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CONTRIBUTED PAPERS

Tropical and subtropical Asia's valued tree species under threat

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Abstract

Tree diversity in Asia's tropical and subtropical forests is central to nature-based solutions. Species vulnerability to multiple threats, which affect provision of ecosystem services, is poorly understood. We conducted a region-wide, spatially explicit assessment of the

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vulnerability of 63 socioeconomically important tree species to overexploitation, fire, overgrazing, habitat conversion, and climate change. Trees were selected for assessment from national priority lists, and selections were validated by an expert network representing 20 countries. We used Maxent suitability modeling to predict species distribution ranges, freely accessible spatial data sets to map threat exposures, and functional traits to estimate threat sensitivities. Species-specific vulnerability maps were created as the product of exposure maps and sensitivity estimates. Based on vulnerability to current threats and climate change, we identified priority areas for conservation and restoration. Overall, 74% of the most important areas for conservation of these trees fell outside protected areas, and all species were severely threatened across an average of 47% of their native ranges. The most imminent threats were overexploitation and habitat conversion; populations were severely threatened by these factors in an average of 24% and 16% of their ranges, respectively. Our model predicted limited overall climate change impacts, although some study species were likely to lose over 15% of their habitat by 2050 due to climate change. We pinpointed specific natural areas in Borneo rain forests as hotspots for in situ conservation of forest genetic resources, more than 82% of which fell outside designated protected areas. We also identified degraded areas in Western Ghats, Indochina dry forests, and Sumatran rain forests as hotspots for restoration, where planting or assisted natural regeneration will help conserve these species, and croplands in southern India and Thailand as potentially important agroforestry options. Our results highlight the need for regionally coordinated action for effective conservation and restoration.

KEYWORDS
climate change analysis, conservation hotspots, conservation priorities, restoration hotspots, restoration priorities, spatially explicit threat assessment, species distribution modeling, tree species, vulnerability mapping

Especies de Árboles Valoradas y Amenazadas de Asia Tropical y Subtropical

Resumen: La diversidad de árboles en los bosques tropicales y subtropicales de Asia es un eje central para las soluciones basadas en la naturaleza. La vulnerabilidad de las especies ante las múltiples amenazas, las cuales afectan el suministro de servicios ambientales, es un tema poco comprendido. Realizamos una evaluación regional espacialmente explícita de la vulnerabilidad de 63 especies de árboles de importancia socioeconómica ante la sobreexplotación, incendios, sobrepastoreo, conversión del hábitat y cambio climático. Los árboles se seleccionaron para su evaluación a partir de listas nacionales de prioridades, y las selecciones fueron validadas por una red de expertos de 20 países. Usamos el modelado de idoneidad Maxent para predecir el rango de distribución de las especies, conjuntos de datos espaciales de libre acceso para mapear la exposición a las amenazas y rasgos funcionales para estimar la susceptibilidad a las amenazas. Con base en la vulnerabilidad a las amenazas actuales y al cambio climático, identificamos las áreas prioritarias para su conservación y restauración. En general, el 74% de las áreas más importantes para la conservación de estos árboles quedó fuera de las áreas protegidas y todas las especies estaban seriamente amenazadas en promedio en el 47% de su distribución nativa. Las amenazas más inminentes fueron la sobreexplotación y la conversión del hábitat; las poblaciones estuvieron seriamente amenazadas por estos factores en promedio en el 24% y 16% de su distribución, respectivamente. Nuestro modelo predijo un impacto general limitado del cambio climático, aunque algunas especies estudiadas tuvieron la probabilidad de perder más del 15% de su hábitat para el 2050 debido a este factor. Identificamos áreas naturales específicas en las selvas de Borneo como puntos calientes para la conservación in situ de los recursos genéticos forestales, más del 82% de los cuales estaban fuera de las áreas protegidas designadas. También identificamos áreas degradadas en los Ghats Occidentales, los bosques secos de Indochina y las selvas de Sumatra como puntos calientes para la restauración, en donde la siembra o la regeneración natural asistida ayudarán a conservar estas especies. Además, identificamos campos de cultivo al sur de India y Tailandia como potenciales opciones importantes de agrosilvicultura. Nuestros resultados resaltan la necesidad de acciones regionales coordinadas para la conservación y restauración efectivas.

PALABRAS CLAVE:
análisis del cambio climático, especies de árboles, evaluación espacialmente explícita de amenazas, mapeo de vulnerabilidades, modelado de distribución, prioridades de conservación, prioridades de restauración, puntos calientes de conservación, puntos calientes de restauración

亚洲热带及亚热带地区有价值的树种面临威胁

【摘要】保护亚洲热带和亚热带森林的树木多样性是基于自然的解决方案的关注重点。物种面对多种威胁的脆弱性会影响生态系统服务的供给, 但目前人们对此仍知之甚少。我们对63种具有社会经济意义的树种面对过度开发、火灾、过度放牧、栖息地转换和气候变化的脆弱性进行了全区域空间显式评估。我们进行评估的树种来自国家优先保护名录, 树种的选择得到代表 20个国家的专家网络的认可。研究使用Maxent适宜性模型预测了物种分布范围, 并用可获取的空间数据集绘制了威胁暴露情况, 用功能特征估计了威胁敏感性。我们利用暴露地图和敏感性估计结果得到了物种特异的脆弱性地图, 并根据物种对当前威胁和气候变化的脆弱性, 确定了保护和恢复的优先区域。总的来说, 对这些树种的保护最重要的区域有 74%在保护区之外, 所有树种平均在其原生分布区 47%的范围内受到严重威胁。最紧迫的威胁是过度开发和栖息地转换;树木种群平均在其24%和16%的范围内受到这些因素的严重威胁。我们的模型预测得到的气候变化整体影响有限, 尽管一些物种到2050年可能会因气候变化而失去超过15%的栖息地。我们发现婆罗洲雨林中特定的自然区域应作为森林遗传资源原地保护的热点地区, 该区域82%以上的面积位于已有保护区之外。我们还确定了西高止山、中南半岛旱林和苏门答腊雨林的退化地区为恢复热点地区, 在这些地区种植树木或辅助自然再生将有助于保护树种, 而印度南部和泰国的耕地则是潜在的重要农林地。我们的结果强调了为有效保护和恢复而采取区域性协调行动的必要性。**【翻译: 胡怡思;审校: 聂永刚】**

