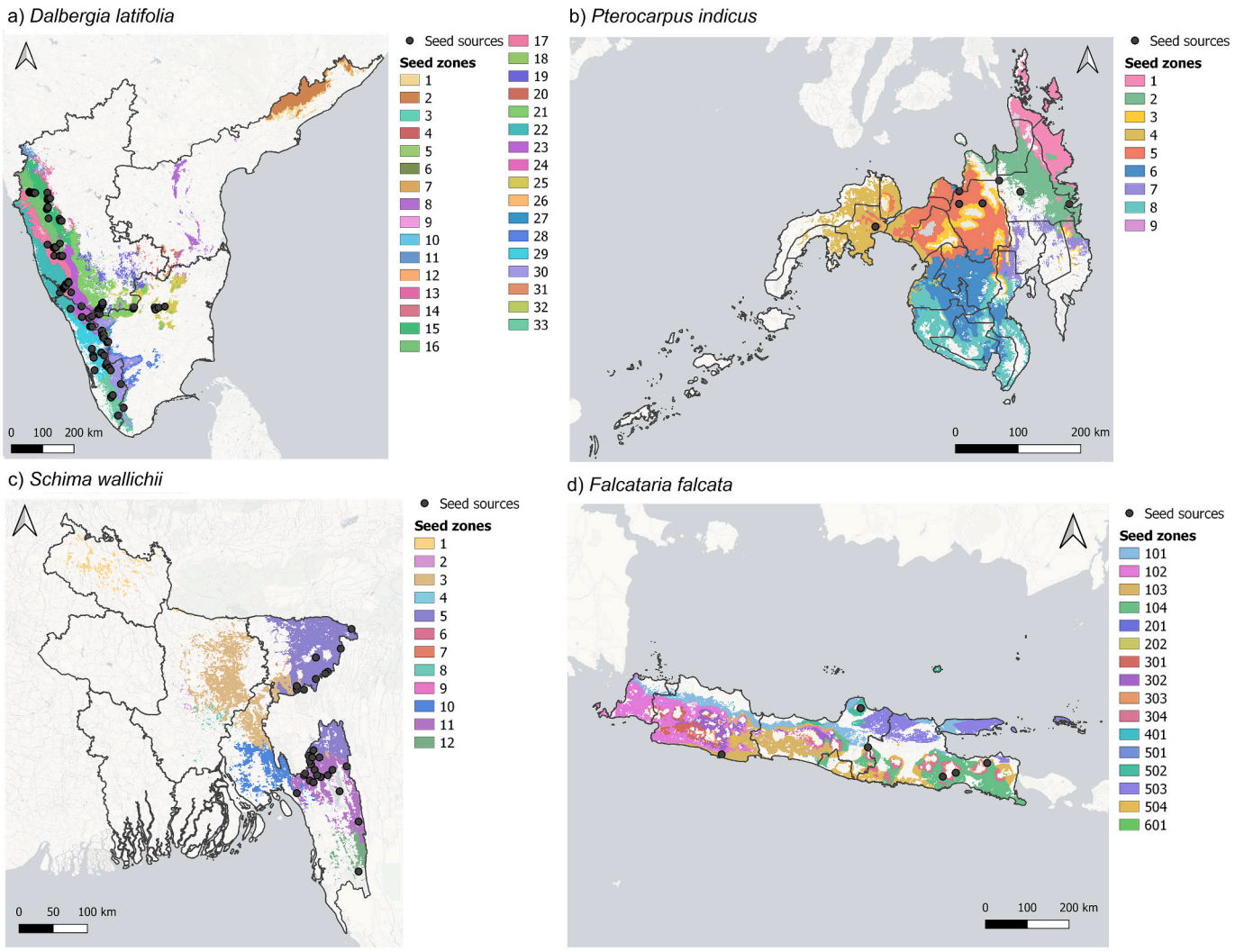

Fig. 3. Visual representation of the seed source gap analysis, showing the seed sources (black dots) and seed zones within the distribution range of four of the pilot species, using one species per target region as example: (a) *Dalbergia latifolia* in the four southern states of India, (b) *Pterocarpus indicus* in Mindanao (Philippines), (c) *Schima wallichii* in Bangladesh and (d) *Falcataria falcata* in Java (Indonesia). The shown borders indicate the boundaries of the first-level administrative divisions ('states' in India, 'provinces' in Mindanao and Java, 'divisions' in Bangladesh).

