# The potential for using rare, native species in reforestation– A case study of yews (Taxaceae) in China

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## ABSTRACT

Ecosystem restoration is regarded as one of the most cost-effective ways of mitigating the effects of the ongoing climate- and anthropogenic changes and slow or revert the loss of biodiversity. Forest restoration has much potential to conserve forest specialist species and ecosystem services, by using multiple, native tree species to promote a high local diversity of trees, with likely positive effects on overall biodiversity and on ecosystem resilience. In this study, we assessed the potential of using two rare, native species of the yew family (Taxaceae) in forest restoration in China. Species of this family are only rarely used in reforestation despite their potential contribution to tree functional diversity as long-lived, shade-tolerant, evergreen understory trees with fleshy seed cones of value to frugivorous animals. By using species distribution modelling methods, we analysed national and local scale occurrence data for *Taxus cuspidata* and *Torreya grandis* to determine the climate-based potential ranges as well as important factors for growth on a local scale. The analyses showed that both species have large potential ranges driven mainly by precipitation and by comparing these ranges with the areas that have potential for sustaining forests, we found large areas available for forest restoration where these species could be included. On the local scale, we found that low light levels and low competition from co-occurring trees are more important for the growth of seedlings compared to the adult individuals of both species. If the ecological requirements for seedlings are ensured, i.e. by creating moderately shaded environments in which seedlings can escape competition, both Taxaceae species have high potential for reforestation in China and will increase the ecological qualities of a restored forest, and at the same time, the conservation of rare tree-species in their native ranges is ensured. Conclusively, both *Ta. cuspidata* and *To. grandis* are shade-tolerant, slow-growing trees that, by creating an evergreen scrubby layer, add to forest structural complexity and stability, thereby helping support ecosystem services and biodiversity, e.g. microhabitat and resources for birds and other animals.

## 1. Introduction

Forests are important in sustaining much of the world's biodiversity, the functioning of the biosphere, and the livelihoods of millions of people. Globally, forests cover approximately 30% of the land area and a third of this is relatively undisturbed by human activities (FAO and UNEP, 2020). The value of forests have become increasingly more important considering the ongoing climate changes, as they mitigate

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effects by retaining water, storing carbon dioxide and so on (FAO and UNEP, 2020). In the past 30 years, deforestation has been a major problem leading to a net loss of 178 million hectares of forest worldwide (FAO and UNEP, 2020). Furthermore, Bastin et al. (2019) highlight the climate-change related threat to forests by estimating a loss of ~ 223 million hectares of potential forest area under future climate conditions (2050 s). Hence, there is a strong need to protect intact forests, but also to restore degraded forests and forests in deforested areas (Jacobs et al., 2015; Watson et al., 2018).

Ecosystem restoration is increasingly highlighted as an effective and relatively cheap solution to mitigate biodiversity loss and climate change (Turner, Oppenheimer and Wilcove, 2009; Bastin, Yelena, et al., 2019; Lewis et al., 2019; Leclère et al., 2020), with several recent studies showing that the restoration of forests have great impacts on carbon sequestration (Feng et al., 2013; Lu et al., 2018). The importance of ecosystem restoration is highlighted by the recent announcement from the United Nations declaring the period 2021–2030 'The Decade on Ecosystem Restoration'. Here, restoration of forest ecosystems, by planting trees or by promoting spontaneous regeneration of woody species, is one of several strategies suggested to be important in accomplishing this goal (Chazdon and Uriarte, 2016, https://www.decadeonrestoration.org/what-ecosystem-restoration).