关键词: 物种脆弱性地图, 物种分布模型, 气候变化分析, 空间显式威胁评估, 优先保护, 优先恢复, 保护热点地区, 恢复热点地区, 树种

INTRODUCTION

Forests and trees are a crucial part of nature-based solutions to reduce the exposure and vulnerability of human communities and societies to environmental changes (Seddon et al., 2020). Forested landscapes in South and Southeast Asia directly or indirectly support hundreds of millions of people. The region's forests host some of the largest trees in the tropics and are among the most carbon-dense and floristically diverse terrestrial ecosystems (Slik et al., 2015), meaning they play a critical role in mitigating climate change (Lewis et al., 2019). Trees in- and outside these forests contribute substantially to local livelihoods and national economies (Oldekop et al., 2020), nutrition security, low-carbon food systems (Jansen et al., 2020), and maintaining human health in general. However, species' and populations' threat status and capacity to adapt to a changing environment remain poorly understood and vary based on ecological traits and genetic diversity. As the pressures on the remaining natural forests mount (FAO, 2014; Hughes, 2017) and countries operationalize ambitious restoration targets (United Nations General Assembly, 2019), there is an urgent need for species- and context-specific approaches to set conservation and restoration priorities. Existing global-scale priority maps that combine data (e.g., on forest cover, carbon stocks, and restoration costs and benefits) (Strassburg et al., 2020) can help narrow down target areas for ecosystem restoration investments. However, information on which trees can survive and thrive and where this can occur under current and projected conditions is critical (Lughadha et al., 2020). Global conservation priorities are typically biased toward vertebrate diversity (Brooks et al., 2006; Pelletier et al., 2018), which does not adequately represent priority areas for conserving plant diversity and can, therefore, lead to inappropriate decisions, and data on tree species distributions are of poor quality (Serra-Diaz et al., 2017).

We mapped the natural distribution and vulnerability to multiple threats of 63 native tree species of socioeconomic importance in 20 countries in South and Southeast Asia and identified climate-sensitive and population-specific priority areas for conservation and restoration activities.

METHODS

Study region

The vulnerability assessment covered 20 countries in tropical and subtropical Asia that together form the Indo-Malayan floristic realm. This was also the area that the expert network Asia Pacific Forest Genetic Resources Programme (APFORGEN) (http://www.apforgen.org/) was able to assess because accurate species occurrence points and detailed knowledge on the natural and naturalized distribution of important tree species are available. APFORGEN seeks to enhance technical and scientific cooperation, training, and information exchange among member countries by linking and providing technical support to national forest programs, research institutions, nongovernmental organizations, and individuals interested in the conservation and management of forest genetic resources in the region. We included Papua New Guinea in the spatial analysis because several of the study species that occurred in Indonesian West Papua had continuous distribution across the border with Papua New Guinea.

Selection of tree species

Study species were selected through a participatory, expert-driven process as part of a research project called APFORGIS (Establishing an Information System for Conserving Native Tree Species and Their Genetic Resources in Asia-Pacific). National coordinators of the APFORGEN network identified national species experts to participate in a regional workshop in 2018 to select the study species. The experts created an initial list of 72 regionally important tree species of common interest to multiple countries that would benefit from coordinated conservation efforts across their native distribution based on existing national priority lists and the following selection criteria on which they jointly agreed: native to tropical and subtropical Asia; cross-border distribution (natural occurrence in at least two countries); socioeconomically important for timber or nontimber forest products or provision of other key ecosystem services, such as erosion control, soil improvement, and shade; of conservation concern or considered a priority in forest and landscape restoration; and existence of at least basic knowledge on reproductive biology (e.g., pollen and seed dispersal patterns, mating systems) to enable identifying patterns among species that share similar characteristics. Some species were widely cultivated, but many were found exclusively in the wild. The species belonged to 27 families, the most species-rich family being Fabaceae (17 species), followed by Dipterocarpaceae (13 species) and Thymelaeaceae (three species).We focused on transboundary species because improving the conservation status of their genetic resources rangewide requires jointly developed and validated cross-border assessments that provide a foundation for collaborative follow-up actions.

Tree species occurrence data

Tree species occurrence points were compiled from several sources (Appendix S1), mainly APFORGEN members and other individual researchers from the target countries, but also from scientific articles and Bioversity International's Collecting Mission Database (http://bioversity.github.io/geosite/). We standardized the data with the occurrence data collation template developed in the Southern African Development Community (SADC) Crop Wild Relatives project (http://www.cropwildrelatives.org/sadc-cwr-project/) and implemented a three-step cleaning process (Appendix S2) to ensure high data quality. The cleaned data set contained 10,258 occurrence points for the 72 initial tree species (Appendix S3).

Species distribution modeling

To reduce the negative effects of spatial sampling bias on model accuracy, we used the SDMtoolbox 2.2 for ArcGIS (Brown, 2014) and spatially filtered (i.e., thinned) the occurrence points at three spatial resolutions (5, 10, and 15 km) according to high, medium, and low environmental heterogeneity. The heterogeneity classes were based on the natural breaks of percentage of eigenvalues of a principal component analysis applied on a set of 28 environmental predictor variables (Appendix S2). Spatial filtering is a quick and efficient way to substantially improve the reliability of predictions of species distribution models (SDMs). After spatial filtering, 63 tree species had more than 20 presence points, which is generally considered sufficient to build accurate distribution models (Wisz et al., 2008). The other nine tree species were excluded from modeling. The cleaned and filtered data set, with 6740 tree occurrence points, was used for modeling (Appendix S3).

We tested the 28 potential predictor variables at a spatial resolution of 2.5 arc minutes (approximately 4.5 km at the equator) for multicollinearity across the study area because correlation among variables may negatively affect model performance (Heikkinen et al., 2006). We calculated the variance inflation factor (VIF) with the R package usdm (Naimi et al., 2014) and retained only variables with VIFs <10. With this method, we obtained a subset of 15 climatic, edaphic, and topographic variables with reduced correlation as input for the SDMs (Appendix S2).

To model the potential distribution of the 63 priority tree species, we chose the maximum entropy (Maxent 3.4.1) algorithm (Phillips et al., 2018) because of its high performance with presence-only data (Elith et al., 2011), especially at relatively small sample sizes (Wisz et al., 2008). Because default settings might lead to overfitting (Radosavljevic & Anderson, 2014), we executed Maxent across a range of different settings in the R package ENMeval (Muscarella et al., 2014) to balance goodness of fit with model complexity and to evaluate models with spatially independent partitions. When comparing different evaluation metrics, Maxent models selected with the Akaike information criteria corrected for small sample sizes (AICc) estimate habitat suitability under current and future conditions more accurately than models selected with other methods (Warren & Seifert, 2011). For each species, we, therefore, selected the model with the lowest AICc value (i.e., $\Delta AICc = 0$) for subsequent spatial analysis. We also calculated the most widely used performance metric for SDMs, area under the receiver operating characteristic curve (AUC), to facilitate comparison with other studies. The models were evaluated using four-fold cross-validation with spatially independent checkerboard partitioning of presence and background records (Muscarella et al., 2014). Background points were randomly selected for each species separately, from a geographic extent similar to the one for its occurrence points, to improve the discriminatory power of models in the core distribution area (Acevedo et al., 2012) and transferability in place and time (Phillips, 2008). For this purpose, we created for each species a convex hull around the presence locations and extended it to 20% of the longest axis between presence points. To avoid omitting large areas where species may be present, we converted the suitability maps into presence-absence maps at a spatial resolution of 2.5 arc minutes (approximately 4.5 km at the equator) based on the 10th percentile training presence omission threshold.