Fig. 3; Figs. B.1-B.21). Across all species, an average of only 34% of seed zones within the species predicted distributions had designated seed sources, and 24% of the species had no seed sources at all. Seed sources covered the environmental range of the selected species best in Bangladesh, where 40–75% of seed zones had at least one designated seed source. The situation was the worst in Mindanao, Philippines, where only two of the five study species had any designated seed sources, followed by Java, Indonesia, where only three of five species had seed sources. Although the study area in South India was much larger and with more seed zones than in the other countries, Java and Mindanao still had more gaps in seed source availability. Comparison with land cover data showed that most seed sources were located inside forests, except for 10 % of the seed sources in Bangladesh and 42% in India. The average area affected by these seed source gaps varied between 0.3 Mha in Bangladesh to 17.9 Mha in Southern India (Table B.2, Appendix B).

Overlay of seed zone maps with community-based forest management (CBFM) data in Mindanao, Philippines, showed that all identified gaps in seed source availability could potentially be filled by CBFM areas, which were available in all seed zones within the target species distribution (Fig. 4). None of the existing seed sources fell within CBFM boundaries. To facilitate practical use of the seed zone maps, third-level administrative divisions (generally equivalent to districts or sub-districts, depending on the country) were assigned to the seed zone covering the largest portion of their area. Consequently, districts or sub-districts within a state or province often fell into several different seed zones, and in some cases were more closely aligned with districts or sub-districts in neighboring states or provinces than with those in their own jurisdiction (Fig. 5; Figs. B.22-B.25 for the other countries).

The number of seed sources falling in areas predicted to be suitable by the distribution models under current and future climatic conditions are shown in Table B.1. Vast majority, 97% of the seed sources, were predicted to remain within suitable habitat for the species under future climates, with only *Aglaia chittagonga* in Bangladesh, and *Pterocarpus marsupium* and *Terminalia bellirica* in India predicted to lose at least 10% of existing seed sources (Appendix B, Table B.1). However, when the seed zones were projected to the predicted climate of the 2050s, notable shifts were observed in the predicted boundaries of some zones, suggesting that in future, existing seed sources may fall in different seed zones than currently. For example, in Bangladesh, several southern seed zones (e.g. nos. 8, 10, 12) expanded substantially to the north while the northern zones (e.g. nos. 3, 4, 5) contracted (Fig. 6; see Figs. B.26-B.28

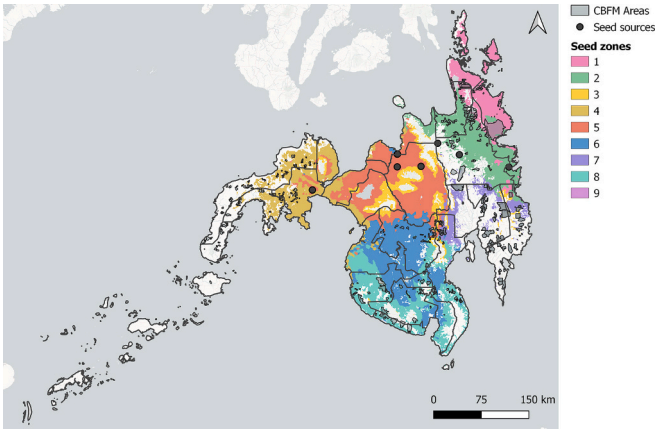

Fig. 4. Using community-based forest management (CBFM) areas (shown as a grey overlay) to identify potential new seed sources, showing *Pterocarpus indicus* in Mindanao (Philippines) as an example. The seed zone map shows those areas within the modelled distribution of *Pterocarpus indicus* that are not deforested (according to the GLAD-GLC land cover map, Potapov et al., 2022). The shown borders indicate the boundaries of the first-level administrative divisions (provinces).

