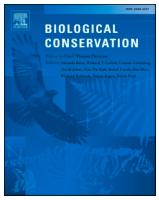
Biological Conservation 270 (2022) 109560

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon



Range-wide priority setting for the conservation and restoration of Asian rosewood species accounting for multiple threats and ecogeographic diversity

Hannes Gaisberger [a,b,*], Tobias Fremout [i,j], Thea So [c], Bansa Thammavong [d], Chaloun Bounithiphonh [d], Tran Thi Hoa [e], Zheng Yongqi [f], Tania Kanchanarak [g,h], Suchitra Changtragoon [k], Sineath Sreng [c], Huang Ping [f], Tin Hang Hung [l], Pyae Pyae Win [m,n], Ida Hartvig [o,p], Ida Theilade [q], David Boshier [l], John MacKay [l], Chris Kettle [b,r], Riina Jalonen [g]

[a] Department of Geoinformatics, Paris Lodron University, Schillerstr. 30, 5020 Salzburg, Austria
[b] Bioversity International, Via di San Domenico 1, 000153, Rome, Italy
[c] Institute of Forest and Wildlife Research and Development, Khan Sen Sokh, Phnom Penh, Cambodia
[d] Forest Research Center, National Agriculture and Forestry Research Institute, Vientiane, Laos
[e] Forest Genetics and Conservation Center for Biodiversity and Biosafety, Institute of Agricultural Genetics, Vietnam Academy of Agricultural Sciences, Hanoi, Viet Nam
[f] Research Institute of Forestry, Chinese Academy of Forestry, Dongxiaofu, Xiangshan Road, Haidian District, 100091 Beijing, China
[g] Bioversity International, c/o TNCPI, Universiti Putra Malaysia, 43400 UPM Serdang, Selangor, Malaysia
[h] The School of Biological Sciences, University of Aberdeen, UK
[i] Division of Forest, Nature and Landscape, KU Leuven, Celestijnenlaan 200E - box 2411, 3001 Leuven, Heverlee, Belgium
[j] Bioversity International, c/o CIP Av La Molina 1895, La Molina, Lima 12, Peru
[k] Department of National Parks, Wildlife and Plant Conservation, 61 Phahonyothin Rd, Lat Yao, Chatuchak, Bangkok 10900, Thailand
[l] Department of Plant Sciences, University of Oxford, Oxford, OX1 3RB, UK
[m] Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw 05282, Myanmar
[n] Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla, Yunnan 666303, China
[o] Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, DK-1958 Frederiksberg C, Denmark
[p] Smithsonian Environmental Research Center, Smithsonian Institute, 647 Contees Wharf Rd, Edgewater MD 21037, MD, USA
[q] Department of Food and Resource Economics, University of Copenhagen, Rolighedsvej 23, DK-1958 Frederiksberg C, Denmark
[r] Department of Environmental System Science, ETH, Zurich, Switzerland

ARTICLE INFO

Keywords:
Threat assessment
Distribution and vulnerability mapping
Ecogeographic diversity
Dalbergia ssp.
Conservation planning
Climate change

ABSTRACT

Understanding the impact of multiple anthropogenic threats on tree species is urgently needed for estimating population decline and enabling coordinated and efficient conservation actions. We applied a spatially explicit framework to assess the vulnerability of three highly valuable Asian rosewood species (*Dalbergia cochinchinensis, D. cultrata, D. oliveri*) to five key threats across their native ranges in six countries of the Greater Mekong Subregion. All three species face significant threat levels from at least one of the five threats in more than 75% of their native ranges, including within existing protected areas. Overexploitation is the single most important threat (53–60%), followed by habitat conversion (17–41%) and fire (20–28%). About 21% of the distribution range of *D. cultrata* is under medium to very high threat from climate change, which is predicted to have less impact on *D. oliveri* and on *D. cochinchinensis*. Based on our threat assessment we delineated species-specific priority areas for conservation and restoration that we subdivided by ecoregions as a surrogate for adaptive variation within species. Half of the ecoregions were classified as priority for improving the conservation of adaptive variation in one or more of the species. We propose spatially explicit follow-up actions that include *in situ* conservation, restoration, and *ex situ* conservation to improve the effectiveness of current conservation measures to capture adaptive variation within species. Transboundary coordination will be important to effectively address conservation threats. The study can act as a model for regional planning for other valuable tree species.

* Corresponding author at: Department of Geoinformatics, Paris Lodron University, Schillerstr. 30, 5020 Salzburg, Austria.
E-mail address: hannes.gaisberger@stud.sbg.ac.at (H. Gaisberger).

https://doi.org/10.1016/j.biocon.2022.109560
Received 9 September 2021; Received in revised form 18 February 2022; Accepted 13 April 2022
Available online 28 April 2022

1. Introduction

Multiple anthropogenic threats drive local extinctions of tropical tree species (Abel-Schaad et al., 2018; Fremout et al., 2020; Gaisberger et al., 2021; Gallagher et al., 2021). In addition to the mounting pressure from global warming, forest habitats in the Greater Mekong are being rapidly destroyed by industrial-scale illegal logging and agricultural expansion (Foley, 2020). The resulting loss of genetic diversity limits the opportunities to restore viable, productive populations and reduces the species' ability to adapt to and survive under a changing environment (Sork et al., 2010). Species-specific conservation and management plans that consider the within-species (intraspecific) variation in traits and responses to threats are needed, but high species diversity coupled with limited resources in lower-income countries constrain the development and application of such planning. For example, even basic information about the current distribution of tropical tree species is often lacking (Botanical Gardens Conservation International (BGCI), 2021; Serra-Diaz et al., 2017; Gaisberger et al., 2021). Efficient and practical priority setting is urgently needed to not only prevent further population decline but also to reverse the trend and push back highly threatened species from the brink of extinction.

The precarious status of Asian rosewoods (*Dalbergia spp.*) illustrates how conservation and management of even the most highly valued tropical tree species is fraught with such challenges. Sought for their beautiful reddish timber used for making luxury furniture, wood carvings and instruments, *Dalbergia spp.* can fetch prices as high as US $50,000 m^{-3} (Winfield et al., 2016). High demand for the species has driven illegal logging across the Greater Mekong. Trade initially focused on Siamese rosewood (*Dalbergia cochinchinensis*), but as the species has become increasingly rare, exploitation shifted to other species such as Burmese rosewood (*Dalbergia oliveri*) and other genera such as *Pterocarpus spp*. *Dalbergia* species were recognized as threatened as early as in 1998 on the IUCN Red List of Threatened Species (IUCN, 2021) but their exploitation has only intensified since then (Winfield et al., 2016). In 2017, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) placed the entire genus of *Dalbergia* on its Appendix II, restricting international trade to reduce pressure on the remaining natural populations.

Tree population decline can be driven by intense reduction or fluctuations in the number of mature individuals (IUCN Standards and Petitions Committee, 2019) or other processes that limit reproduction, regeneration, or genetic diversity of offspring. Illegal logging is the most severe threat to many *Dalbergia spp.* (Winfield et al., 2016), and mature trees that produce the valued heartwood are often completely wiped out in the region's landscapes. While the species are capable of coppicing (So et al., 2010), the common practice of digging out stumps limits regeneration, and even when clonal reproduction occurs, it does not help maintain genetic diversity. *Dalbergia* ssp. are also affected by land conversion to agriculture (Liu et al., 2019), eliminating both mature trees and regeneration, as well as grazing and fire that limit regeneration potential in the seasonally dry tropical forests (Prasad, 2001). Impacts of climate change on the species remain unknown but may affect seedling establishment and regeneration (Hung et al., 2020) and intensify the impacts of other threats such as more frequent fires. Assessing the vulnerability of species to multiple threats is fundamental for the planning of cost-effective restoration and conservation actions (Butt et al., 2016).