Validation of SDMs

Because our focus was the conservation status of tree species within their natural distribution ranges, we excluded states or provinces from the modeled distribution areas where the species did not occur or were naturalized. The area exclusion was based on an expert workshop in Sri Lanka in March 2019 and a review of literature and public databases (e.g., The International Union for the Conservation of Nature [IUCN] Red List of Threatened Species (https://www.iucnredlist.org) and the Plants of the World Online database (www.plantsoftheworldonline.org). We further excluded the mangrove biome (Dinerstein et al., 2017) as unsuitable from the modeled distribution ranges, except for *Rhizophora apiculata*, the only mangrove species in this study. We restricted this species' modeled distribution to 10 km inland from the coastline (Natural Earth, 2021). For the other two habitat-specific species, *Gonystylus bancanus* and *Myristica malabarica*, we restricted modeled distribution to 10 km into the matrix surrounding peatlands (Xu et al., 2018). We refer to the resulting SDMs as validated SDMs.

Spatial threat analysis

We characterized the vulnerability of the 63 tree species to overexploitation, fire, overgrazing, habitat conversion, and climate change as a function of threat exposure and species sensitivity (Fremout et al., 2020; Gaisberger et al., 2017) and created species-specific vulnerability maps for which the extent was restricted to the respective validated SDMs.

For the current threats overexploitation, fire, overgrazing, and habitat conversion, we constructed exposure layers to estimate patterns and intensity of threat throughout the study region from freely available spatial data sets (Appendix S2) based on a set of assumptions derived from the literature and expert knowledge (Appendix S2). The climate-change exposure layers were created by projecting the SDMs of the 63 species to downscaled future climate conditions for 2050 (2041–2060 period), as predicted by global circulation models (GCMs) from the sixth Coupled Model Intercomparison Project (CMIP6) (Eyring et al., 2016), under different shared socioeconomic pathways (SSPs). We followed Brunner et al. (2020) to select the five GCMs with the highest combined weight of performance and independence among those available at the WorldClim website (https://worldclim.org/), which resulted in the selection of the following GCMs: MIROC6, BCC-CSM2-MR, IPSL-CM6A-LR, CNRM-ESM2-1, and MRI-ESM2-0. To assess the robustness of the vulnerability mapping method, we carried out a sensitivity analysis by creating reference-, best-, and worst-case scenario exposure maps for each of the considered threats. The methodological decisions made during the creation of the exposure layers are a key element of uncertainty compared with other sources for this kind of vulnerability assessment (Fremout et al., 2020). The climate-change reference exposure map was created using the SSP245 scenario, whereas SSP126 and SSP585 were used for the best- and worst-case exposure maps, respectively. Further details on the construction of the exposure layers are in Appendix S2.

To estimate the sensitivity of the priority tree species to the five key threats, we applied a method developed by Fremout et al. (2020) in which explicit relations between tree functional traits and resistance against threats were established based on a literature study and expert judgment. The capacity to resist each threat was linked to several traits, each with a corresponding weight in accordance with the expected magnitude of its influence on species sensitivity to the threat in question, ranging from 1 (very low) to 5 (very high). We focused on a set of 10 key traits with medium to very high importance (Appendix S2). A partial sensitivity score (Appendix S2) was created for each single trait level, corresponding to the expected nature of its influence on species sensitivity, varying between 0 (maximally decreasing sensitivity) and 1 (maximally increasing sensitivity). For example, bark thickness was given a very high trait weight when estimating species sensitivity to fire because it is the most important trait in determining tree sensitivity to fire (Schubert et al., 2016). Species with thick (>10 mm), intermediate (5–10 mm), and thin bark (< 5 mm) were given partial fire sensitivity scores of 0.5, 0.75, and 1, respectively. Both the partial threat sensitivity scores and the trait weights were adapted from Fremout et al. (2020) (Appendix S2). The trait information for the 63 priority tree species (Appendix S4) was compiled through an extensive literature search (Appendix S5).

The overall sensitivity score (between 0 and 1) for each species-threat combination was calculated as the weighted mean of the partial sensitivity scores based on the abovementioned trait weights (Appendix S2). In turn, the species-specific threat vulnerability maps were constructed on a cell-by-cell basis as the product of the species-specific threat sensitivity score (0–1) and the threat exposure value (0–1), restricted to validated SDMs (Appendix S2). The threat vulnerability values ranged from 0 (no vulnerability) to 1 (maximum vulnerability) and were categorized into one of five classes (no threat, low, medium, high, and very high) by applying the thresholds of 0.01, 0.25, 0.50, and 0.75. We calculated the proportion of the species' distribution area assigned to the five vulnerability classes for each of the threats individually and in combination. To define the most vulnerable species, we ranked them according to decreasing proportion of distribution area with high and very high threat vulnerability. Because multiple stressor interactions, ranging from synergistic to antagonistic effects, are complex and difficult to predict for real-world applications (Côte et al., 2016) and for reasons of simplicity, we defined the combined vulnerability of an area, corresponding to an individual pixel, as the highest vulnerability among the individual layers.

Priority areas for single species

The combined current threat and climate-change vulnerability maps were used to generate species-specific priority maps for conservation and restoration activities. We delineated areas recommended for in situ conservation of populations in areas where both current and climate-change threat levels were low; restoration activities, such as active planting or assisted natural regeneration of populations, in areas where current threat levels were high but climate-change threat levels were low; and ex situ conservation of populations in areas where climate-change threat levels were high through relocation to suitable areas (assisted migration) or collection and storage of seeds in seed banks.

In situ conservation of tree populations was prioritized in areas with low vulnerability to current threats and to climate change. In areas with low vulnerability, the likelihood that human disturbance has led to increased inbreeding and limited genetic variability is reduced (Lowe et al., 2005), whereas the low threat from climate change enhances the likelihood of continued seed production and regeneration under future conditions. We restricted the prioritized area for in situ conservation to areas where the SDMs predicted occurrence of highly suitable areas (suitability values ≥ 0.7, range 0–1), with the aim to identify populations that were likely to have maximal fitness and adaptive capacity (Nagaraju et al., 2013).

Priority areas for the combination of species

In addition to the species-specific maps, we created maps combining priority sites for all tree species in which we delineated areas recommended for in situ conservation, restoration activities, and ex situ conservation based on the number of species and the proportion of species per grid cell (Appendix S2). We also constructed combined priority maps by calculating the proportion of species per grid cell for which the grid cell in question was recommended for conservation or restoration. To increase visibility on the maps and to identify foci of conservation and restoration activities, we defined hotspots as areas where the recommended priority activities of at least 10 tree species overlapped. The combined priority activity hotspot maps were overlaid on an ecoregions map (Dinerstein et al., 2017) to identify the respective biomes and ecoregions in tropical and subtropical Asia in which the conservation and restoration hotspots were predicted to occur. In addition, we created a map of protected areas for the study region by using designated protected areas from the United Nations Environment Programme World Conservation Monitoring Centre and IUCN (2020) that we updated with national protected areas from Bangladesh, Cambodia, and India, provided by contributing species experts. We eliminated spatial overlaps and overlaid the final map of protected areas with the in situ map of areas of conservation priority to assess the proportion of the species' native distribution range that was under some type of protection. The restoration priority map was overlaid with a cropland area map (Latham et al., 2014) to identify areas that are predominantly agricultural land. All area calculations were carried out after transformation into cylindrical equal area's projection.

