

Article

Climate Niche Modelling for Mapping Potential Distributions of Four Framework Tree Species: Implications for Planning Forest Restoration in Tropical and Subtropical Asia

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Abstract: Selecting tree species to plant for forest ecosystem restoration is critical but problematic. Knowing tree species' climatic niches can help, but such information is limited for most tropical tree species. Consequently, the research presented here explored the use of climate and species record location data, to map the potential distribution of four tree species across tropical and subtropical Asia based on their modelled climatic niches. All were framework species, of proven effectiveness for forest restoration: *Choerospondias axillaris* (Roxb.) B.L. Burtt and A.W. Hill, *Ficus hispida* L.f., *Hovenia dulcis* Thunb., and *Prunus cerasoides* Buch.-Ham. ex D. Don. Potential species distributions were projected onto maps of known climatic conditions using the maximum entropy algorithm in Maxent software to predict where the climate is conducive for including each species in forest restoration trials. The models predicted species location very well for *F. hispida* and *H. dulcis* and fairly well for *P. cerasoides* and *C. axillaris*. Climatically suitable areas for *C. axillaris* were located mostly north of the equator, whilst those of *F. hispida*, *H. dulcis* and *P. cerasoides* extended south of the equator. The importance of each climatic niche variable differed among species. Driest-month precipitation was critical for *F. hispida*, as well as mean dry-season temperature for *C. axillaris* and *P. cerasoides* and cold-season precipitation for *H. dulcis*. In addition to aiding species selection for forest restoration, potential distribution maps based on climatic niche models can indicate where novel species for tree plantations might be successful and where species might become invasive. Applying such techniques to a large number of species will be needed to significantly improve species selection for forest ecosystem restoration.

Keywords: maxent; *Choerospondias axillaris*; *Ficus hispida*; *Hovenia dulcis*; *Prunus cerasoides*; framework species method



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1. Introduction

Tropical forest-ecosystem restoration can be defined as management interventions on degraded forestlands to maximize biomass accumulation and the recovery of forest structural complexity, biodiversity, and ecosystem functioning within prevailing climatic and soil limitations [1]. Its significance for mitigating both biodiversity loss (e.g., [2,3]) and global climate change (by carbon sequestration [4]) is now well-recognized, under such global schemes as the Bonn Challenge (targeting restoration of 350 million hectares by 2030 [5]) and the UN's "Decade on Ecosystem Restoration" (2021–2030) [6]. Its role in climate change mitigation first rose to prominence with the inclusion of "enhancement of carbon stocks" into the UN's REDD+ initiative [7], with safeguards to ensure biodiversity conservation and community participation (safeguards [d] and [e] in UNFCCC COP16 [8]). Conventional monoculture plantations of fast-growing, often exotic, tree species satisfy neither of these safeguards [9,10]. Forest ecosystem restoration sequesters carbon 40 times more efficiently than plantations and six times more efficiently than agroforestry systems [4].

Despite this, about two thirds of the area pledged under the Bonn Challenge and other planned national initiatives are (or will be) plantations and agroforests, with only one third undergoing more natural ecological restoration [4]. Consequently, the need to develop effective techniques to restore tropical forest ecosystems is urgent, including protocols for the selection of indigenous forest tree species that will thrive in the prevailing climatic conditions of deforested sites.

In northern Thailand, the framework species method (FSM) of forest restoration (Figure 1) has been adapted, tested, and successfully used to restore various forest types on “moderately” degraded sites, i.e., where natural regeneration is too sparse to achieve canopy closure within 3–5 years (i.e., Stage 3 degradation, *sensu* Elliott et al. [1]). Framework species are selected from among those that are characteristic of the target ecosystem for high rates of survival and growth in the exposed conditions of deforested sites. They should also have dense spreading crowns, capable of rapidly shading out competitive herbaceous weeds, and they should attract seed-dispersing wildlife to foster biodiversity recovery (by producing fleshy fruits or nectar-rich flowers at a young age). An additional advantageous characteristic in the fire-prone seasonal tropics is resilience after fire. Selected species are propagated in nurseries from locally collected seeds for 6–18 months. Then, they are planted in restoration sites and maintained for two to three years (weeding and fertilizer application three times each rainy season) until canopy closure. The technique was first developed in Queensland, Australia [11] and it has been trialed to restore various forest ecosystem types in Thailand [1], Cambodia [12], Indonesia [13], China [14], Tanzania [15], and the Philippines [16].

It has proved to be highly successful in achieving ecological objectives. With careful species selection, weeds are shaded out and canopy closure can be achieved within 2–3 years and biodiversity recovery is rapid. For example, the species richness of the bird community during restoration of evergreen forest in northern Thailand increased from about 30 before planting to 88 after 6 years, representing about 54% of bird species recorded in nearby mature forest [17], and the birds brought in tree seeds. Sinhaseni reported that 73 species of nonplanted trees recolonized the plot system within 8–9 years, most having germinated from seeds dispersed from nearby forest by birds (particularly bulbuls), fruit bats, and civets [18]. Furthermore, Kavinchan et al. and Jantawong et al. recently demonstrated remarkably rapid recovery of ecosystem carbon dynamics. Net inputs of carbon into the soil from litterfall, the overall accumulation of soil organic carbon, and the accumulation of above-ground carbon in the trees returned to levels that are typical of old-growth natural forest within 14–16, 21.5, and 16 years, respectively [19,20]. However, since the technique relies on attracting seed-dispersing animals to foster biodiversity recovery, its use is limited where seed sources (remnant forest) are too distant and/or where seed-dispersing animals have been extirpated [21]. Its adoption is also limited by the lengthy and in-depth research needed to identify framework tree species.