Population genetic studies show high levels of intraspecific diversity between populations of *Dalbergia oliveri* and *D. cochinchinensis*, indicating limited geneflow and potentially high local adaptation (Hartvig et al., 2018). This differentiation may result partly from the complex relief and biogeographical history in the Greater Mekong Subregion (Woodruff, 2010). The Mekong River and other large water bodies also act as barriers to the species' dispersal (Sander et al., 2018). Population genetic studies have identified several distinct clusters of populations, often extending across national border zones (Hartvig et al., 2018). Therefore, local extinction of the species observed throughout the subregion suggest permanent loss of genetic diversity and adaptive capacity. In the absence of range-wide genetic data, environmental distances are valid surrogates in conservation planning for representing genetic variation (Hanson et al., 2017). Ecoregions, encompassing geographic areas with similar environmental conditions, are useful to delineate areas in which plant species face little disruption of population genetic patterns or loss of local adaptation (Miller et al., 2011).

Interest for planting *Dalbergia spp.* is growing rapidly in the subregion. In Cambodia, *D. cochinchinensis* is among the most planted tree species (Institute of Forest and Wildlife Research and Development, Cambodia, unpublished report). Planted populations can both relieve the pressure on the natural populations and help conserve their genetic diversity. However, their productivity and conservation value depend on the genetic diversity of the planting material and its suitability to the environmental conditions (Broadhurst, 2013). Seed sourcing for planting these species relies on declining natural populations, illustrating how conservation and restoration are intertwined and need to be considered together.

In this study we present a spatially explicit framework based on habitat suitability modelling, threat exposure estimates and a trait-based sensitivity scoring approach (Fremout et al., 2020) to assess the vulnerability of three highly valuable Asian rosewood species (*Dalbergia cochinchinensis, D. cultrata, D. oliveri*) to current threats (overexploitation, fire, overgrazing, habitat conversion) and climate change across their native ranges in six countries (Cambodia, China, Laos, Myanmar, Thailand and Vietnam). Based on threat vulnerability levels we delineated species-specific priority areas for conservation and restoration. We refined the results by subdividing the priority areas by ecoregions as surrogate for genetic diversity to capture adaptive variation within species. The objectives of this study were to (i) assess the vulnerability of three economically important Asian rosewood species to key threats, (ii) identify species-specific and ecoregional conservation and restoration priorities to conserve adaptive variation within species, and (iii) explore opportunities for cooperation and synergies between countries in their conservation efforts across the species' ranges.

2. Materials and method

2.1. Habitat suitability modelling

Species occurrence data was collected from scientific and grey literature, national and global databases, and individual research projects (Table A1). The initial dataset with 565 occurrence records underwent a three-step cleaning process to ensure quality control and a spatial filtering process to reduce the negative effects of uneven sampling (Supplementary text). The final occurrence dataset of the three *Dalbergia* species used for spatial analysis consisted of 355 occurrence points (Table A2).

We tested 31 potential predictor variables (Table A3) that included bioclimatic variables from the CHELSA v2.1 database (Karger et al., 2017), edaphic variables from the SoilGrids v1 database (Hengl et al., 2017) and topographic variables (Danielson and Gesch, 2011), 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 using a stepwise procedure. A subset of 18 remaining predictors (Table A3) at a spatial resolution of 30 arcsec (*ca.* 0.9 km at the equator) were used to model the habitat suitability of the three *Dalbergia* species using the maximum entropy algorithm (Maxent) (Phillips et al., 2018).

As default settings might lead to overfitting (Radosavljevic and Anderson, 2014), we executed Maxent across a range of different settings using the R package ENMeval (Muscarella et al., 2014), to balance goodness-of-fit with model complexity and to evaluate models with spatially independent partitions. For each species we therefore selected

the model with the lowest Akaike information criteria (AICc) value (*i.e.*, $\Delta AICc = 0$) as best performing model for subsequent spatial analysis. We also calculated a widely used performance metric for SDMs, the area under the receiver operating characteristic curve (AUC), in order to facilitate comparison with other studies. The models were evaluated using 4-fold cross-validation using spatially independent checkerboard partitioning of presence and background records (Muscarella et al., 2014). Background points were randomly selected from a geographic extent similar to the one of the occurrence points, which is aimed at improving the discriminatory power of models in the core distribution area (Acevedo et al., 2012), as well as the transferability in place and time (Phillips, 2008). For this purpose, we created for each of the three species a convex hull around the presence locations, extended with a buffer corresponding to 20% of the longest axis between presence points. To avoid omitting large areas where species may be present from our analysis, we converted the suitability maps into presence-absence maps using the 10th percentile training presence omission threshold.

The resulting maps were validated through an online consultation with species experts and a review of literature and existing species databases. As part of this process, modeled distribution ranges of the species in states or provinces and in ecoregions not confirmed as part of their natural distribution (*e.g.*, due to barriers to dispersal such as mountain ranges) were identified and excluded from the maps.

2.2. Threat exposure

For each of the five threats (overexploitation, fire overgrazing, habitat conversion, and climate change), threat exposure estimates were constructed using freely accessible spatial datasets (Table A4), according to the methodology described in Gaisberger et al. (2021) and in Table A5. The exposure estimates, aimed to reflect the expected impacts at population level (Table A4), were created as grid layers with values ranging from 0 (no threat exposure) to 1 (maximum threat exposure). They reflect current exposure levels, except for climate change, in which case they reflect expected future levels. To assess the exposure to climate change, we projected the distribution models of the three *Dalbergia* species to predicted climate conditions for 2055 (2041–2070 period), using the following downscaled General Circulation Model (GCM) predictions, obtained from the CHELSA database (https://chelsa-climate.org/cmip6/; Karger et al., 2017): GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1–2-HR, MRI-ESM2–0, and UKESM1–0-LL. The climate change exposure maps were created by calculating the number of different GCMs predicting presence of suitable habitat across the validated distribution ranges. All grid layers used to construct the exposure maps had a spatial resolution of 30 arcsec (*ca.* 0.9 km at the equator). To assess the robustness of the threat mapping methodology, we carried out a sensitivity analysis by creating reference-, best- and worst-case scenario exposure maps (Figs. A1–A2) for each of the considered threats (details in Table A5).

2.3. Sensitivity and vulnerability

To estimate the sensitivity of the three *Dalbergia* species to the five key threats we applied a sensitivity scoring approach (Fremout et al., 2020) in which explicit relations between tree functional traits and resistance against threats were established based on literature and expert judgement. We focused on a subset of 10 key traits with 'medium' to 'very high' importance, which we compiled through a separate literature study (Table A6). The details of the data used to estimate species sensitivities and the final trait-based sensitivity scores are available in Gaisberger et al. (2021) and Tables A7 and A8.