RESULTS

Species-specific threat assessment

We created tuned and validated distribution maps for 63 selected tree species across their native ranges in South and Southeast Asia (Figure 1). The validation AUC values of the best performing SDMs per species (with lowest AIC values) ranged from 0.92 to 0.99 (Appendix S2), indicating excellent accuracy. On average, over two-thirds (70%) of the total modeled distribution area of about 9.4 million km^2 occurred in the tropical and subtropical moist broadleaf forests and about 17% in tropical and subtropical dry broadleaf forests.

The sensitivity analysis of the vulnerability mapping method indicated that the priority conservation and restoration maps were relatively sensitive to the decisions made when creating the exposure layers. An average of 30% (SD 7) of the grid cells within species' distribution ranges changed from one category to another compared with the reference maps for the best-case priority maps and 29% (5) for the worst-case priority maps.

The spatially explicit threat assessment revealed that all 63 species were highly or very highly threatened by at least one of the five threats in an average of 47% (SD 15) of their native distribution ranges (Figure 2). Overexploitation emerged as the single most important threat, with populations being highly or very highly threatened in an average of 24% (15) of their native distribution ranges. This was followed by an average of 16% (10) for habitat conversion, 9% (11) for overgrazing, 7% (6) for fire, and 4% (6) for climate change. When also considering medium threat levels, the affected areas increased to 76% (14) for at least one of the five threat factors, 63% (17) for overexploitation, 39% (6) for habitat conversion, 19% (22) for overgrazing, 16% (10) for fire, and 8% (10) for climate change. Threat maps of the most vulnerable tree species to each of the five threats are in Appendix S2.

Among the species that were rarely cultivated or found only in the wild, the five most threatened species were *Afzelia xylocarpa* (highly or very highly threatened by at least one of the five factors in 70% of its distribution area; range between best-case and worst-case scenario 48–87%) [Figure 3]; climate change predominant threat); *Shorea roxburghii* (68% of its distribution; range 41–85%) and *Dalbergia oliveri* (65% of its distribution; range 41–84%) (habitat conversion single most important threat); and *M. malabarica* (67% of its distribution; range 50–90%) and *Aquilaria*

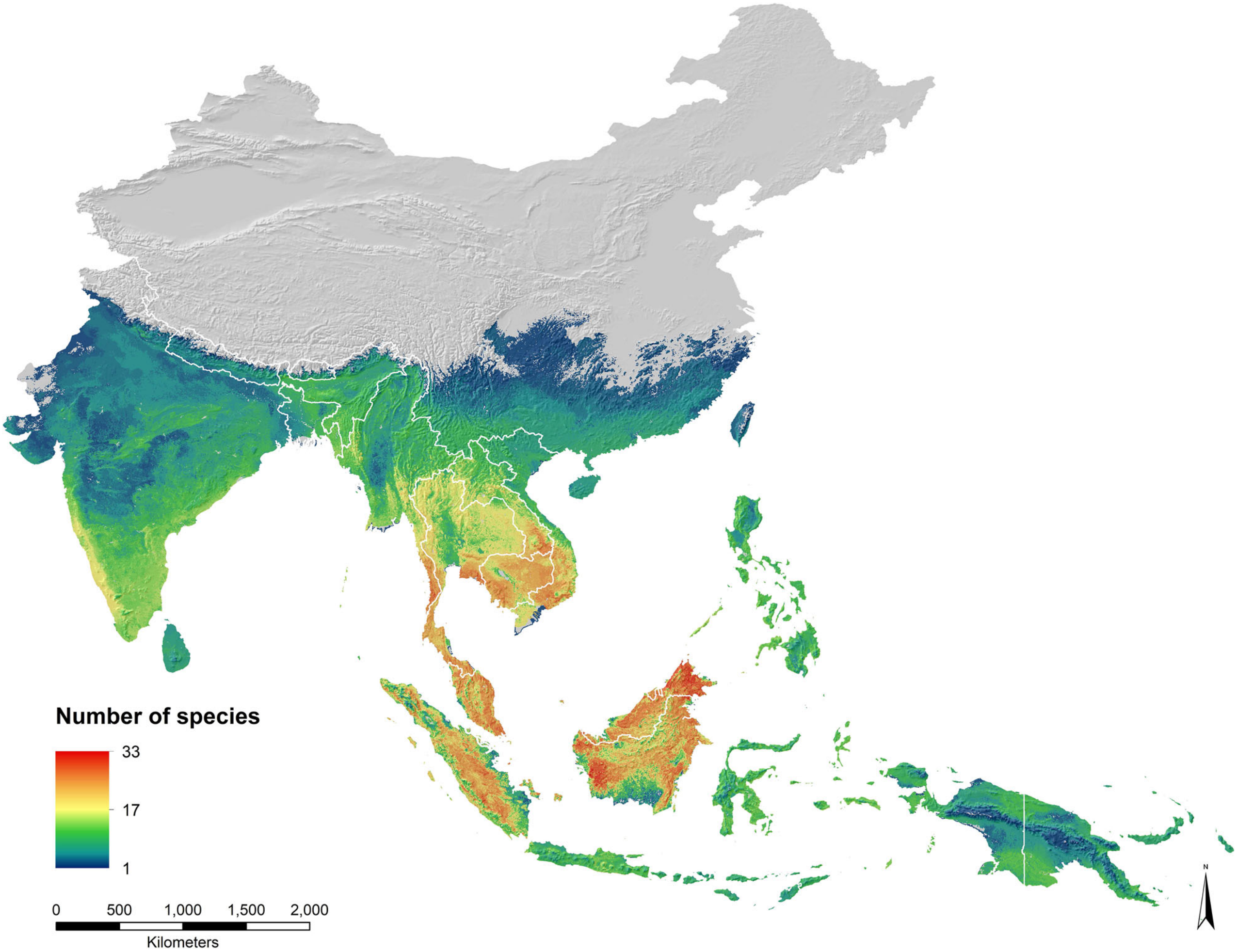

FIGURE 1 Number of socioeconomically important tropical and subtropical Asian tree species ($n = 63$) per grid cell (approximately 4.5×4.5 km) in the study of priority areas for conservation and restoration. The natural distribution ranges of species were estimated by validated species distribution models

crassna (63% of its distribution; range 38–85%) (overexploitation single most important threat).