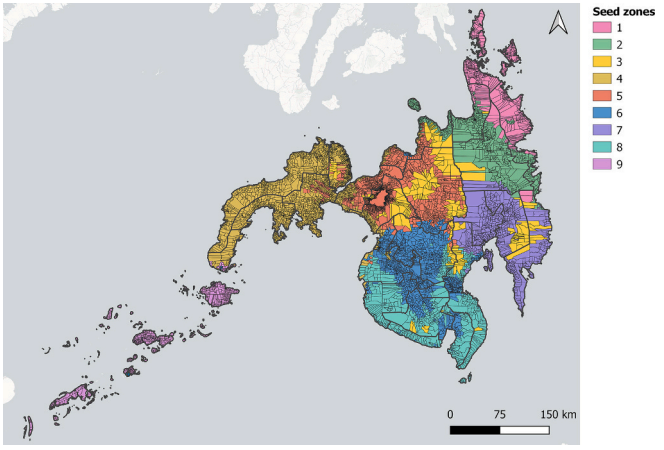

Fig. 5. Seed zones for Mindanao, Philippines, fixed to the third-level administrative divisions (barangays), indicated by the thin lines. Each barangay is assigned to the seed zone that covers the highest number of grid cells within that barangay. The borders of the first-level administrative divisions (provinces) are indicated by the thick lines.

for the other countries). All divisions except Khulna, Barisal, and Rangpur experienced major changes in the type and extent of seed zones.

4. Discussion

Our results reveal widespread gaps in the availability of native tree seed sources to deliver forest and landscape restoration as a nature-based solution to the global crises. Gaps in seed source availability were found in all countries and for all studied species, even though they were widely used and commercially or culturally important native species. While our results only cover four countries in tropical Asia, reviews (Nyoka et al., 2015) and indicator studies on the status of tree seed systems for restoration across Sub-Saharan Africa (Giacomini et al., 2023) and Latin America (Atkinson et al., 2021) indicate that similar gaps are likely in other regions in the Global South, and merit analysis to identify and address them as a precondition for achieving national restoration targets.

Interestingly, although two of the study countries, Indonesia and the Philippines, have in place regulations to allow registering seed sources also on private or communal lands, these countries had much fewer seed sources than the other two countries, where seed sources are currently only designated on government-managed land. Although Mindanao has numerous CBFM areas, we did not find any designated seed sources under CBFM for the selected species in this study. As there are several CBFM areas in each of the seed zones of Mindanao, local communities could play an important role in filling gaps in seed source availability, but the reasons for the low registration of seed sources on private and communal lands must first be understood. Lack of economic incentives arising from lack of seed distribution networks, dependency on government projects, market distortions, and regulatory hurdles is a significant barrier (Harrison et al., 2008; Lillesø et al., 2018; Nirsatmanto and Sunarti, 2021). Evidence from countries where local communities have played relatively active roles in tree seed supply chains suggests that to improve the economic viability of small-scale seed enterprises, it is important to create demand for native tree seed outside government-led restoration programmes, help local seed suppliers demonstrate seed quality, and build social capital for collaboration within community organizations and supplier networks (Harrison et al., 2008; Gregorio et al., 2016; Schmidt et al., 2019; Urzedo et al., 2019; Valette et al., 2020).

Comparing species distributions with land cover data helps identify additional forest areas that may harbor suitable seed source populations of selected species, and that could, thus, be prioritized for field surveys. Our results suggest that known natural populations of the selected species may be sufficient to fill in identified gaps in Java and Mindanao islands, but field surveys are necessary to ensure that population sizes are adequate to produce quality and genetically diverse seed (Broadhurst et al., 2006). Seed collection should not represent a threat to natural populations, many of which are simultaneously affected by land use change, climate change, and related impacts on biotic interactions such as seed predation (Marchioro et al., 2023). Systematic assessments of seed source availability such as presented here help ensure that seed demand can be sustainably met in both current and changing environmental conditions. With the highly ambitious global restoration targets, it is necessary to complement natural seed sources by establishing seed orchards for native species with clear market demand (Lillesø et al., 2018; Pedrini et al., 2020). In our study, this was already common in India, where 42% of designated seed sources were outside of forests: on research stations and in some cases on agricultural land. Establishing seed orchards can be a viable income generation activity for smallholder farmers, as it increases seed production capacity (Zinnen et al., 2021), allows easier access, and can provide income opportunities for women and other vulnerable social groups for whom seed collection in the wild may not be a realistic enterprise due to social norms, mobility or time constraints, or safety concerns (Elias et al., 2024).