Species-specific 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 the expert corrected species distribution area. The grid cells of the vulnerability maps were categorized into five classes (no threat, low, medium, high, and very high) using the thresholds of 0.01, 0.25, 0.50 and 0.75. As multiple stressor interactions, ranging from synergistic to antagonistic effects, are complex and difficult to predict for real-world applications (Côte et al., 2016), for simplicity we defined the combined vulnerability of an area, corresponding to an individual pixel, as the highest vulnerability among the individual layers. To identify the overall vulnerability of a species, we calculated the proportion of distribution area under 'medium' to 'very high' vulnerability to current and predicted climate change threats individually and in combination.

2.4. Priority action maps for conservation and restoration

Based on the vulnerability to current threats (overexploitation, fire, overgrazing and habitat conversion) and to climate change, we present the following conservation and restoration planning strategy (Fremout et al., 2020). We recommend (i) *in situ* conservation of populations in areas where both current and climate change threat levels are low, (ii) restoration activities such as active planting or assisted regeneration of populations in areas where current threat levels are high but climate change threat levels are low, and (iii) *ex situ* conservation of populations in areas where climate change threat levels are high, in order to safeguard the genetic resources that might disappear due to climate change by 2055. The remaining combinations of current and climate change threat levels were classified as (iv) 'no single priority action' areas and may benefit from a combination of conservation and restoration approaches (*e.g.*, passive restoration) depending on the site context.

We restricted the prioritized area for *in situ* conservation to areas where the modeled distribution showed highly suitable habitat (values ≥ 0.7) as predicted by the Maxent models, with the aim to identify populations that are likely to have maximal fitness and adaptive capacity (Nagaraju et al., 2013). In addition, the priority action maps were overlaid with a protected areas map (UNEP-WCMC and IUCN, 2018), updated with protected areas for Cambodia (Gaisberger et al., 2021), to assess the proportion of species' native distribution ranges that are currently under some type of protection and with a land cover map (Latham et al., 2014) to identify areas that are 'natural' or converted to agricultural land use. We defined as 'natural' all areas that were not classified as 'cropland'. The distinction between converted and non-converted areas is important as these land use types may require different conservation and restoration strategies. Large-scale ecological restoration projects are more likely to be implemented in non-converted areas whereas agroforestry might be the more appropriate restoration strategy in areas already converted to agriculture (Fremout et al., 2020).

2.5. Ecoregional diversity

We partitioned the modeled distribution ranges of the three *Dalbergia* species by ecoregions (Dinerstein et al., 2017), as surrogate for adaptive genetic variation (Miller et al., 2011), and combined it with the priority action maps to obtain subdivisions of species distribution areas likely to represent patterns of intraspecific adaptive variation (Fig. A3). Modeled distribution area not prioritized for restoration or *ex situ* conservation was classified as 'stable'. Ecoregions were defined as priority for improving the conservation of adaptive variation when less than 10% of the potential distribution area was stable and within protected areas. Three possible follow-up actions were identified for these priority ecoregions: (i) designating additional protected areas or conservation units in areas prioritized for *in situ* conservation that remain outside the existing protected area network, (ii) restoring the species' populations in areas prioritized for restoration (degraded or converted lands but remaining suitable for the species under climate change), and (iii) conserving the species *ex situ* through seed collection and field gene banks, especially when conservation targets could not be met through the other means (*i.e.* >90% of the potential distribution area becoming unsuitable for the species under climate change). A combination of these actions could be applied in each ecoregion to meet the conservation

threshold. All area calculations were carried out after transformation into Cylindrical Equal Area's projection.

3. Results

3.1. Modeled species distribution

The cross-validated AUC values of the best performing SDM per species (with lowest AICs values) ranged from 0.85 to 0.93, indicating excellent accuracy.

3.2. Exposure and vulnerability to key threats

We created exposure maps for each of the five threats (over-exploitation, fire overgrazing, habitat conversion, and climate change) across the distribution ranges of the target species (Figs. A1–A2).

All three *Dalbergia* species show medium to very high threat levels for at least one of the five threats in more than 75% of their potential distribution area (Table 1 and Figs. A4–A6). Overexploitation is the single most important threat (53–60%) and, together with fire (20–28%) and overgrazing (14–16%), is affecting all three species to a similar extent, whereas the vulnerability to the other three threats varies more strongly between the species. Habitat conversion poses an important risk across the species' ranges to *D. cochinchinensis* (41%) and *D. oliveri* (38%) but is less of a risk for *D. cultrata* (17%). In return, *D. cultrata* is more threatened by climate change (21%), which is predicted to have less effects on *D. oliveri* (13%) and on *D. cochinchinensis* (7%).

3.3. Conservation and restoration priorities across the species' native ranges

Based on the threat levels of current threats and climate change we mapped priority areas for conservation and restoration actions for the three *Dalbergia* species (Fig. 1, Table 2). On average 12% (range 11–12%) of the distribution ranges are prioritized for *in situ* conservation, 27% (range 15–42%) for restoration activities, and 6% (range 3–9%) for *ex situ* conservation. The sensitivity analysis indicated that an average of 22% (±2 SD) of the grid cells of the priority area maps within species' distribution ranges changed from one category to another compared with the reference maps for the best-case priority maps and 27% (±3) for the worst-case priority maps.

At least 10% of the species' predicted distribution in each of the countries falls within protected areas, except for *D. cochinchinensis* in Vietnam, and *D. cultrata* and *D. oliveri* in China, Myanmar and Vietnam (Table 2). Cambodia has the highest proportion of the species' potential distribution ranges under protection, ranging from 38 to 57%. However, species are in some cases severely threatened also within the protected area network: for example, 42% of the current distribution of *D. cultrata* within protected areas in Cambodia is prioritized for restoration due to high vulnerability to current threats. Similarly, 28–52% of the species distribution ranges in protected areas in Cambodia are predicted to become unsuitable for the species due to climate change and are prioritized for *ex situ* conservation.

Areas prioritized for *in situ* conservation account for 11–12% of the total distribution ranges. More than 95% of these areas occur outside of the current protected areas for *D. cultrata* in China and in Myanmar and for *D. oliveri* in Myanmar. Restoration priority areas for *D. cochinchinensis* are mostly located in Thailand (56%) and Cambodia (46%) and those for *D. oliveri* in Cambodia (38%) and Vietnam (35%). The largest portion of distribution range prioritized for *ex situ* conservation is located in Vietnam (49%) for *D. cultrata*.

3.4. Ecoregional diversity

The conservation status of the three *Dalbergia* species varies largely by ecoregion. For *D. cochinchinensis*, 6 of the 11 ecoregions (55%) have less than 10% of the species predicted distribution in stable protected areas. For *D. cultrata*, the proportion is 10 of 20 ecoregions (50%) and for *D. oliveri,* 9 of 19 ecoregions (47%) (Tables 3 and A10). Three ecoregions with predicted species distribution have less than 1% of stable protected areas: Northern Thailand-Laos moist deciduous forests for *D. cochinchinensis*, Irrawaddy dry forests for *D. cultrata* and *D. oliveri*, and Yunnan Plateau subtropical evergreen forests for *D. cultrata*. The stable protected area is also very small (<100 km^2) for individual species in three other ecoregions. Two ecoregions are identified as priority for improving the conservation of adaptive variation for all three species: Northern Indochina subtropical forests and Northern Khorat Plateau moist deciduous forests (Fig. 2). One ecoregion in Myanmar and three ecoregions in Vietnam have no stable protected areas in that country for one or more of the target species.