In areas where high to very high vulnerability to current threats coincided with low vulnerability to climate change, we recommend implementing restoration activities, ranging from assisted natural regeneration to tree planting. Assisted natural regeneration aims at accelerating succession by removing or reducing barriers to forest regeneration, such as competition with weedy species or recurring disturbances (e.g., fire and cattle grazing). If this measure is not sufficient, enrichment planting can be used to speed up the process and to ensure sufficient diversity of the restored forest (Shono et al., 2007). Areas with high to very high vulnerability to current threats were assumed to be most in need of restoration, whereas the low climate change vulnerability increased the probability of survival of the planted or regenerating trees under future climate conditions. Seed collection for ex situ conservation in gene banks and conservation stands or supporting assisted migration programs (whereby seeds are planted in areas that are expected to remain suitable in the future) is recommended in areas with high to very high vulnerability to climate change to safeguard the genetic resources that might otherwise disappear in the future.

Priority areas for conservation and restoration

Across all 63 tree species, on average 10% (range 5–19%) of the distribution area was prioritized for in situ conservation and 40% (range 21–58%) for restoration activities, whereas on average, 3% (range 3–4%) of the distribution area was predicted to become unsuitable as a result of climate change. Three examples of priority action maps of rarely or uncultivated species identified as highly endangered are in Appendix S2.

Nearly three-quarters (74%; range 74–79%) of the areas prioritized for in situ conservation were located outside existing protected areas. Conservation priority areas were concentrated in tropical and subtropical moist broadleaf forests (90% of priority areas with a range of 87–93%, compared with 70% of the combined species ranges in these forests). In contrast, areas prioritized for conservation were underrepresented in tropical and subtropical dry broadleaf forests (7%; range 5–11%; compared

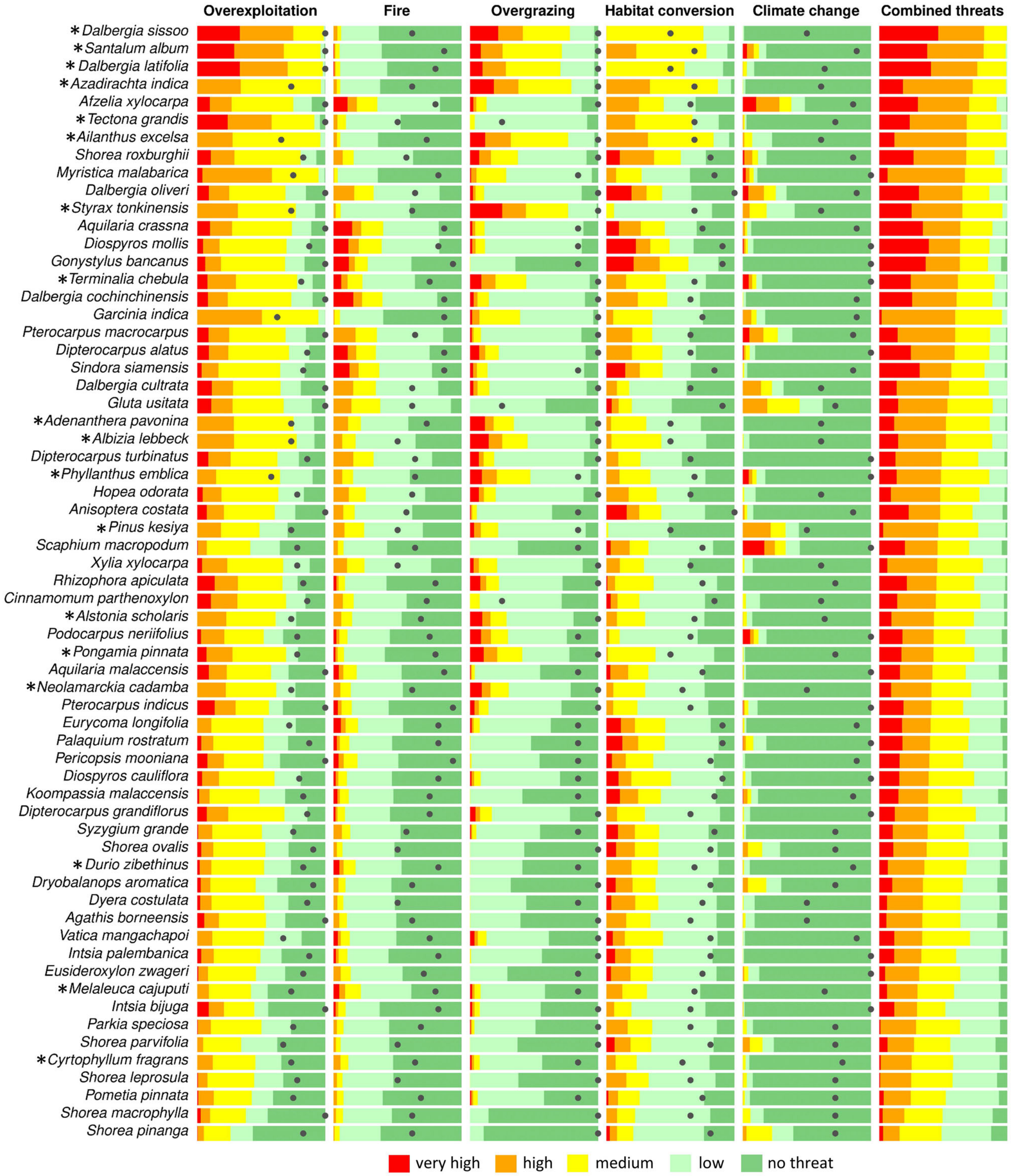

FIGURE 2 Threat sensitivity and vulnerability estimates for 63 tree species relative to five threats and the five threats combined (gray dots, sensitivity values; bars, relative share of distribution range of each species by level of threat [very high, high, medium, low, and no threat]; *, widely cultivated species). Species are in decreasing order of share of distribution range under high or very high vulnerability to combined threats

with the combined species ranges of 17%). Major in situ conservation hotspots (Figure 4) were in Tenasserim-South Thailand semi-evergreen rain forests in Myanmar and Thailand; Central and Southeast Indochina dry forests, close to the borders between Thailand, Laos, Cambodia, and Vietnam; Cardamom Mountains rain forests between Thailand and Cambodia; Peninsular Malaysian rain forests; and Borneo lowland and montane rain forests in Malaysia (Sabah, Sarawak) and Indonesia