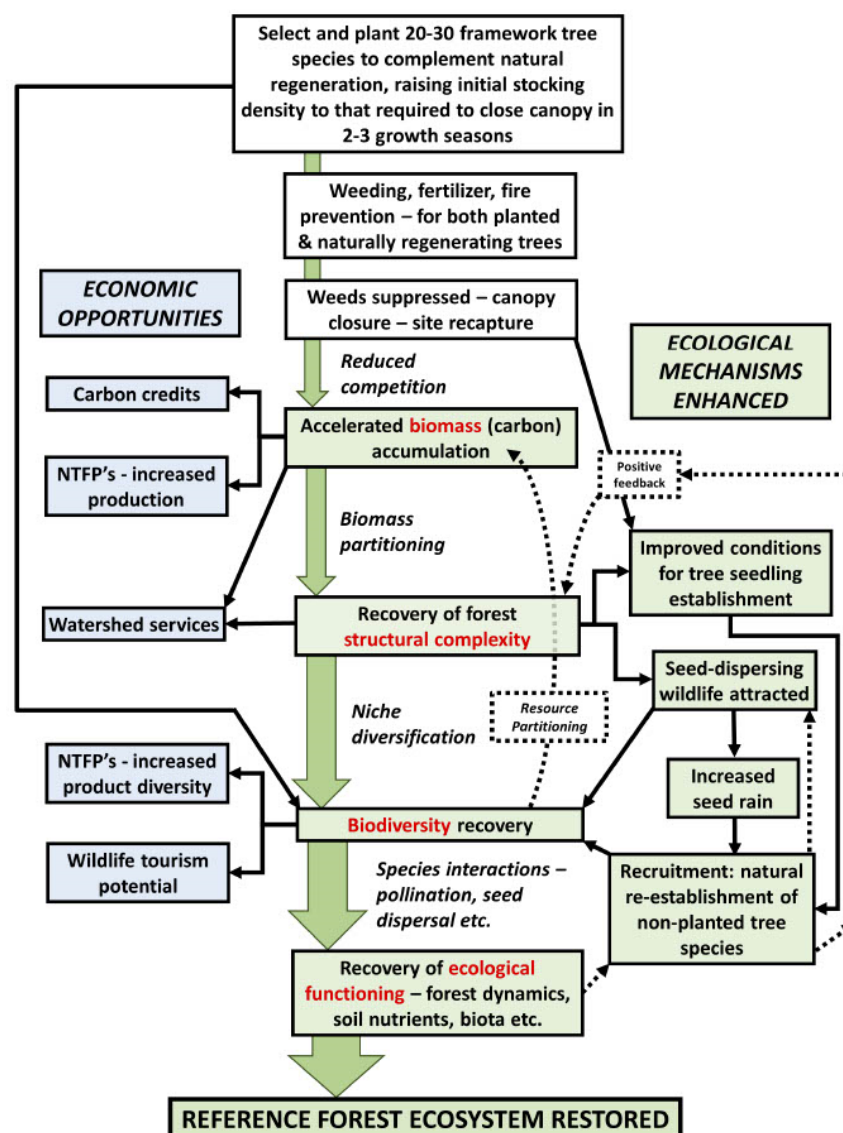


Figure 1. How the framework species method accelerates forest ecosystem restoration. Reprinted with permission from Stephen D. Elliott, first published in Jantawong et al. 2022 [22]. Dotted lines indicate positive feedback loops, by which planted framework tree species intensify key mechanisms of natural regeneration: weed suppression, seed-rain enhancement, and creation of conditions conducive to the establishment of recruit tree species.

A critical step in adapting the framework species method to restore a greater diversity of forest types over a wider range of climatic zones is the selection of “candidate” framework species for trialing. This is particularly difficult where target (or “reference”) forest ecosystems have been extirpated from landscapes and where local records of indigenous species are sparse. Under such circumstances, matching the climatic niches of indigenous tree species with climate maps provides an alternative way to determine where trials of candidate frameworks the tree species are likely to be successful and can greatly facilitate species–site matching to increase the likelihood of success of forest restoration projects [23–25].

Herbarium labels are an underutilized source of information that could greatly facilitate and improve forest restoration practices, particularly species–site matching [26]. Modern labels usually have the GPS coordinates of the collection locality, whereas old labels usually have written descriptions. Satellite imagery and/or field checks can often be used to convert such descriptive notes into GPS coordinates, which can then be used

for mapping and modelling species distributions. Old, large herbaria (mostly in Europe) usually store multiple specimens of each species from many localities, and are thus invaluable in determining tree distributions. Models of species' climatic suitability, based on herbarium data, provide a way to expand forest restoration into wider areas [27].

In the study presented here, we mapped the potential distributions of four tree species, previously proven to be “excellent” framework species for restoring upland evergreen forest in northern Thailand [28], using location data from herbarium specimen labels and the Global Biodiversity Information Facility [29], climatic data for each recorded location, and the maximum entropy approach [30]. The maximum entropy algorithm (MaxEnt) allows the use of a small amount of presence-only occurrence data. Development of MaxEnt modelling is still being researched. Modelling species' niches using MaxEnt relies on the quality of sample data and requires attention at many stages of model calibration [31]. In our study, MaxEnt was selected in preference to new modelling approaches [32,33] due to its 15 years of development and its superiority in terms of computational time and ease of use. The aim of this study was to assist with species selection for FSM trials by mapping the potential distribution of four known framework tree species, thus exploring their potential inclusion in forest restoration trials

2. Materials and Methods

2.1. Studied Species

Four species were selected for this study: *Choerospondias axillaris* (Roxb.) B.L. Burt and A.W. Hill (Anacardiaceae), *Ficus hispida* L.f. (Moraceae), *Hovenia dulcis* Thunb. (Rhamnaceae), and *Prunus cerasoides* Buch.-Ham. ex D. Don (Rosaceae) (Table 1, Figure 2). All had been tested in multiple field trials (FORRU-CMU Database) to restore seasonal, upland, evergreen forest (>1000 m from the sea level) in northern Thailand, resulting in their being ranked as “excellent” framework species [28]. All had excellent or acceptable growth and survival over the first two growing seasons after planting out in deforested sites and suppressed weeds well beneath their crowns. All demonstrated excellent or acceptable resilience after forest fires and were attractive to seed-dispersing animals (by producing fleshy fruits or bird nest sites within a few years after planting [34].

Table 1. Information of the four species. Overall, they are excellent framework tree species for forest restoration.