The area prioritized for *in situ* conservation is sufficient to reach the 10% threshold for stable protected area in three of the 25 total species-ecoregion combinations that are prioritized for additional conservation measures (Table A10). This includes the Northern Indochina subtropical forests (Fig. 2A) for *D. cultrata.* The remaining 22 ecoregions (or species-ecoregion combinations) would require restoration outside of the current protected area network to meet the conservation target, including the Northern Indochina subtropical forests for *D. cochinchinensis* and *D. oliveri* (Fig. 2A) and the Northern Khorat Plateau moist deciduous forests (Fig. 2B) for all three species. This corresponds to an estimated restoration need of about 1.1 million ha across the species' combined ranges. The majority of the priority areas for restoration remain as natural habitat, except for the Chao Phraya lowland moist deciduous forests (for *D. cochinchinensis*), the Irrawaddy dry forests (for *D. cultrata* and *D. oliveri)* and the Peninsular Malaysian rain forests (for *D. oliveri)*, where large portions of potential habitat have been converted to cropland. Fig. 1 shows maps of other areas within the landscapes where the species would benefit from restoration activities, independently of the conservation status within the ecoregion or country. At country level, more than 40% of the species' potential distribution is prioritized for restoration for *D. cochinchinenis* in Thailand (56%) and in Cambodia (46%) (Table 2).

None of the ecoregions are prioritized for *ex situ* conservation with the set (high) threshold of >90% of the distribution area becoming unsuitable by 2055. The ecoregions most threatened by climate change are the Northern Triangle subtropical forests in Myanmar (53% becoming unsuitable for *D. cultrata*) and the Southern Annamites montane rain forests in Cambodia, Laos and Vietnam (49% also for *D. cultrata*). Four other ecoregions are predicted to lose over 20% of the species' current distribution area: Northern Indochina subtropical forests (Fig. 2A) for *D. cochinchinenis*, Irrawaddy dry forests for *D. cultrata* and Mizoram-Manipur-Kachin rain forests and Myanmar coastal rain

Table 1
Potential distribution area with 'medium' to 'very high' threat vulnerability. The range between best-case and worst-case scenario is indicated in brackets. The corresponding maps can be found in Figs. A4–A6.

Species	Over-exploitation (%)	Fire (%)	Over-grazing (%)	Habitat conversion (%)	Climate change (%)	Threats combined (%)
D. cochinchinensis	60 (47–69)	28 (14–39)	14 (7–27)	41 (41–42)	7 (6–7)	80 (69–86)
D. cultrata	53 (36–66)	20 (6–34)	16 (12–33)	17 (16–18)	21 (21–21)	75 (57–86)
D. oliveri	57 (42–66)	20 (8–34)	15 (5–21)	38 (38–39)	13 (8–13)	75 (61–83)

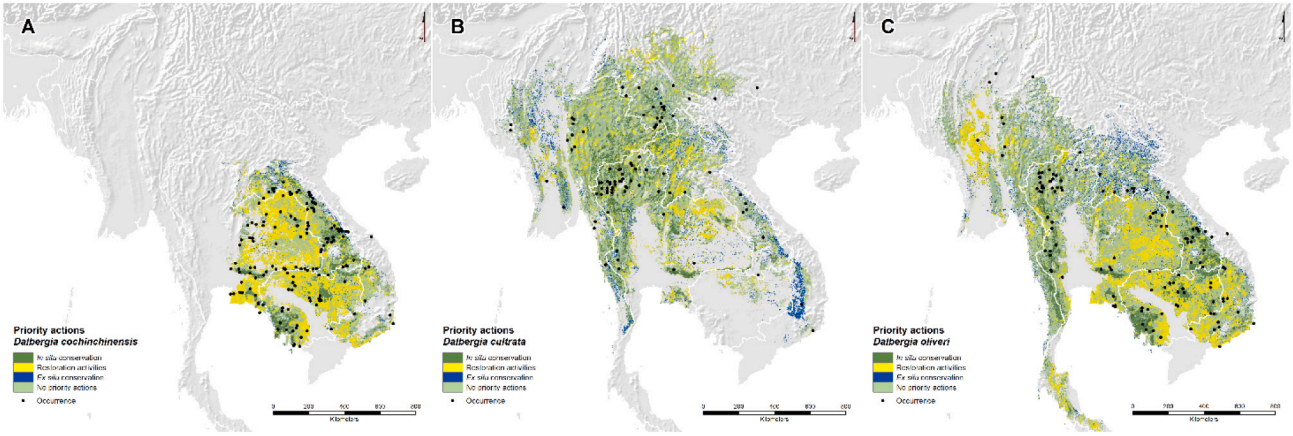


Fig. 1. Priority action maps for conservation and restoration of (A) *D. cochinchinensis,* (B) *D. cultrata and* (C) *D. oliveri*.

Table 2
Priority areas for *in situ* conservation, restoration activities and *ex situ* conservation for the three *Dalbergia* species by country.

Species	Country	Predicted distribution			Priority for *in situ*		Priority for restoration		Priority for *ex situ*
		km^2	% protected	% protected and stable	% of total area	% in protected areas	% of total area	% in natural habitats	% of total area
Dalbergia cochinchinensis	All	441,912	21	17	12	72	42	37	3
D. cochinchinensis	Cambodia	131,387	39	27	16	84	46	70	1
D. cochinchinensis	Laos	100,596	20	18	19	49	21	72	7
D. cochinchinensis	Thailand	157,258	12	11	6	96	56	5	1
D. cochinchinensis	Vietnam	52,667	9	8	5	55	31	38	4
D. cultrata	All	871,792	13	11	12	40	15	52	9
D. cultrata	Cambodia	20,471	57	43	2	61	21	91	10
D. cultrata	China	160,781	<1	<1	6	<1	13	79	4
D. cultrata	Laos	132,820	16	14	8	30	17	92	11
D. cultrata	Myanmar	300,279	2	2	12	3	12	49	8
D. cultrata	Thailand	231,009	31	29	20	80	20	17	6
D. cultrata	Vietnam	26,432	7	3	<1	57	5	51	49
D. oliveri	All	997,383	18	16	11	63	25	31	7
D. oliveri	Cambodia	145,220	38	30	22	82	38	59	1
D. oliveri	China	34	5	1	–	–	1	12	23
D. oliveri	Laos	151,484	17	15	15	44	12	71	19
D. oliveri	Myanmar	253,113	2	2	6	4	19	25	9
D. oliveri	Thailand	362,686	23	21	10	86	27	10	4
D. oliveri	Vietnam	84,847	9	8	6	44	35	30	6

forests for *D. oliveri. Ex situ* conservation may also be necessary in areas with little protected areas and few natural habitats remaining, independently of potential threat from climate change, such as the Chao Phraya lowland moist deciduous forests in Thailand, the Irrawaddy dry forests in Myanmar and the Peninsular Malaysian rain forests.

4. Discussion

This article provides a framework for quantitatively assessing the conservation status of tree species and their intraspecific diversity across species ranges, considering multiple threats. Our method uses freely available spatial datasets, species occurrence and trait data combined with expert knowledge, making it well suited for tropical countries with high tree diversity and limited published information.