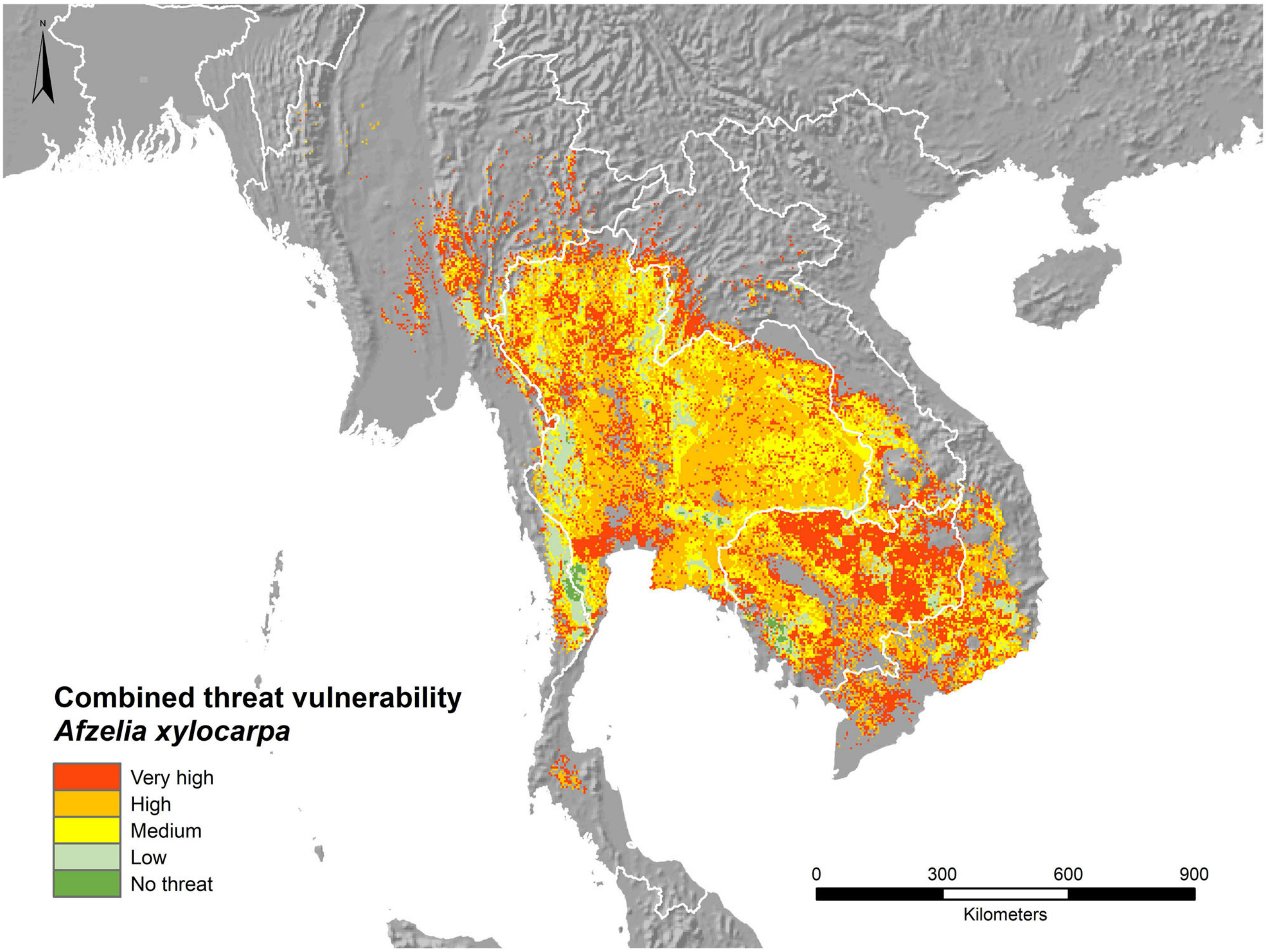

FIGURE 3 Vulnerability of the socioeconomically important tree *Afzelia xylocarpa* in the Greater Mekong Subregion to the combined threats of overexploitation, fire, overgrazing, habitat conversion, and climate change

(Kalimantan). The largest aggregation of hotspots for in situ conservation was predominantly outside existing protected areas in northern Tenasserim rain forests in Myanmar and in Borneo lowland and montane rain forests.

Areas predicted to become unsuitable for species because of climate change were proportionally represented in tropical and subtropical moist broadleaf forests (68%; range 68–71%), whereas they were more concentrated in tropical and subtropical dry broadleaf forests (26%; range 24–27%). In the entire region, sites with high threat level due to climate change overlapped for fewer than 10 of the study species and occurred widespread across the combined distribution range (Appendix S2).

A little more than half of the hotspots for restoration were in areas predominantly converted to agriculture (54%; range 47–57%). The remaining portion was in natural areas, where threat levels were high due to threats, such as overexploitation or fire. Restoration priority areas were almost proportionally represented in tropical and subtropical moist broadleaf forest (67%; range 66–68%), where most of the studied species grew, and overrepresented in tropical and subtropical dry broadleaf forests (24%; range 22–24%). Major restoration hotspots (Figure 5) were in Western Ghats moist deciduous and montane rain forests; East and South Deccan Plateau dry and the southern Deccan thorn scrub forests; Central and Southeast Indochina dry forests in Thailand, Cambodia, and Laos; Chao Phraya lowland moist deciduous forests in Thailand; Tenasserim-South Thailand and Peninsular Malaysian rain forests; and Sumatran lowland rain forests of Indonesia. Contiguous restoration hotspots in degraded natural lands (i.e., not converted to agriculture) (Figure 5) were in Western Ghats forests; Central and Southeast Indochina dry forests in northern Thailand, Cambodia, and Laos; and Sumatran lowland rain forests.

The proportion of area recommended for in situ conservation was highest in Indonesia, which represented about 40% of the total area recommended for in situ conservation, compared with 27% of the total predicted species distribution ranges in the country (Table 1). Only 17% of this area was inside designated protected areas (Figure 4). India had the highest proportion of priority areas for restoration; on average, 33% of the distribution ranges of the studied tree species were recommended for