Species	Family	Elevation (m asl) ¹		Framework Species Assessment ²				
		Lower	Upper	Survival ³	Growth ⁴	Weed Suppression ⁵	Fire Resilience ⁶	Attraction to Seed Dispersers ⁷
<i>Choerospondias axillaris</i> (Roxb.) B.L. Burt and A.W. Hill	Anacardiaceae	460	1600	E	E	A	E	Flowering and fruiting from 4th year. Fruits attract seed-dispersing mammals.
<i>Ficus hispida</i> L.f.	Moraceae	60	1525	E	A	E	E	Figs from 3rd year attract seed-dispersing birds/squirrels.
<i>Hovenia dulcis</i> Thunb.	Rhamnaceae	1025	1300	E	E	E	E	Fruit and infructescence attract seed-dispersing birds but flowers late: >8 years after planting.
<i>Prunus cerasoides</i> Buch.-Ham. ex D. Don	Rosaceae	1050	1750	E	E	E	A	Flowers, fruit, and bird nests within 3 years. Fruits attract seed-dispersing birds.

¹ CMU-B Herbarium Database; ² Elliott et al., (2003) [28]; ³ E > 70% (mean at end of 2nd growing season); ⁴ E > 2:0 m, A = 1:5–1.99 m (mean height at end of 2nd growth season); ⁵ E > 33%, A 16.5%–33% (mean reduction in weed cover beneath tree crown at end of 2nd growth season); ⁶ E > 70%, A = 50%–69.9% (mean survival after fire); ⁷ Forest Restoration Research Unit (2005) [34].

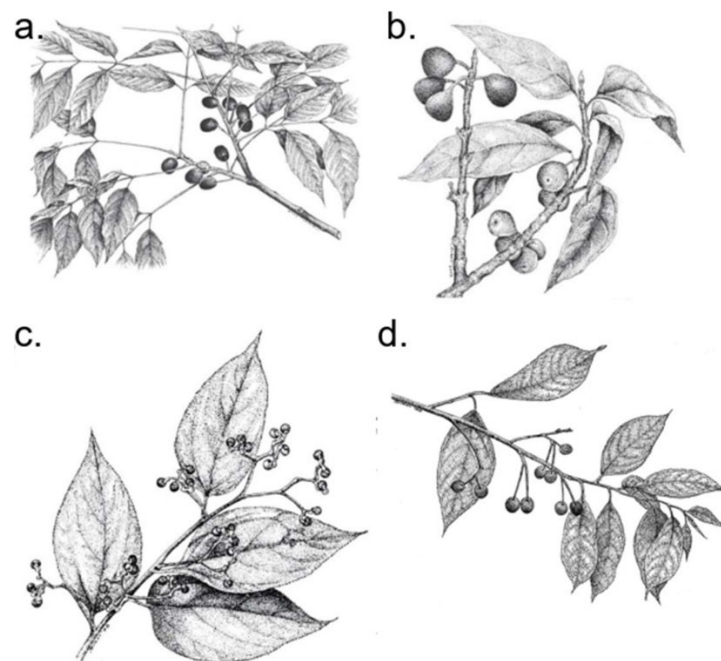


Figure 2. Foliage and fruit of four studied species: (a) *Choerospondias axillaris* (Roxb.) B.L. Burttt and A.W. Hill, (b) *Ficus hispida* L.f., (c) *Hovenia dulcis* Thunb., and (d) *Prunus cerasoides* Buch.-Ham. ex D. Don.

2.2. Data Collection

Species location records were gathered from specimen labels at the herbarium of the Royal Botanic Gardens, Kew, United Kingdom and the Global Biodiversity Information Facility [29]. Specimen labels were photographed at Kew from September to November 2014 and the data were subsequently transcribed into a spreadsheet. For those labels without GPS coordinates, location descriptions were checked with US GeoNames [35] and Google Earth Pro (Google Inc., Mountain View, CA, USA) to determine most likely GPS coordinates. Location data from specimens that could not be matched with any location database were discarded.

Species location records in the GBIF datasets were downloaded using the “gbif” function in the “dismo” package [36] written in the R programming language [37]. Search terms were accepted species names [38]. Locations where the species had been artificially introduced were removed. The numbers of records from each of the two data sources are listed in Table 2 for each species. The native geographical ranges differed among the four species (Table 2).

Table 2. Species and the number of data points at different steps of data preparation.

Species	Herbarium Records	GBIF Records with Coordinate Data ¹	Records within the Native Range	Subsampled Records	Native Geographical Extent of Location Data	Range Description
<i>C. axillaris</i>	57	361	183	116	Longitude 77–142° E Latitude 18–40° N	India to China Southeast/south-central China to Thailand
<i>F. hispida</i>	60	1221	756	236	Longitude 76–154° E Latitude 20° S–38° N	India to Australia Australia to Southeast/south-central China
<i>H. dulcis</i>	70	637	391	101	Longitude 77–136° E Latitude 11–36° N	India to Japan Japan and China to Thailand
<i>P. cerasoides</i>	46	213	139	68	Longitude 76–113° E Latitude 6–31° N	India to Thailand South China to Thailand
Total	234	2432	1481	524		

¹ 1 September 2019.

Current climatic data (1960–1990) were obtained from Worldclim V. 1 [39]: a set of global climate layers with a 2.5 arc minute resolution (approximately 20 km²). Nineteen bioclimatic variables (Table 3) were downloaded: (1) annual mean temperature, (2) mean diurnal range (mean of monthly (max temp–min temp)), (3) isothermality, (4) temperature seasonality (standard deviation *100), (5) max temperature of warmest month, (6) min temperature of coldest month, (7) temperature annual range, (8) mean temperature of wettest quarter, (9) mean temperature of driest quarter, (10) mean temperature of warmest quarter, (11) mean temperature of coldest quarter, (12) annual precipitation, (13) precipitation of wettest month, (14) precipitation of driest month, (15) precipitation seasonality (coefficient of variation), (16) precipitation of wettest quarter, (17) precipitation of driest quarter, (18) precipitation of warmest quarter, and (19) precipitation of coldest quarter.