The predicted shifts in seed zones under future climate change scenarios underscore the need to consider climate change during seed selection in order to help build adaptive capacity into restored ecosystems. Restoration practitioners worldwide report a lack of knowledge on how to prepare their projects for a changing climate (Bosshard et al., 2021; Jalonen et al., 2018, 2023), highlighting a need for practical tools to assist with planning. The future seed zone maps presented here are indicative of general trends only, because of the uncertainty of climate projections (we used an ensemble of five models in this study) and the characteristics of the applied environmental clustering method (Fremout et al., 2021). Provenancing strategies which take into account climate change typically recommend a combination of seed sources based on the predicted changes at the target planting site, to cope with uncertainty (Prober et al., 2015). Decision-support tools for species and provenance selection are emerging which are able to provide such spatially explicit guidance to restoration practitioners (e.g., Fremout et al., 2022; St. Clair et al., 2022). Overall, while our study only covered 21 pilot species, the fact that 97% of existing seed sources were

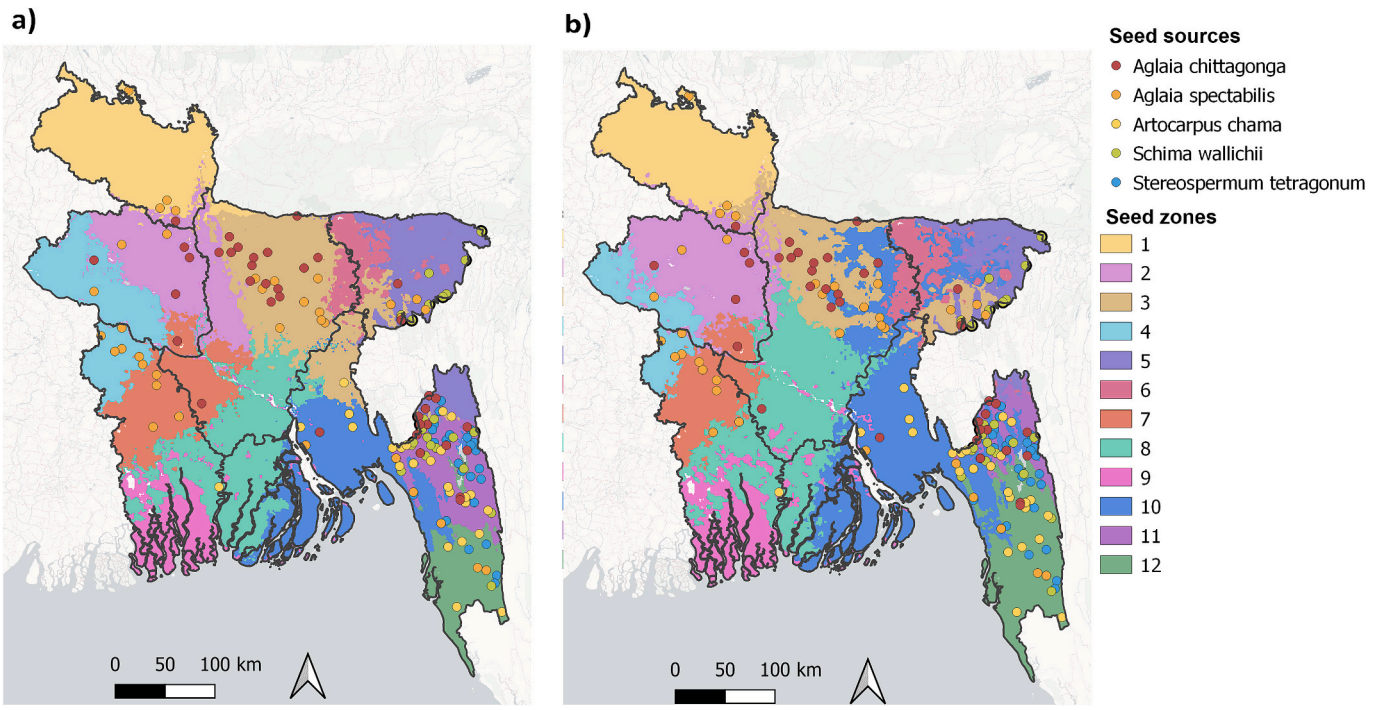

Fig. 6. Present (a) and future (b) seed zones of Bangladesh, overlaid with the seed sources of the five target species of Bangladesh. The future seed zones shown correspond to the average climatic conditions for the period 2041–2060 based on an ensemble of climate predictions of five general circulation models (ACCESS-CM2, GISS-E2–1-G, INM-CM5–0, MIROC6 and MPI-ESM1–2-HR) under SSP3.7–0 climate change scenario. The shown borders indicate the boundaries of the first-level administrative divisions (divisions).