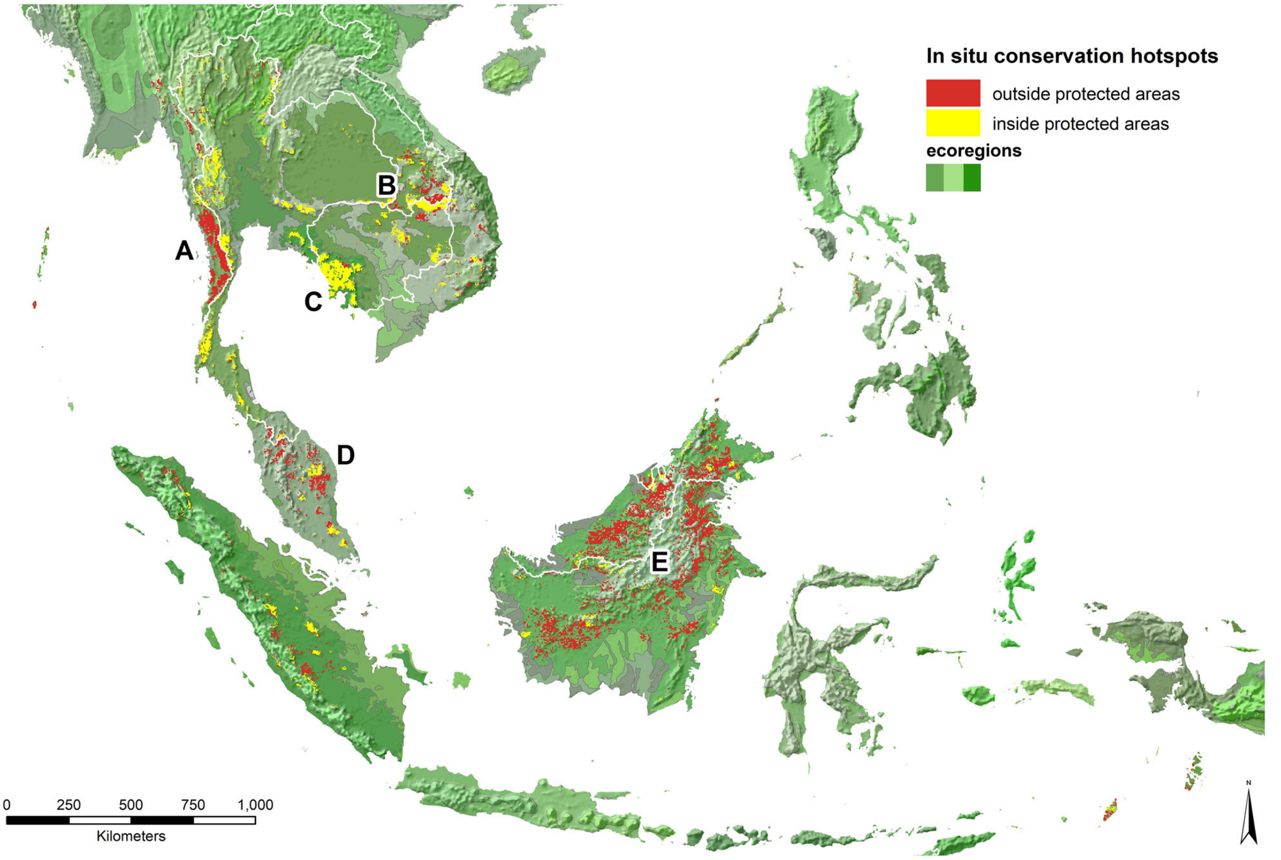

FIGURE 4 In situ conservation hotspots for the 63 priority tree species in Southeast Asia (red, in situ conservation hotspots overlap for at least 10 tree species outside protected areas; yellow, in situ conservation hotspots overlap for at least 10 tree species inside protected areas; a–e, major in situ conservation hotspots; green, ecoregions)

restoration (compared with 21% of total species ranges in the country) (Figure 5), followed by Indonesia (18%) and Thailand (11%). Priority restoration areas for degraded natural habitats were mainly in Indonesia, where they accounted for 13% of the combined species ranges. Countries with the largest share of species' combined habitat likely to become unsuitable due to climate change by 2050, and, therefore, prioritized for ex situ conservation, were India (21%), Indonesia (20%), Thailand (15%), Myanmar (11%), Laos (8%), and Vietnam (7%). The remaining countries were expected to lose on average <6% of the current combined distribution ranges of the studied tree species.

All vulnerability, priority conservation, and restoration maps of the 63 studied tree species and the priority activity maps for the combination of species are freely available from Tree Diversity Platform (https://www.tree-diversity.org/interactive-map).

DISCUSSION

Although the selected tree species represent diverse ecological traits and uses, all 63 were highly threatened by at least one of the five threat factors across an average of nearly half (47%) of their native distribution ranges. This indicates the need to increase targeted conservation and restoration activities for tropical and subtropical Asia's native tree diversity and to simultaneously prevent local extinctions of valuable species and their genetic diversity as well as support human communities and societies in adapting to environmental changes as they strive to meet socioeconomic development goals. We based recommend for conservation and restoration for local, national, and regional levels on our results.

First, our results help identify highly valued species at risk of extirpation and inform the design of species conservation and development plans in the context of progressive climate change. Given the high pressure from multiple threats, some populations and their genetic resources likely cannot be conserved over long term in natural habitats or as remnant trees in human-modified landscapes; rather, they will require complementary ex situ conservation measures, such as specifically established conservation or restoration stands or field gene banks, to avoid their permanent loss. In contrast to crop seeds, conservation of seeds in seed banks is seldom feasible because the seeds of many tropical trees do not germinate ex situ and lose viability quickly (Sacandé et al., 2004). Cultivation of socioeconomically important species within their natural ranges, especially in collaboration with local communities, can contribute to conservation and livelihood benefits, but it requires policy support and market mechanisms to help

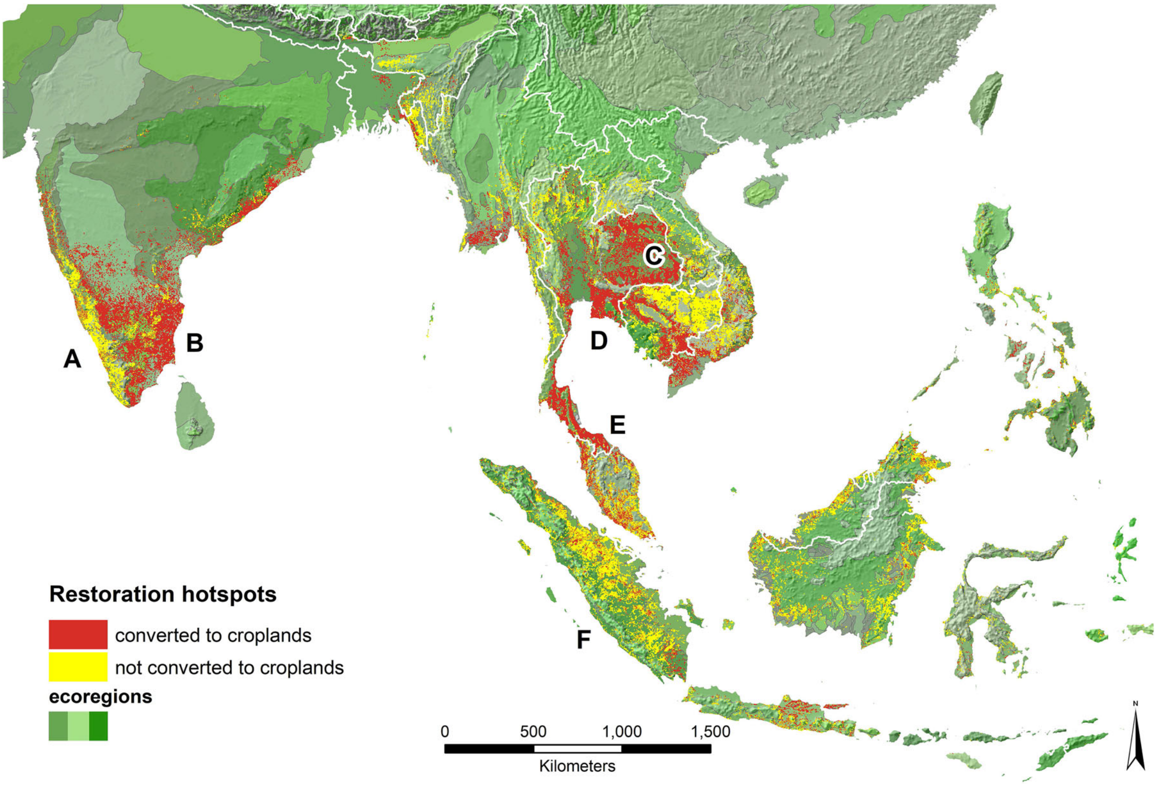

FIGURE 5 Restoration hotspots for the 63 important tree species in South and Southeast Asia (red, restoration hotspots overlap for at least 10 tree species that have been converted to cropland; yellow, restoration hotspots overlap for at least 10 tree species that are not under cultivation; a–f, major restoration hotspots; green, ecoregions)