Table 3. Nineteen climatic variables and their abbreviations. After removing collinearity among the variables, 10 variables were used in the model (variables with ✓).

Abbreviation	Variables (Unit)	Note	Used in Modelling
Bio1	Annual mean temperature (°C)		
Bio2	Mean diurnal range (mean of monthly) (°C)	max temp–min temp	✓
Bio3	Isothermality (%) ¹	(Bio2/Bio7) × 100	✓
Bio4	Temperature seasonality (°C) ²	standard deviation	
Bio5	Max temperature of warmest month (°C)		
Bio6	Min temperature of coldest month (°C)		
Bio7	Temperature annual range (°C)	Bio5–Bio6	
Bio8	Mean temperature of wettest quarter (°C)		✓
Bio9	Mean temperature of driest quarter (°C)		✓
Bio10	Mean temperature of warmest quarter (°C)		✓
Bio11	Mean temperature of coldest quarter (°C)		
Bio12	Annual precipitation (mm)		
Bio13	Precipitation of wettest month (mm)		✓
Bio14	Precipitation of driest month (mm)		✓
Bio15	Precipitation seasonality (%) ³	coefficient of variation	✓
Bio16	Precipitation of wettest quarter (mm)		
Bio17	Precipitation of driest quarter (mm)		
Bio18	Precipitation of warmest quarter (mm)		✓
Bio19	Precipitation of coldest quarter (mm)		✓

¹ A value of 100 indicates the diurnal temperature range is equivalent to the annual temperature range. A value less than 100 represents a smaller level of temperature variability within an average month relative to the year. ² The larger the standard deviation, the greater the variability of temperature. ³ The ratio of the standard deviation of the monthly total precipitation to the mean monthly total precipitation. A measure of the variation in monthly precipitation totals over the course of the year.

2.3. Species Location Record Preparation

For each species, duplicate records and locations in the ocean were removed. Then, to account for sampling bias, species location records were systematically subsampled [40]. Grid cells were created at one-degree resolution throughout each species' known range, and then only one record per grid cell was randomly sampled (Figure S1). The numbers of records retained in each cleaning step are presented in Table 2.

2.4. Climatic Data Preparation

To generate a list of noncorrelated variables to use in the model, correlations among 19 variables were identified using Pearson's correlation coefficient (Table S1). The analyses were carried out using the function "removeCollinearity" in the "virtualspecies" package [41] in R programming language. Pearson's correlation coefficient was used to compute a distance matrix, which was then used to construct an ascendant hierarchical classification (Figure S2) of the 19 variables. Variables that were 85% correlated were grouped together. Single variables not correlated to any other variables were automatically selected, along with one randomly selected variable from each of the groups, resulting in a total of

10 noncorrelated variables being included in the model. The extent of the climatic variables that were used in MaxEnt modelling was unique for each species, according to the extent of species occurrence. Climatic data were converted to ASCII raster files.

2.5. Modelling

Climatic niche models were calibrated in Maxent 3.4.1 [42]. The operations performed were (i) calibration, (ii) cross-validation, and (iii) projection. Maxent calculated the frequency distributions of all climatic variable values, firstly for all species location record points (species climate frequency) and secondly for a sample of 10,000 randomly selected background points within the species' range boundaries (geographical climate frequency). If a species shows *no* climatic preference within its range, then the two proportional frequency distributions would be very similar, because the species would be distributed randomly across its range. If a species is associated with a certain climatic variable value, then the species frequency, at that value, would be higher than the geographical frequency and vice versa. Therefore, the ratio between the two proportional frequency distributions can be used to derive the climatic suitability of each point on the map for growth of a species, within its range.

For model calibration, we applied a “regularization multiplier” of two. The regularization multiplier controls how closely fitted the output distribution is around species record locations. Values of less than 1 result in very tight fit around species record locations, whereas higher values result in wider dispersion [43]. Regularization multipliers of two to four are suggested to reduce “over-fitting” the models [44].

The models were subjected to 10-fold cross-validation. Species location records were randomly split into 10 equal-sized groups (called “folds”). For each species, 10 models were run, each one using data from nine folds (training) with the omitted fold used for validation (by determining if the models reliably predicted species presence at the record locations in the omitted folds). Each of the 10 models was run for up to 500 iterations.

The predictive accuracy of each model was estimated using the area under the receiver-operating characteristic curve (AUC). AUC is interpreted as how much the model can distinguish between species location and background points. An AUC close to 0.5 indicates that model performance is equivalent to random guessing. AUCs greater than 0.8 indicate high model performance [45]. The AUCs were generated and averaged over 10 models for each species.

To identify locations suitable for supporting each species (habitats matching the species' climatic niche requirements) beyond its current range, the climatic conditions across the whole of tropical and subtropical Asia (latitude 11°S to 40°N and longitude 60°E to 160°E) were used. Maxent model outputs (cloglog outputs) were imported into the R programming language and potential distribution maps were generated. The results were re-grouped into four classes of climatic suitability as: (i) <0.1 = “unsuitable”, (ii) $0.1–0.3$ = “low suitability”, (iii) $0.3–0.6$ = “suitable”, and (iv) >0.6 = “highly suitable” (see [46]).

In addition, the relative contributions of each climatic variable to explain variance in the MaxEnt models were estimated. The values of each climatic variable on training species location and background data were randomly permuted. Then, the model was re-evaluated using the permuted data and decreases in training AUC were measured (permutation importance) [44]. The permutation importance values were normalized to percentages. A high value of permutation importance indicated that the model depended on the variable to a high degree [44] (see Appendix S1).

3. Results

3.1. Model Performance and Potential Distributions of Four Studied Species

The models predicted species location fairly well for *P. cerasoides* and *C. axillaris*, and very well for the other two species. Average AUCs ranged from 0.782 for *P. cerasoides* to 0.830 for *H. dulcis* (Table 4, Figure S3). The predicted distributions of suitable habitats according to climatic conditions are presented in Figures 3–6. Overall, areas with climates

highly suited for *C. axillaris* tended to be located north of the equator, including parts of China, Vietnam, Thailand, Myanmar, India, Bhutan, and Nepal (Figure 3), whilst those of *H. dulcis*, *F. hispida*, and *P. cerasoides* extended more equally both north and south of the equator (Figures 4–6).