The results from this study reveal that all three *Dalbergia* species (*D. cochinchinensis*, *D. cultrata*, *D. oliveri*) are at risk across large parts of their distribution ranges in the Greater Mekong Subregion, with overexploitation being the most important threat followed by habitat conversion and fire. This provides the most comprehensive spatially explicit conservation assessment of the studied species since they were classified as threatened by the IUCN Red List in the late 1990s. Although protected areas cover between 13 and 21% of the species' predicted ranges, *Dalbergia spp.* are under pressure within these areas from both current threats and future climate change. Moreover, the existing protected areas are highly concentrated, leaving many parts of these species' ranges without protection. Populations outside the existing protected area network are rapidly dwindling, and in the vast majority of the studied ecoregions, areas identified as priority for *in situ* conservation are insufficient to reach the conservation goal of 10% stable protected area. Both conservation of the remaining populations and species restoration are urgently needed and require the collaboration between countries and stakeholders. The results presented were used to update the IUCN Red List assessments for the three species in collaboration with the Global Tree Assessment project (Barstow et al., 2022a, 2022b; Contu et al., 2022).

To fill the current gaps in the existing protected area network, the priority areas for *in situ* conservation should be surveyed to confirm the presence of viable populations of the species and to delineate genetic conservation units, starting from the currently least protected ecoregions. High modeled habitat suitability has been associated with high genetic diversity (Nagaraju et al., 2013). Populations growing in the most suitable areas for each species can therefore be particularly valuable for *in situ* conservation. Because of the high genetic differentiation between populations (Hartvig et al., 2018), conservation measures

Table 3
Priority ecoregions with least stable protected areas (≤2%) for one or more *Dalbergia* species. Data for all three species is included for the two ecoregions (highlighted in grey) identified as priority for conserving all three species: 'Northern Indochina subtropical forests', and 'Northern Khorat Plateau moist deciduous forests' (Fig. 2).

Ecoregion	Country	Species	Predicted distribution			Priority for *in situ*		Priority for restoration		Priority for *ex situ*
			km²	% protected	% protected and stable	% of total area	% in protected areas	% of total area	% in natural habitats	% of total area
Chao Phraya lowland moist deciduous forests	Thailand	*D. cochinchinensis*	8,549	2	1	1	89	86	2	<1
Irrawaddy dry forests	Myanmar	*D. cultrata*	10,857	1	<1	<1	-	21	3	27
		D. oliveri	16,485	<1	<1	<1	-	71	1	6
Myanmar coastal rain forests	Myanmar	*D. cultrata*	18,955	1	1	8	3	8	71	12
		D. oliveri	20,004	1	1	2	-	14	28	21
Northern Indochina subtropical forests	China, Laos, Myanmar, Thailand, Vietnam	*D. cochinchinensis*	1,140	1	1	1	1	11	92	39
		D. cultrata	279,868	3	2	10	6	13	69	5
		D. oliveri	115,637	5	3	1	9	12	50	18
Northern Khorat Plateau moist deciduous forests	Laos, Thailand	*D. cochinchinensis*	15,269	2	2	1	25	59	20	<1
		D. cultrata	7,866	2	2	1	21	34	16	3
		D. oliveri	11,959	2	1	<1	31	31	20	19
Northern Thailand-Laos moist deciduous forests	Laos, Thailand	*D. cochinchinensis*	1,348	<1	<1	-	-	30	98	2
Northern Triangle subtropical forests	Myanmar	*D. cultrata*	599	1	1	<1	-	1	100	53
Yunnan Plateau subtropical evergreen forests	China	*D. cultrata*	67,618	<1	<1	1	-	18	81	2

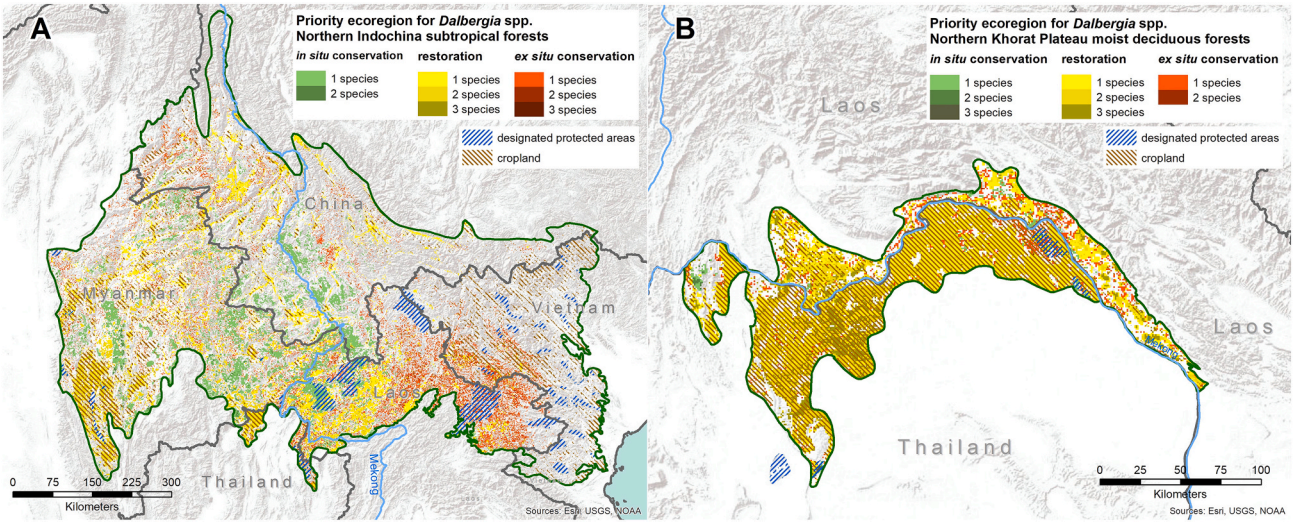


Fig. 2. Priority ecoregions for *D. cochinchinensis, D. cultrata and D. oliveri* with priority action areas for *in situ* conservation, restoration and *ex situ* conservation. (A) 'Northern Indochina subtropical forests' and (B) 'Northern Khorat Plateau moist deciduous forests'.

should be expanded also to underrepresented areas to avoid a potential loss of unique adaptative variation. Less diverse populations at the species' range margins can harbor unique, important traits *e.g.*, for climate change adaptation (Angert et al., 2020; Hartvig et al., 2020) and should be studied further.

In situ priority areas are usually relatively remote, as accessibility is one of the main factors contributing to overexploitation. Opportunity costs from conservation are therefore more limited than in areas with higher accessibility and land use pressures (Carrasco et al., 2017). On the other hand, remoteness increases the costs of monitoring tree populations and therefore also the risk of illegal logging of valuable species (Xue et al., 2019). Remote and under-resourced protected areas can also be particularly vulnerable to encroachment as they may restrict the informal access rights of local forest-dependent land users (Geldmann et al., 2019). Areas prioritized for *in situ* conservation are potentially well-suited for community forestry, as threats to the target species are more limited than elsewhere and conservation of genetic diversity does not preclude sustainable use. Field surveys indicate that community forests in Cambodia harbor some of the largest remaining populations of *D. cochinchinensis* and *D. oliveri* in the country (Institute of Forest and Wildlife Research and Development, Cambodia, unpublished report). Seed collection and seedling production are potential opportunities for employment and sources of income, given the increasing interest for planting *Dalbergia spp.* in the region and the high price of seed that can fetch up to US$ 250–300 kg^{-1}. Linking communities to seed markets is crucial for sustaining the benefits and the commitment to protecting seed sources (Valette et al., 2020).