predicted to remain suitable in a changing climate indicates that investments in developing seed sources yields long-term benefits. When investments in establishing new seed sources are made, it is useful to model the target species distributions into future climates to ensure the long-term viability of the seed sources.

Seed zones do not follow administrative boundaries, and filling in gaps in seed source availability requires coordination and collaboration between multiple scales and multiple state and non-state actors (Chazdon et al., 2021) – especially if opportunities for community participation in seed supply networks are to be strengthened. New or improved governance models are, thus, required. Theory on scale-sensitive governance (Wiegant et al., 2022) and experiences in the study countries suggests that useful models include (i) *Task-specific organizations* to develop standards and develop and maintain information systems on tree seed (e.g., Directorate of Forest Tree Seed in Indonesia, and Regional Tree Seed Centres in the Philippines). Potential challenges that need to be considered when implementing this model include difficulty of enforcing set standards, and a lack of sensitivity to local needs (Urzedo et al., 2019; Wiegant et al., 2022); (ii) *Decentralization* of seed source management from national or state forestry departments to community organizations (with mechanisms to designate seed sources outside government-managed lands already existing in Indonesia and the Philippines; DENR, 2010; Ministry of Environment and Forestry, 2010, 2020). Documented challenges to consider include higher-level actors imposing unfeasible or locally irrelevant targets on local actors, lack of technical or financial support to enhance local capacities for implementation, and lack of checks and balances that may result in local actors deviating from agreed goals (Gregorio et al., 2016; Nirsatmanto and Sunarti, 2021; Wiegant et al., 2022). (iii) *Polycentric governance* where sub-national jurisdictions sharing the same seed zones interact to set goals for seed production and distribution, and to foster seed supply by private and community actors. We are not familiar of such current polycentric governance mechanisms in our study countries, as they did not have seed zones defined prior to this study. However, such mechanisms would be increasingly valuable as demands for native tree seed grow while the progressive climate change calls for seed transfer to assist ecosystems to adapt (Prober et al., 2015).

Our methodology for analyzing gaps in the availability of tree seed sources was proven to be robust, allowing comparisons of seed source needs between species, seed zones and countries and offering actionable information to help prioritize management actions on the ground. The methodology combines all elements of the well-established indicator framework of *pressures* (land use change, climate change), *state* (extent of species' suitable habitat, number of populations that fulfil criteria of seed sources e.g. in terms of population size and lack of disturbance), and *responses* (registration of seed sources as genetic reserves, extent of community forestry) (Graudal et al., 2020), which can be emphasized in the analysis in different ways depending on the local context and management priorities. The methodology is cost-effective, using primarily existing data, and can be easily adjusted to capture trends over time and to different spatial scales, including assessing complementarities in seed source availability between neighboring countries which can be important in resource-constrained, species-rich countries in the Global South (APFORGEN, 2023). The methodology is based on environmental modelling and does not replace field studies, but rather complements them by helping to target them better. It should also be noted that the distribution models may not be able to accurately predict species distributions in mangrove or peat swamp forests, and so our analysis was restricted to mineral soils only.

The main constraint to the application of the methodology in this pilot study was the lack of occurrence data on target tree species, which is still common for tropical tree species (Serra-Diaz et al., 2017). Several initially selected species had to be removed from the analysis due to data gaps, including the endangered *Bouea oppositifolia* and *Dipterocarpus alatus* in Bangladesh, and the critically endangered *Xanthostemon philippinensis* in the Philippines. Although the Global Biodiversity Information Facility (GBIF, www.gbif.org) is an important source of information, many herbaria are not yet represented in the data and are a potentially massive source of new information. Many specimens (even if found on GBIF) also remain to be georeferenced before they can be