Table 4. Area under the receiver-operating characteristic curve (AUC), averaged over 10 models with one standard deviation and the importance of permutation of bioclimatic variables contributing to climatic niche models of each species. The first three most important variables and the average suitable range and optimum value of those variables are presented.

Species	Average AUC (1 Standard Deviation)	Permutation Importance (Normalized Percentage) and Suitable Range of Variables					
		The First	Suitable Range (Optimal Value)	The Second	Suitable Range (Optimal Value)	The Third	Suitable Range (Optimal Value)
<i>C. axillaris</i>	0.783 (0.062)	Mean temperature of driest quarter (36.3%)	4.7–18.8 °C (13.9 °C)	Precipitation of driest month (19.3%)	8.8–81.6 mm (22.5 mm)	Precipitation of wettest month (11.8%)	161.0–397.7 mm (215.3 mm)
<i>F. hispida</i>	0.811 (0.039)	Precipitation of driest month (20%)	≥7.9 mm (14.3 mm)	Precipitation seasonality (17.4%)	21–95% (72.4%)	Mean temperature of driest quarter (°C) (15.4%)	11.3–27.0 °C (25.6 °C)
<i>H. dulcis</i>	0.830 (0.059)	Precipitation of coldest quarter (32.3%)	≥87 mm (558 mm)	Precipitation of warmest quarter (24.2%)	448.0–2127.2 mm (526.0 mm)	Mean temperature of wettest quarter (9.6%)	18.5–25.1 °C (23.1 °C)
<i>P. cerasoides</i>	0.782 (0.079)	Mean temperature of driest quarter (59.5%)	4.3–18.8 °C (11.1 °C)	Mean temperature of warmest quarter (27.9%)	12.7–25.6 °C (18.4 °C)	Isothermality (9.6%)	43.3–62.6% (49.2%)

The model predicted that the most suitable climatic conditions for *C. axillaris* occur mostly in SE China and northern Vietnam, where most of the records are located (Figure 3). The population in Thailand appears to exist under suboptimal climatic conditions, towards the southern limit of the species' range. Although the species has spread westward along the Himalayas, it has yet to be recorded in highly suitable climatic areas in Pakistan, Afghanistan, and Tajikistan, nor has it colonized highly suitable climatic areas in southern Indonesia and Papua New Guinea.

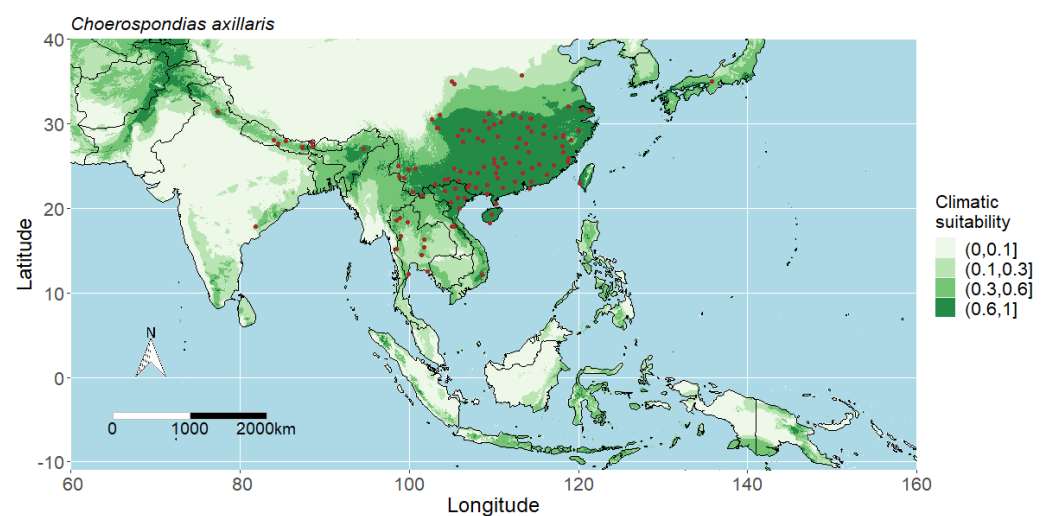


Figure 3. *Choerospondias axillaris*: confirmed records (brown circles) and potential current climate suitability, modelled from climatic variables (green)—darker green represents higher climatic suitability. Four classes of climatic suitability are (i) <0.1 = “unsuitable”, (ii) $0.1–0.3$ = “low suitability”, (iii) $0.3–0.6$ = “suitable”, and (iv) >0.6 = “highly suitable”.

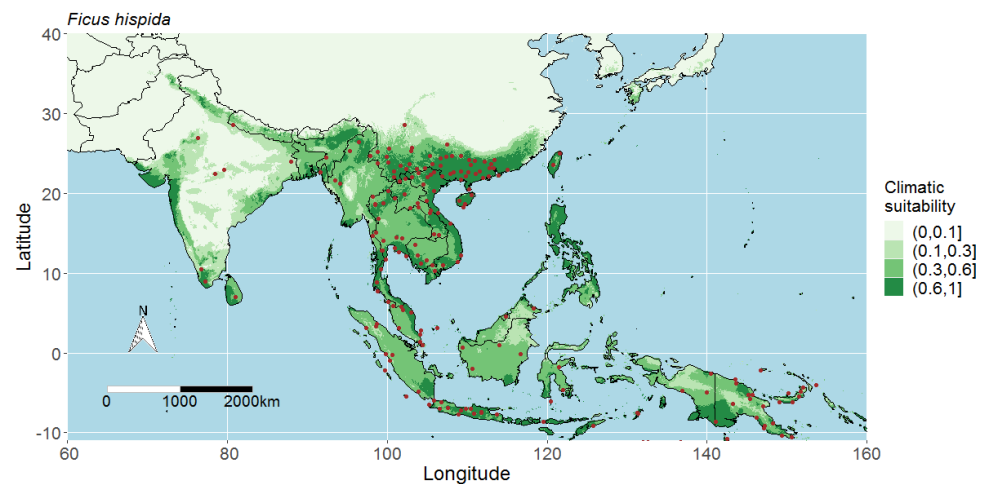


Figure 4. *Ficus hispida*: confirmed records (brown circles) and potential current climate suitability, modelled from climatic variables (green)—darker green represents higher climatic suitability. Four classes of climatic suitability are (i) <0.1 = “unsuitable”, (ii) $0.1–0.3$ = “low suitability”, (iii) $0.3–0.6$ = “suitable”, and (iv) >0.6 = “highly suitable”.