shift pressure from natural populations. This need was recognized in the Glasgow Leaders' Declaration on Forests and Land Use (UNFCCC, 2021), which pertains to 90% of the world's forests. Attention to representativeness of genotypes and geneflow between wild and cultivated populations is also required (Ashton et al., 2014; Gaisberger et al., 2020). Such efforts are compatible with current forest and landscape restoration targets and could be supported with restoration-related investments, but the current widespread lack of genetic diversity in restoration plantings limits their value for species conservation (Jalonen et al., 2018).

Second, although our results optimistically predict relatively limited climate change impacts for most species, the species' vulnerability to climate change varied widely and populations of some species may be pushed beyond their tolerable limits in some ecoregions as soon as by 2050, even without considering the potentially synergistic effects of multiple threat interactions. Assisted migration programs may be needed to safeguard the genetic diversity of such species and populations. Remaining natural populations of widely cultivated species contain valuable genetic variation for tree improvement (Lohr et al., 2016) because climate change is making new demands on species adaptation (Keenan, 2015). At the same time, impacts of population decline of vulnerable, socioeconomically important tree species on local livelihoods and ecosystem service provision need to be analyzed.

Third, in Asia's highly species diverse countries, the combined multispecies maps help identify target areas, where conservation actions generate the most synergy between species and, thus, optimize the use of land and resources. Specifically, the identified priority conservation areas outside of current protected area networks should be of the highest priority because these populations are unprotected, unmonitored, and expected to be of high genetical diversity. Therefore, these populations could serve as important seed sources for fulfilling the seed demands for multimillion hectare land restoration commitments and for rebuilding resilience in degraded ecosystems (Atkinson et al., 2021). Moreover, the priority action maps allow identifying synergies between countries in genetic resources conservation because responsibilities can be shared for ecoregions that extend beyond country boundaries. Countries can also enhance their collaboration in maintaining seed sources and exchanging genetic material to meet restoration targets or serve other planting programs for high-value native species.

Fourth, our results support the implementation of restoration efforts by informing the selection of target species and restoration strategies for specific contexts, which is especially important for the many tree species in the Asian tropics that have seeds that cannot be stored for long periods (i.e., recalcitrant seeds) (Kettle, 2009). They provide information on the species' current and future suitability and the extent to which they are threatened and thus benefit from restoration.

TABLE 1 Conservation and restoration priorities for 63 important tree species in South and Southeast Asia by country[a]

Country	Number of species	Share of cumulative distribution area (%)	In situ conservation priority area (%)	Share of protected areas (%)	Restoration priority area (%)	Share of cropland (%)	Ex situ conservation priority area (%)
Indonesia	33	27.2	40.5	17.1	17.7	23.9	20.5
India	19	21.0	1.9	31.8	32.8	77.0	20.0
Thailand	30	9.3	7.3	81.5	10.8	79.7	15.0
Malaysia	33	8.2	13.7	12.7	6.7	34.9	3.7
Myanmar	31	7.2	8.1	12.7	5.4	36.2	11.3
China	16	6.1	2.6	0.2	7.2	16.4	5.4
Vietnam	29	4.5	1.9	43.0	5.1	48.1	6.6
Cambodia	28	4.3	5.5	83.0	5.5	34.7	6.0
Laos	28	3.8	5.3	36.0	2.6	9.8	8.1
Papua New Guinea	12	3.2	9.8	2.8	0.4	16.1	1.2
Philippines	16	2.9	2.3	49.3	2.4	47.7	0.8
Bangladesh	15	1.0	0.1	8.6	2.1	72.9	0.5
Nepal	9	0.4	0.0	20.4	0.6	52.9	0.4
Sri Lanka	9	0.4	0.4	81.8	0.4	44.7	0.0
Brunei	29	0.2	0.5	35.9	0.1	3.8	0.1
Timor-Leste	11	0.1	0.1	26.2	<0.1	59.1	0.1
Bhutan	14	0.1	0.1	49.0	<0.1	12.6	0.1
Singapore	23	<0.1	<0.1	13.3	<0.1	6.1	<0.1

[a]Includes countries with at least five occurring species. Calculations are based on the sum of the grid cells of the modeled distribution ranges of coinciding species. Countries are in decreasing order of share of total distribution area.

Species-site matching remains a common bottleneck limiting the effectiveness of restoration efforts (Brancalion & Holl, 2020). The combined conservation and restoration priority map, together with the species-specific priority maps, help to identify seed sources for restoration that are less vulnerable and, therefore, likely to maintain higher genetic variability, resulting in better growth, survival, and productivity. Because predicted high-quality habitat is likely to be correlated with high species abundance (Acevedo et al., 2017), it should be easier to collect seeds in these areas from a large number of trees, which is crucial to ensure the collected material is sufficiently genetically diverse (Thomas et al., 2014). Moreover, our method allows the identification of priority restoration areas in natural forests and woodlands at high risk of degradation, which are often excluded from global analyses because degradation remains poorly characterized and is not easily distinguished with remote sensing (Gao et al., 2020). Degraded natural ecosystems can contribute substantially to several global challenges (IPBES, 2018) and are likely easier and cheaper to restore than areas converted to croplands (Crouzeilles et al., 2020). Restoration hotspots in unconverted land amounted to approximately 63 million ha (7% of the total modeled area), indicating that they could greatly contribute to meeting global restoration goals in the region (CBD, 2011; CBD, 2021). In already converted land, agroforestry is likely often a more feasible solution for maintaining species populations across their environmental ranges, especially because all target species are socioeconomically important, but implementation depends on opportunity and operation costs. An important next step would be to complement our results with estimates of restoration costs and benefits (Strassburg et al., 2020).

Development of species-specific decision support is necessarily knowledge intensive. Trait-based approaches can help assess impacts of threats on groups of species sharing similar traits, including lesser known species. That we could not create stable distribution models for nearly 13% of the prioritized species due to the lack of occurrence data confirms the persistence of data gaps for even the most important species (Serra-Diaz et al., 2017), and efforts are needed to gather additional information.

Our vulnerability and conservation and restoration priority maps were created with the aim to be easily interpretable by practitioners and policy makers to support the planning of effective, efficient, tree-based conservation and restoration actions. Our spatially explicit analysis, coupled with the species-specific climate change threat factors, makes our method an ideal complement to the IUCN Red List assessments (BGCI, 2021).

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