Restoration of *Dalbergia spp.* populations outside of the current protected area network is necessary for recovering and maintaining adaptive variation within species across large parts of their ranges. Mainstreaming these and other threatened, socio-economically important tree species in broader land restoration programs would be important to align resources, help meet conservation targets and improve biodiversity benefits of restoration initiatives (Strassburg et al., 2020). Our restoration priority maps can help identify areas where the species distributions overlap with ongoing or planned restoration and tree planting programs. Although *Dalbergia spp.* can regenerate through coppicing, active planting is likely needed in most areas given the species' highly threatened status and the lack of genetic recombination in clonal reproduction (Hartvig et al., 2020). Capacities of farmers, other land managers and restoration practitioners need to be strengthened to ensure that planted populations are established using genetically diverse and adapted seed to contribute to genetic conservation and result in resilient populations that can subsequently serve as sources of quality seed (Jalonen et al., 2018). The scarcity of viable seed source populations in most priority ecoregions underlines the importance of good seed selection and collection practices. Remaining viable seed sources, including conservation stands in natural forests and *ex situ* seed sources, need to be mapped and conserved across the species ranges to enable restoration. Establishing seedling or clonal seed orchards using material from multiple natural populations can contribute to conserving genetic diversity while building up seed production (Dudley et al., 2020). Consequently, conservation and restoration are intertwined and need to be planned in coordination.

Our results indicate that *ex situ* conservation is important for the long-term conservation of species' adaptive variation in ecoregions that are predicted to be severely affected by climate change. Responses to heat and drought stress vary between the species despite their relatedness (Hung et al., 2020), illustrating the need for species-specific analyses before synergies for conservation action can be identified. *D. cultrata* in particular is at risk at the margins of its current distribution because of the combined effects of climate change and current threats. These areas should be targeted by germplasm collection to avoid the potential loss of adaptive variation. Our maps will help to focus collection efforts in areas where climate threat levels are high but current threat levels are low and where it is therefore likely that viable remnant populations can still be found. *Ex situ* conservation of tree genetic resources does not preclude sustainable use, and, apart from seed banks, conservation units can include plantations, provenance trials, seed orchards, agroforestry and trees on farm. Common garden studies and genomic studies can help to understand species' capacity to adapt to climate change and identify opportunities for selection and breeding to support adaptation. Climate change should also be considered in the management plans for protected areas where the species are predicted to be affected. This would also benefit other species within vulnerable protected areas.

Eleven out of the 21 ecoregions (52%) in the studied area extend over country boundaries, with the conservation status sometimes differing drastically across the border. None of the species is sufficiently protected within individual ecoregions in individual countries. Synergies between countries are, therefore, likely to improve the conservation status as well as helpful to share and stretch resources (Wang et al., 2021). Each ecoregion should have several conserved populations to avoid the risk of genetic erosion (Hoban et al., 2020). For severely threatened species, such as *Dalbergia spp.*, identifying such reserves in collaboration between countries within an ecoregion is particularly important as remaining populations are scarce. Regional collaboration would also support efforts to address illegal cross-border trade, the main driver of loss of *Dalbergia spp.* in the region (EIA, 2016). Within countries, improving the conservation status of *Dalbergia* species in existing protected areas requires addressing persistent challenges in how these areas are designed (Kukkonen and Tammi, 2019) and managed (Cuong et al., 2017; Graham et al., 2021), including through enforcement of the law and addressing corruption (Milne, 2015). Our results contribute to better targeting conservation efforts within and between protected areas, for example by highlighting protected areas where populations of *Dalbergia spp.* require better monitoring and restoration.

Transboundary collaboration for conservation actions is constrained by a lack of methods for identifying national roles, responsibilities and complementarities (Schmeller et al., 2008). Species distribution modelling contributes to such analyses, but the lack of distribution data in a standardized form limits its potential and constitutes a major bottleneck for many native Asian tree species (Serra-Diaz et al., 2017; Gaisberger et al., 2021). Our experience shows that collaborative projects on species of common interest can facilitate the compilation and standardization of previously unpublished data to enable range-wide conservation assessments. Collaboration among national experts is also crucial for validating the resulting distribution maps and for identifying opportunities and recommendations for concrete collaborative actions. Results from the spatial analysis help target field survey to areas with high predicted potential for conservation and most synergies between species or countries. This saves both resources and time which is important in the race against local extinctions of *Dalbergia spp.* and other severely threatened species.

CRediT authorship contribution statement

Hannes Gaisberger: Conceptualization, Data curation, Formal analysis, Methodology, Software, Investigation, Validation, Visualization, Writing - original draft, Writing - review & editing. **Thea So:** Investigation, Validation, Resources, Writing – review & editing. **Bansa Thammavong:** Investigation, Validation, Resources, Writing - review & editing. **Chaloun Bounithiphonh:** Investigation, Validation, Resources, Writing - review & editing. **Tran Thi Hoa:** Investigation, Validation, Resources, Writing - review & editing. **Zheng Yongqi:** Investigation, Validation, Resources, Writing - review & editing. **Tania Kanchanarak:** Data curation, Investigation, Writing - review & editing. **Tobias Fremout:** Methodology, Investigation, Software, Writing - review & editing. **Suchitra Changtragoon:** Investigation, Validation. **Sineath Sreng:** Investigation, Validation. **Huang Ping:** Investigation, Validation, Writing - review & editing. **Tin Hang Hung:** Validation, Writing - review & editing. **Pyae Pyae Win:** Investigation, Validation. **Ida**

Hartvig: Investigation, Validation, Writing - review & editing. **Ida Theilade:** Investigation, Validation, Writing - review & editing. **David Boshier:** Funding acquisition, Investigation, Project administration. **John MacKay:** Funding acquisition, Investigation, Project administration. **Chris Kettle:** Supervision, Funding acquisition, Writing - review & editing. **Riina Jalonen:** Conceptualization, Methodology, Data curation, Investigation, Formal analysis, Project administration, Supervision, Validation, Funding acquisition, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to the following experts for sharing occurrence data of the studied species: Alison KS Wee, Chhang Phourin, Ferry Slik, Fran Lambrick, Greuk Pakkad, Hugo Volkaert, Josep Serra-Diaz, Jens Svenning, Lutz Lehmann, Mu Mu Aung, Nguyen Hoang Nghia, Simon Laegaard, Stephen Elliott, Voradol Chumchamroom, Wichan Eiadthong (deceased). This work was supported by the UK Darwin Initiative [grant number 25-023], the Government of the Federal Republic of Germany through the Federal Ministry of Food and Agriculture (BMEL) [grant number GenR 2017-5), and the CGIAR Trust Fund Contributors (https://www.cgiar.org/funders/) through the CGIAR Research Program on Forests, Trees and Agroforestry. Additional funding was provided through EuropeAid [grant number CSO-LA/2019/161819-3/7], the Franklinia Foundation, the Carlsberg Foundation [grant number CF19-0234], and the National Natural Science Foundation of China [grant number 31761143002].