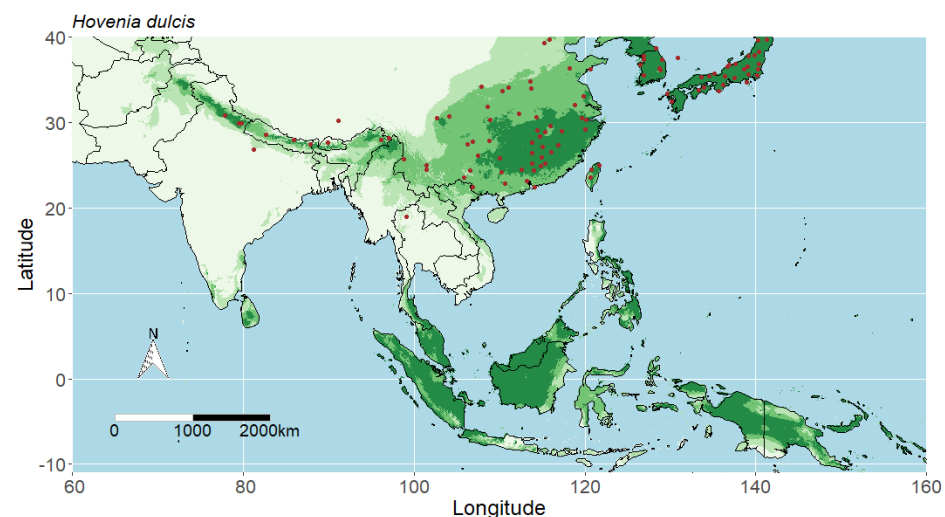


Figure 5. *Hovenia dulcis*: confirmed records (brown circles) and potential current climate suitability, modelled from climatic variables (green)—darker green represents higher climatic suitability. Four classes of climatic suitability are (i) <0.1 = “unsuitable”, (ii) $0.1–0.3$ = “low suitability”, (iii) $0.3–0.6$ = “suitable”, and (iv) >0.6 = “highly suitable”.

Areas with highly suitable climatic conditions for *F. hispida* were widely spread from southern China through Indomalaya to Papua New Guinea (latitudes 30° N and 11° S) (Figure 4), although the highest density of records was concentrated in southern China and Indochina. Most of the Philippines appears to have suitable climatic conditions for this species, but *F. hispida* has not yet been recorded there. The records in central India exist under apparently unfavorable climatic conditions, on the western edge of the species’ range.

The model predicted suitable climatic conditions for *H. dulcis* both inside and outside the species’ native range. Figure 5 shows two disjunct climatically suitable zones—a northern zone where the species is present and a southern zone where the species has yet to be recorded. The northern zone includes SE China, Taiwan, S. Korea, and Japan. The southern zone includes Malaysia, Indonesia, southern Philippines, and Papua New Guinea. The outlying population in northern Thailand appears to exist under suboptimal climatic conditions at the southernmost edge for the species’ current range.

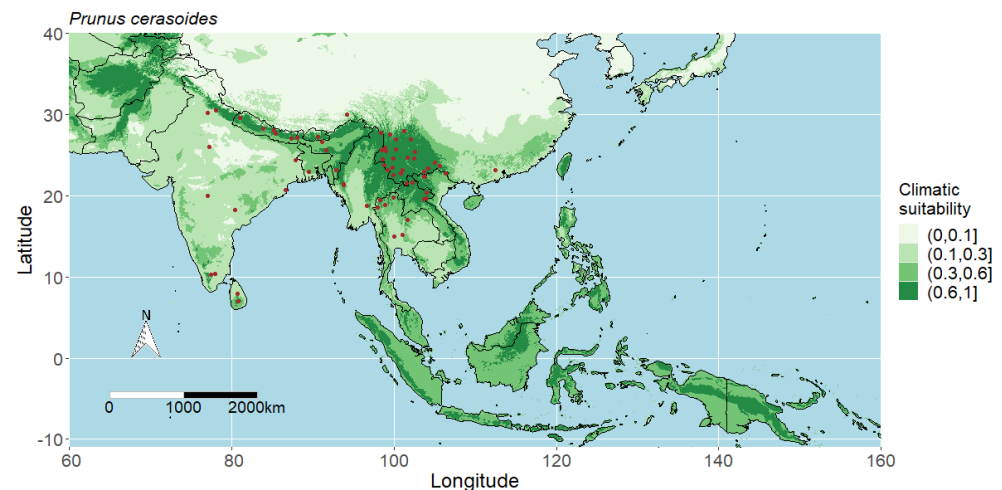


Figure 6. *Prunus cerasoides*: confirmed records (brown circles) and potential current climate suitability, modelled from climatic variables (green)—darker green represents higher climatic suitability. Four classes of climatic suitability are (i) <0.1 = “unsuitable”, (ii) $0.1–0.3$ = “low suitability”, (iii) $0.3–0.6$ = “suitable”, and (iv) >0.6 = “highly suitable”.

The recorded range of *P. cerasoides* is centered in SW China and northern Thailand and Lao PDR, spreading westward along the Himalayas (Figure 6). Scattered records exist under suboptimal climatic conditions in India and Sri Lanka at the western edge of the species’ range. Suitable (but unoccupied) climatic areas south of Thailand occurred sparsely and mostly in highland areas of the Indonesian islands, Borneo, the Philippines, and eastern Papua New Guinea.