incorporated into species distribution models. Collaboration with local agencies can help gain access to species occurrence data outside of public domain. Regional collaboration and data sharing helps meet thresholds for data needs that apply for species ranges rather than administrative boundaries (Gaisberger et al., 2021), and citizen science has untapped potential to contribute to filling gaps (Callaghan et al., 2021). The methodology also requires other data, all of which is not necessarily readily available in the public domain (e.g., coordinates of seed sources or shapefiles of CBFM areas), however, national forestry experts from the public sector were able to access the data for the current analysis without difficulty. Now that the seed zone maps for each country have been developed, the analysis can be easily extended to cover other species without the need of advanced spatial analysis skills, provided that species distribution maps are available. Our results indicate that similar analyses should be prioritized also in other countries in the Global South, and the published methodology for delineating seed sources (Fremout et al., 2021) allows expanding such analyses also to countries currently lacking seed zone maps.

5. Conclusion

After years of global attention and multi-billion dollar investments to restoration since the Bonn Challenge (2011-), our results highlight how the fundamental role of seed availability and quality in restoration success continues to be overlooked in the race to reforest the planet. Because of the lack of attention to seed origin, we are missing crucial opportunities to help forest-dependent communities, seed source owners, local seed collectors and entrepreneurs add value to restoration efforts by producing suitably adapted seed of diverse native species, while gaining income and incentives for sustainable forest management. We are also missing opportunities to synergize forest restoration and forest conservation efforts, by making sure that natural seed sources required for restoration are protected, and that restoration efforts incorporate genetic diversity to contribute to species conservation. We recommend that governments and organizations supporting restoration in the Global South prioritize investments in developing (i) seed zone maps to guide seed sourcing and help identify context-specific opportunities for involving indigenous peoples and local communities in seed supply, (ii) publicly available registries of seed sources and seed suppliers, (iii) accessible mechanisms to register seed sources on private and communal lands, (iv) strategies to identify and fill gaps in seed source availability, including working with community forestry groups and establishing seed orchards, (v) policy and legislative frameworks that help create demand for quality seed of native species, such as regulations mandating restoration of degraded ecosystems and seed quality standards, and (vi) collaboration mechanisms such as multi-stakeholder platforms and seedling buy-back programmes that facilitate the participation of indigenous peoples and local communities in seed supply chains. These concrete actions, supported by the methodology and results of this study, will help implement and monitor progress towards the Targets of the Kunming-Montreal Global Biodiversity Framework on ecosystem restoration and the conservation of the genetic diversity of wild species, and can be included in National Biodiversity Strategies and Action Plans as countries update those.

CRediT authorship contribution statement

Riina Jalonen: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Tobias Fremout:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Rekha R. Warrier:** Writing – review & editing, Validation, Investigation, Funding acquisition, Data curation. **Vivi Yuskianti:** Writing – review & editing, Validation, Investigation, Funding acquisition, Data curation. **Enrique Tolentino:** Writing – review & editing, Validation, Investigation, Funding acquisition, Data curation. **Cristino Tiburan:** Writing – review & editing, Validation, Investigation, Funding acquisition, Data curation. **Md. Zahidur Rahman Miah:** Writing – review & editing, Validation, Investigation, Funding acquisition, Data curation. **Md. Tauhidor Rahaman:** Writing – review & editing, Validation, Investigation, Data curation. **Peter Wilkie:** Writing – review & editing, Validation, Investigation, Funding acquisition. **Dede J. Sudrajat:** Writing – review & editing, Validation, Investigation, Data curation. **Denny:** Writing – review & editing, Validation, Investigation, Data curation. **Christopher J. Kettle:** Writing – review & editing, Investigation, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Riina Jalonen reports financial support was provided by UK Darwin Initiative. Riina Jalonen reports financial support was provided by CGIAR Fund Donors. Funding support was received jointly by all authors: Riina Jalonen, Tobias Fremout, Rekha R. Warrier, Vivi Yuskianti, Enrique Tolentino jr., Cristino Tiburan jr., Md. Zahidur Rahman Miah, Md. Tauhidor Rahaman, Peter Wilkie, and Christopher J. Kettle. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2026.111811.

Data availability

The processed data required to reproduce the above findings are available to download from: https://doi.org/10.7910/DVN/JESQWT.

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