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109560.

References

Abel-Schaad, D., Iriarte, E., López-Sáez, J.A., Pérez-Díaz, S., Sabariego Ruiz, S., et al., 2018. Are Cedrus atlantica forests in the Rif Mountains of Morocco heading towards local extinction? The Holocene 28. https://doi.org/10.1177/0959683617752842.

Acevedo, P., Jimenez-Valverde, A., Lobo, J.M., Real, R., 2012. Delimiting the geographical background in species distribution modelling. J. Biogeogr. 39, 1383–1390. https://doi.org/10.1111/j.1365-2699.2012.02713.x.

Angert, A.L., Bontrager, M.G., Aringgren, J., 2020. What do we really know about adaptation at range edges? Annu. Rev. Ecol. Evol. Syst. https://doi.org/10.1146/annurev-ecolsys-012120-091002.

Barstow, M., et al., 2022. Dalbergia cochinchinensis. In: The IUCN Red List of Threatened Species. Submitted assessment (FINAL CITATION TO BE PROVIDED DURING PROOF STAGE).

Barstow, M., et al., 2022. Dalbergia oliveri. In: The IUCN Red List of Threatened Species. Submitted assessment (FINAL CITATION TO BE PROVIDED DURING PROOF STAGE).

Botanical Gardens Conservation International (BGCI), 2021. State of the World's Trees. BGCI, Richmond, UK. https://doi.org/10.5822/978-1-61091-756-8. Submitted assessment (FINAL CITATION TO BE PROVIDED DURING PROOF STAGE).

Broadhurst, L.M., 2013. A genetic analysis of scattered yellow box trees (Eucalyptus melliodora A.Cunn. ex Schauer, Myrtaceae) and their restored cohorts. Biol. Conserv. 161 https://doi.org/10.1016/j.biocon.2013.02.016.

Butt, N., Possingham, H.P., De Los Rios, C., Maggini, R., Fuller, R.A., et al., 2016. Challenges in assessing the vulnerability of species to climate change to inform conservation actions. Biol. Conserv. 199, 10–15. https://doi.org/10.1016/j.biocon.2016.04.020.

Carrasco, L.R., Webb, E.L., Symes, W.S., Koh, L.P., Sodhi, N.S., 2017. Global economic trade-offs between wild nature and tropical agriculture. PLoS Biol. 15 https://doi.org/10.1371/journal.pbio.2001657.

Contu, S., et al., 2022. Dalbergia cultrata. In: The IUCN Red List of Threatened Species. Submitted assessment (FINAL CITATION TO BE PROVIDED DURING PROOF STAGE).

Côte, I.M., Darling, E.S., Brown, C.J., 2016. Interactions among ecosystem stressors and their importance in conservation. Proc. R. Soc. B 283, 20152592. https://doi.org/10.1098/rspb.2015.2592.

Cuong, C.Van, Dart, P., Dudley, N., Hockings, M., 2017. Factors influencing successful implementation of biosphere reserves in Vietnam: challenges, opportunities and lessons learnt. Environ. Sci. Policy 67. https://doi.org/10.1016/j.envsci.2016.10.002.

Danielson, J., Gesch, D., 2011. Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010). U.S. Geol. Surv. Open-File Rep. 2011–1073 2010, 26 https://doi.org/citeulike-article-id:13365221.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., et al., 2017. In: An Ecoregion-based Approach to Protecting Half the Terrestrial Realm XX, pp. 1–12. https://doi.org/10.1093/biosci/bix014.

Dudley, N., Jones, T., Gerber, K., Ross-Davis, A.L., Sniezko, R.A., et al., 2020. Establishment of a genetically diverse, disease-resistant Acacia koa A. Gray seed orchard in Kokee, Kauai: early growth, form, and survival. Forests 11, 1–13. https://doi.org/10.3390/f11121276.

Environmental Investigation Agency (EIA), 2016. CITES CoP17 - Analysis of the Demand-driven Trade in Hongmu Timber Species: Impacts of Unsustainability and Illegality in Source Region.

Foley, S., 2020. Threats to Mekong Forest Ecosystems: last chance for the indo-burma biodiversity hotspot. In: Goldstein, M.I., Della Sala, D.A. (Eds.), Encyclopedia of the World's Biomes. Elsevier, pp. 168–184. https://doi.org/10.1016/B978-0-12-409548-9.11940-2. ISBN 9780128160978.

Fremout, T., Thomas, E., Gaisberger, H., Van Meerbeek, K., Muenchow, J., et al., 2020. Mapping tree species vulnerability to multiple threats as a guide to restoration and conservation of tropical dry forests. Glob. Chang. Biol. 26, 3552–3568. https://doi.org/10.1111/gcb.15028.

Gaisberger, H., Fremout, T., Kettle, C., Vinceti, B., Kemalasari, D., et al., 2021. Tropical and subtropical Asia's valued tree species under threat. Conserv. Biol., e13873 https://doi.org/10.1111/cobi.13873.

Gallagher, R.V., Allen, S., Mackenzie, B.D.E., Yates, C.J., Gosper, C.R., et al., 2021. High fire frequency and the impact of the 2019–2020 megafires on Australian plant diversity. Divers. Distrib. 27 https://doi.org/10.1111/ddi.13265.

Geldmann, J., Manica, A., Burgess, N.D., Coad, L., Balmford, A., 2019. A global-level assessment of the effectiveness of protected areas at resisting anthropogenic pressures. Proc. Natl. Acad. Sci. U. S. A. 116 https://doi.org/10.1073/pnas.1908221116.

Graham, V., Geldmann, J., Adams, V.M., Grech, A., Deinet, S., et al., 2021. Management resourcing and government transparency are key drivers of biodiversity outcomes in southeast asian protected areas. Biol. Conserv. 253 https://doi.org/10.1016/j.biocon.2020.108875.

Hanson, J.O., Rhodes, J.R., Riginos, C., Fuller, R.A., 2017. Environmental and geographic variables are effective surrogates for genetic variation in conservation planning. Proc. Natl. Acad. Sci. U. S. A. 114, 12755–12760. https://doi.org/10.1073/pnas.1711009114.

Hartvig, I., So, T., Changtragoon, S., Tran, H.T., Bouamanivong, S., et al., 2018. Population genetic structure of the endemic rosewoods Dalbergia cochinchinensis and D. oliveri at a regional scale reflects the Indochinese landscape and life-history traits. Ecol. Evol. 8, 530–545. https://doi.org/10.1002/ece3.3626.

Hartvig, I., So, T., Changtragoon, S., Thi, H., Somsanith, T., 2020. Conservation genetics of the critically endangered Siamese rosewood (Dalbergia cochinchinensis): recommendations for management and sustainable use. Conserv. Genet. 21, 677–692. https://doi.org/10.1007/s10592-020-01279-1.

Heikkinen, R.K., Luoto, M., Araújo, M.B., Virkkala, R., , et al.Thuiller, 2006. Methods and uncertainities in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30 (6), 751–777.

Hengl, T., De Jesus, J.M., Heuvelink, G.B.M., Gonzalez, M.R., Kilibarda, M., et al., 2017. SoilGrids250m: global gridded soil information based on machine learning. PLoS ONE. https://doi.org/10.1371/journal.pone.0169748.