3.2. Importance of Climatic Variables

The variables that contributed most to explaining the variance in the climatic niche models varied among the species (Table 4, see Appendix S1). The mean temperature of the driest quarter was the most important variable for *C. axillaris* and *P. cerasoides*. The mean temperature of the driest quarter (bio9) was highly correlated with annual mean temperature, minimum temperature of the coldest month, and the mean temperature of the coldest quarter. Precipitation of the driest month was among the top three most important variables for *C. axillaris* and *F. hispida*. Precipitation in the driest month was highly correlated with precipitation in the driest quarter. For *H. dulcis*, the most important variable was precipitation in the coldest quarter.

4. Discussion

4.1. Interpreting the Maps

Based on a comprehensive review of existing records, this study mapped habitat suitability in tropical and subtropical regions for four framework tree species in greater detail than previously reported. The four studied species are previously proven effective at catalyzing forest ecosystem restoration in northern Thailand, when included in mixed-species plantings [28].

Using climatic data from recorded locations, we mapped beyond each species’ recorded range the potential distribution according to climatic conditions conducive for supporting growth of each species (i.e., fundamental climatic niches). Conventionally, outputs from such models have been interpreted as “probability of presence”. However, we interpreted the models’ outputs as an index of “climatic suitability”, since we used only climatic variables in their construction and climate is only part of a species’ fundamental niche. This means that areas on the maps, marked as *climatically* suitable, may be subject to other niche limitations (e.g., unsuitable soil conditions or lack of biotic factors, such as pollinators, seed dispersers, or other essential symbionts). Dispersal barriers, particularly oceans, are

another obvious explanation of why species are absent from areas with a highly suitable climate, hence our substitution of “probability of presence” with “climatic suitability”. This view is supported by Merow et al. (2013) [47], who stated that interpreting Maxent’s predictions as indices of habitat suitability is useful for qualitative exploratory analyses (such as that of the present study).

The maps reliably show where the climate is not suitable for each species. Obviously, planting a species in such locations would be a waste of time and money. However, caution should be exercised when using the maps, to aid species selection decisions for restoration plantings. Although success is highly likely within the species’ now more clearly defined ranges (particularly when mixed with other framework tree species), additional factors must be taken into account when considering climatically suitable areas that are far outside a species’ range, i.e., soil preferences and the presence/absence of essential pollinating and seed-dispersing animals and microbial symbionts. Caution should be applied when considering climatic zones that have long been separated from historical ranges by dispersal barriers (e.g., sea), since where climate is non-limiting, the risk that a species becomes invasive (threatening local flora) is high. This is, of course, anathema to the principles of forest ecosystem restoration [1].

4.2. Predicted Potential Distribution of *Choerospondias Axillaris* and Contributing Variables

Suitable climatic conditions, to support the growth of *C. axillaris*, were predicted in both tropical and subtropical parts of the region north of the equator. This species preferred cooler areas of the subtropics, where mean dry season temperature ranged from 5 to 19 °C. This species can occupy habitats with a wide range of precipitation, suggesting a certain degree of drought tolerance. In Nepal, for example, Guatam ranks this species as moderately drought-tolerant [48].

Topography and suboptimal climatic conditions along the Himalayas may prevent *C. axillaris* from expanding its range west into highly suitable climatic areas in Pakistan, Afghanistan, and Tajikistan. To the south, the Javan sea and a wide band of hostile climatic conditions in northern Indonesia and East Malaysia may have prevented expansion of this species’ range into more climatically suitable areas on Java, the Lesser Sunda Islands, Irian Jaya, and Papua New Guinea. *C. axillaris* produces fleshy fruits that are very attractive to a diverse range of terrestrial and arboreal vertebrate frugivores [49]. This contributes to its framework species status, since such animals disperse seeds into restoration sites from nearby forest remnants, thus promoting biodiversity recovery. However, it may also limit the species’ capability to expand its range over long distances, across large areas where a suitable habitat for such animals does not exist.

C. axillaris is not known to be invasive [50].

4.3. Predicted Potential Distribution of *Ficus Hispida* and Contributing Variables

F. hispida is very widespread, with the present range and geographic extent of its predicted climatic niche closely matching previous reports [51]. Of the four species studied, *F. hispida* had the widest climatic suitability range. In decreasing order of importance, precipitation of the driest month, precipitation seasonality, and mean temperature of the dry season most explained the species’ current geographic range. *F. hispida* inhabits areas where variability in monthly precipitation is low or high, relative to mean annual precipitation (precipitation seasonality ~21%–95%). The species may be highly drought-tolerant, since it is predicted to grow where precipitation of the driest month falls to ~8 mm.

This species occupies most of the areas where the models predicted that climatic conditions fall within the species’ climatic niche, with the notable exception of the Philippines. The models predicted that climatic conditions throughout the Philippines were suitable for *F. hispida*. However, the species has not yet been recorded in the Philippines. Its absence from the Philippines may be explained by the fact that the country was not connected to the rest of the Sunda Shelf islands when sea levels fell during ice ages [52]. Figs of *F. hispida* are highly coevolved with fig pollination wasps (*Ceratosolen solmsi marchali* Mayr in

Chalcidoidea: Agaomidae) [53]. Another possible explanation for the absence of *F. hispida* from the Philippines may be that other factors, i.e., nonclimatic factors, may be detrimental to the survival of the pollinators.

F. hispida is not known to be invasive, although other *Ficus* species are, e.g., *F. macrocarpa* [50].

4.4. Predicted Potential Distribution of *Hovenia Dulcis* and Contributing Variables

High precipitation favors *H. dulcis*. The first two most contributing variables were precipitation of the coldest and warmest quarter. *H. dulcis* requires humidity during the cold season (>87 mm with optimum value of 558 mm) and summer (range ~448–2127 mm with optimum value of 526 mm). In addition, mean temperatures in the wettest quarter ranging from 18 to 25 °C during the rainy season were suitable for this species. Northern Thailand marks the southern limit of *H. dulcis*' known distribution [54].