Hoban, S., Bruford, M., Urban, J.D., Lopes-Fernandes, M., Heuertz, M., et al., 2020. Genetic diversity targets and indicators in the CBD post-2020 global biodiversity framework must be improved. Biol. Conserv. 248, 108654 https://doi.org/10.1016/j.biocon.2020.108654.

Hung, T.H., Gooda, R., Rizzuto, G., So, T., Thammavong, B., et al., 2020. In: Physiological Responses of Rosewoods Dalbergia cochinchinensis and D. oliveri Under Drought and Heat Stresses, pp. 10872–10885. https://doi.org/10.1002/ece3.6744.

IUCN, 2021. The IUCN Red List of Threatened Species. Version 2021-10-13. International Union for Conservation of Nature. Retrieved from. www.iucnredlist.org.

IUCN Standards and Petitions Committee, 2019. Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. Retrieved from. www.iucnredlist.org/documents/RedListGuidelines.pdf.

Jalonen, R., Valette, M., Boshier, D., Duminil, J., Thomas, E., 2018. Forest and landscape restoration severely constrained by a lack of attention to the quantity and quality of tree seed: insights from a global survey. Conserv. Lett. https://doi.org/10.1111/conl.12424.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P., Kessler, M., 2017. Climatologies at high resolution for the earth land surface areas. Sci. Data 4, 170122. https://doi.org/10.1038/sdata.2017.122.

Kukkonen, M.O., Tammi, I., 2019. Systematic reassessment of Laos' protected area network. Biol. Conserv. 229 https://doi.org/10.1016/j.biocon.2018.11.012.

Latham, J., Cumani, R., Rosati, I., Bloise, M., 2014. In: Global Land Cover SHARE (GLC-SHARE) database Beta-Release Version 1.0. Food Agric. Organ. United Nations (FAO), Rome, Italy, pp. 1–39.

Liu, Y., Huang, P., Lin, F., Yang, W., Gaisberger, H., et al., 2019. MaxEnt modelling for predicting the potential distribution of a near threatened rosewood species (Dalbergia cultrata Graham ex Benth). Ecol. Eng. 141 https://doi.org/10.1016/j.ecoleng.2019.105612.

Miller, S.A., Bartow, A., Gisler, M., Ward, K., Young, A.S., et al., 2011. In: Can an Ecoregion Serve as a Seed Transfer Zone? Evidence from a Common Garden Study with Five Native Species, 19, pp. 268–276. https://doi.org/10.1111/j.1526-100X.2010.00702.x.

Milne, S., 2015. Cambodia's unofficial regime of extraction: illicit logging in the shadow of transnational governance and investment. Crit. Asian Stud. 47, 200–228. https://doi.org/10.1080/14672715.2015.1041275.

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENMeval: AnR package for conducting spatially independent evaluations and estimating optimalmodel complexity for MAXENT ecological niche models, 5 (11), 1198–1205. https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12261.

Nagaraju, S.K., Gudasalamani, R., Barve, N., Ghazoul, J., Narayanagowda, G.K., et al., 2013. Do ecological niche model predictions reflect the adaptive landscape of species?: A test using Myristica malabarica Lam., an endemic tree in the Western Ghats, India. PLoS One 8, 1–13. https://doi.org/10.1371/journal.pone.0082066.

Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37 (2), 191–203.

Phillips, S.J., 2008. Transferability, sample selection bias and background data in presence-only modelling: a response to Peterson et al. (2007). Ecography 0 (0). https://doi.org/10.1111/j.2007.0906-7590.05378.x, 080227084236895–0.

Phillips, S.J., Dudik, M., Schapire, R.E., 2018. Maxent software for modeling species niches and distributions (Version 3.4.1). ttps://biodiversityinformatics.amnh.org/open_source/maxent/.

Prasad, R., 2001. Criteria & indicators for sustainable management of dry forests in Asia. Int. For. Rev. 3 (9), 307–316.

Radosavljevic, A., Anderson, R.P., 2014. Making better MAXENT models of species distributions: complexity, overfitting and evaluation. J. Biogeogr. 41 (4), 629–643. https://doi.org/10.1111/jbi.12227.

Sander, N.L., Pérez-Zavala, F., Da Silva, C.J., Arruda, J.C., Pulido, M.T., et al., 2018. Rivers shape population genetic structure in Mauritia flexuosa (Arecaceae). Ecol. Evol. 8, 6589–6598. https://doi.org/10.1002/ece3.4142.

Schmeller, D.S., Gruber, B., Bauch, B., Lanno, K., Budrys, E., et al., 2008. Determination of national conservation responsibilities for species conservation in regions with multiple political jurisdictions. Biodivers. Conserv. 17 https://doi.org/10.1007/s10531-008-9439-8.

Serra-Diaz, J.M., Enquist, B.J., Maitner, B., Merow, C., Svenning, J.-C., 2017. Big data of tree species distributions: how big and how good? For. Ecosyst. 4, 30. https://doi.org/10.1186/s40663-017-0120-0.

So, T., Theilade, I., Dell, B., 2010. Conservation and utilization of threatened hardwood species through reforestation - an example of Afzelia xylocarpa (Kruz.) Craib and Dalbergia cochinchinensis Pierre in Cambodia. Pacific Conserv. Biol. 16, 101–116. https://doi.org/10.1071/PC100101.

Sork, V.L., Davis, F.W., Westfall, R., Flint, A., Ikegami, M., et al., 2010. Gene movement and genetic association with regional climate gradients in California valley oak (Quercus lobata Née) in the face of climate change. Mol. Ecol. 19 https://doi.org/10.1111/j.1365-294X.2010.04726.x.

Strassburg, B.B.N., Iribarrem, A., Beyer, H.L., Cordeiro, C.L., Crouzeilles, R., et al., 2020. Global priority areas for ecosystem restoration. Nature 586, 724–729. https://doi.org/10.1038/s41586-020-2784-9.

UNEP-WCMC, IUCN, 2018. World Database on Protected Areas, WDPA, Version October 2018. www.protectedplanet.net.

Valette, M., Vinceti, B., Gregorio, N., Bailey, A., Thomas, E., et al., 2020. Beyond fixes that fail: identifying sustainable improvements to tree seed supply and farmer participation in forest and landscape restoration. Ecol. Soc. 25 https://doi.org/10.5751/ES-12032-250430.

Wang, L., Yang, B., Bai, Y., Lu, X., Corlett, R.T., et al., 2021. Conservation planning on China's borders with Myanmar, Laos, and Vietnam. Conserv. Biol. 1–12 https://doi.org/10.1111/cobi.13733.

Winfield, K., Scott, M., Grayson, C., 2016. CITES CoP17 information document 48 - global status of Dalbergia and Pterocarpus rosewood producing species in trade. Global Eye. https://doi.org/10.13140/RG.2.2.24590.00321.

Woodruff, D.S., 2010. Biogeography and conservation in Southeast Asia: how 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. Biodivers. Conserv. 19 https://doi.org/10.1007/s10531-010-9783-3.

Xue, X., Nan, C., Deng, C., Liu, X., Wang, Z., et al., 2019. Analysis on the characteristics of illegal cutting and deforestation of Pinus kesiya in Lancang County of Yunnan Province. In: E3S Web of Conferences. https://doi.org/10.1051/e3sconf/201913101124.