Unsuitable climatic conditions in central Thailand and dispersal limitation may prevent spread of the species southwards. The species has not yet been recorded in highly climatically suitable areas, predicted in the Malay Peninsula, Borneo, western Philippines, and most parts of Indonesia. Seed dispersal of this species is by medium-sized birds such as wedge-tailed green pigeons [55,56]. Even though the range of wedge-tailed green pigeons stretches from southern China to Indonesia, dispersal distance by the birds may not be far enough to deliver seeds escaping unsuitable climate conditions of central Thailand.

H. dulcis is well-known as an invasive species in Brazil and Tanzania [57–60]. In Brazil, black capuchin monkeys consume the fruit and may facilitate seed dispersal [58]. Figure 5 illustrates the potential of this species to become invasive in Malaysia, the Philippines, and Indonesia. Bergamin and his team modelled the distribution of *H. dulcis* worldwide under various climate change scenarios [60]. They predicted that the species range is likely to contract slightly at low and medium latitudes, but with a strong potential for range expansion in the northern boreal zone [60]. They stated that “it is essential to implement policies to prevent *H. dulcis* introduction in suitable areas worldwide, as well as local population control, especially in biodiversity hotspots. We concur that this species should not be introduced for forest restoration projects outside of its native range, despite it being an excellent framework tree species in northern Thailand” [28].

4.5. Predicted Potential Distribution of *Prunus Cerasoides* and Contributing Variables

P. cerasoides grows in low-temperature habitats. Mean temperature of the driest quarter was the most important climatic variable. The upper limits of suitable ranges of mean temperature of dry season and summer were relatively low: 19 and 26 °C, respectively. Furthermore, suitable climatic conditions included medium temperature variability within a month relative to the year (~43%–63%). In Thailand, relatively low temperatures are found at high elevations (>1000 m asl.), resulting in the occurrence of *P. cerasoides* in upland evergreen forest, evergreen and deciduous forest, and evergreen and pine forest, particularly in disturbed areas and the forest edge [61]. Our findings suggest that high temperature and high temperature fluctuations limit the distribution of this species.

Despite highly suitable climatic conditions in northern Myanmar, *P. cerasoides* has not been recorded there, abruptly truncating the recorded distribution of the species at the national border between Myanmar, China, and Thailand. This suggests that a lack of collection effort in Myanmar may be responsible for the lack of records there. Its occurrence in the mountains of northern Myanmar is therefore highly likely.

The species has been introduced to Zimbabwe [62], Australia [63], New Zealand [64], and Japan [65]. It is not known to be invasive [50].

4.6. Study Limitations and Future Direction for Species Distribution Modelling for Forest Restoration

One of the limitations of our study may have been sampling bias in herbarium specimen collection. Herbarium specimens are more likely to be collected closer to roads and herbaria [66]. Furthermore, the density and distribution of the species records are likely

to be influenced by both geographical accessibility and political history. For example, the GBIF database contained 0.08 records of vascular plant species per square kilometer in Myanmar compared with 0.25 records per square kilometer in China [29]. This may indicate lower sampling effort in Myanmar in comparison to China. The missing data on species presence affect the differentiation of the environmental conditions between the occurrence points and the background points [67]. In our study, we addressed sampling bias by (1) systematic subsampling and (2) restricting the calibration of the model to the extent of species occurrence data and obtaining the prediction by projecting potential distributions across tropical and subtropical Asia [67]. In this study, we removed duplicate records and used systematic subsampling to account for sampling bias [40]. It is important to remove duplicate records because they lead to overfitting of the models and overestimating habitat suitability in unsuitable sites. In addition, we systematically sampled the occurrence data, to account for sampling bias. However, this subsampling method may underestimate the contribution of highly suitable areas of occurrence, where the high density of records truly reflected the commonness of the species in those areas.

Further studies may include model calibration with more environmental variables and field validations of model predictions. Adding other environmental variables to the models may produce more accurate predictions of species potential distributions, e.g., soil variables [68,69] such as soil type, pH, and nitrogen content [70]. Because some soil properties are likely to be influenced by climatic conditions [71], correlations among the variables should still be considered when selecting variables to include in the models. In addition, independent field validation of models is scarce, especially in forest restoration ecology. To test whether species can grow where models predict suitable habitat, classic transfer experiments should be performed—transplanting seedlings from their home range to the predicted suitable habitat.

Potential distributions of more species should be determined to improve future forest restoration projects. Furthermore, modeling how the distribution of species niches might change as a result of climate change is also important (e.g., [25,72,73]) to help climate-proof future forest restoration initiatives. This includes site selection, the selection of indigenous tree species, and the potential need for assisted species migration.

5. Conclusions

The climatic niches of four tree species were modelled using MaxEnt. Potentially suitable habitats based on climatic conditions were mapped both inside and outside their native ranges across tropical and subtropical Asia. The four species studied—*Choerospondias axillaris*, *Ficus hispida*, *Hovenia dulcis*, and *Prunus cerasoides*—had already been classified as excellent tree species for restoring evergreen seasonal forests [28]. The important variables contributing to their distribution differed among species. Precipitation in the driest month contributed most to determining the distribution of *F. hispida*. Mean temperature of the dry season contributed the most to the species distribution of *C. axillaris* and *P. cerasoides*, while for *H. dulcis* the precipitation of the cold season was the most important contributing factor. The predictive potential distribution maps can be used to facilitate species selection in restoration trials and to determine where not to plant, because a species may become invasive. While this study establishes the usefulness of the techniques used, their application to a much large number of species is needed, to significantly improve species selection for forest restoration initiatives.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f13070993/s1>, Figure S1: An example of systematic subsampling of the occurrence data; Table S1: Pearson's correlation coefficient between each pair of climatic variables of tropical and subtropical Asia region; Figure S2. An ascendant hierarchical clustering classification of 19 bioclimatic variables into 10 internally correlated groups (see Table 2 for full variable names); Figure S3: The area under the receiver-operating characteristic curve (AUC) of each species.; Appendix S1: Analysis of variable contributions of each species.

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