Recently, many international commitments to restore degraded lands have been made and several large-scale restoration projects have been initiated to combat the loss and degradation of forest ecosystems. Examples of such projects are the Bonn Challenge that pledges to restore 350 million hectares of deforested and degraded lands globally by 2030, and the REDD + initiative that uses different policy- and incentive-based strategies to prevent forest loss and degradation worldwide (http://www.bonnchallenge.org/; Kissinger, Herold and De Sy, 2012). However, forest restoration is not the only solution to climate change and biodiversity loss, and in some cases it can even be harmful to the local ecosystem, i.e. afforestation in former grasslands, savannas and open-canopy woodlands, resulting in lower biodiversity and ecosystem services (Veldman et al., 2015, 2017). For example, afforestation to combat desertification in northern regions of China led to severe depletions in soil moisture levels because of unsuitable environments for tree growth in these arid regions (Cao, Chen, et al., 2011; Deng et al., 2016), while afforestation in Shaanxi China using exotic mono-cultures led to decreased vegetation cover, biodiversity and soil moisture compared to abandoned areas (Cao, Chen and Yu, 2009). Moreover, forest restoration is complex and some important aspects to consider when restoring forest ecosystems are the sustenance and maintenance of local livelihoods, the protection of open-canopy ecosystems from afforestation, the promotion of landscape heterogeneity and biodiversity, and the distinction of residual carbon stocks from new carbon stocks (Brancalion and Chazdon, 2017).

In the past ~ 20 years, China has initiated some of the largest reforestation programmes in the world in order to mitigate the effects of many years of intense deforestation. Prior to 2000 BCE, China harboured extensive forests covering up to 60% of the land area, but by 1900 CE forest cover had decreased to just 17% owing to the rapidly growing human population (Zhang, 2000; Liu et al., 2019). During two governmental initiatives in 1958 and 1966–1976, radical deforestation regimes were applied resulting in a forest cover of only 8.2% around 1960. However, the serious effects of this forest destruction was already recognized in the 1970s and reforestation initiatives have since then been implemented (Zhang, 2000; Liu et al., 2019). Following some devastating floods in the late 1990s, the Chinese government implemented several national-scale reforestation programmes to prevent such floods in the future by restoring degraded lands (Delang and Yuan, 2015). The most prominent of these programmes is the "*Grain-for-Green Program*" (GfG), also known as the "*Sloping Land Conversion Program*" (SLCP), that uses cash as incentive for rural households to convert especially sloped agricultural lands into forest, shrub- or grass-land (Delang and Yuan, 2015; Hua et al., 2016). To allow forests to recover

from decades of over-logging and to help restore forest ecosystems and their resilience, the "*Natural Forest Protection Program*" (NFPP) was launched in 1998 and fully implemented by the Chinese government in 2000 (Ren et al., 2015; Sun, Canby and Liu, 2016)**. Natural forest logging bans and harvesting reductions instilled by the NFPP, are some of the largest governmental responses to combat deforestation worldwide (Sun, Canby and Liu, 2016), and the efforts of these Chinese reforestation- and protection programmes resulted in an increase in national forest cover to 22.96% (Xu et al., 2019). In a recent paper assessing the state of the world's forests, Hill et al. (2019) illustrate how forests have changed globally in the past 18 years in terms of both biodiversity and intactness, and here China is shown to harbour several areas of high biodiversity significance, but low intactness, suggesting that these areas could be suitable targets for restoration efforts.

A common feature of Chinese forest restoration programmes and restoration efforts in general is that the emphasis has most often been on short-term economic benefits instead of long-term ecological benefits such as resilience and biodiversity (Brockerhoff et al., 2008; Robbins and Harrell, 2014; Delang and Yuan, 2015). Thus, usually just one or a few fast-growing tree species are used for restoring forests, leading to low survival rates, low resilience to extreme weather events and diseases as well as a lower biodiversity and higher fragmentation compared to the original natural forests they replace (Bennett, 2008; Brockerhoff et al., 2008; Cao, Sun, et al., 2011; Delang and Yuan, 2015; Hua et al., 2018; Liu, Kuchma and Krutovsky, 2018). However, the ability of planted forests to support local biodiversity depends strongly on the original state of the restored land, i.e. if the new forest is planted in a naturally grass covered area it is expected to harbor less biodiversity than the original grassland (Bremer and Farley, 2010). Recently, several studies emphasize the importance of planting multiple, preferably native, species in reforestation projects in order to meet the goals of mitigating climate change effects and restoring biodiversity and ecosystem services (Hooper et al., 2005; Bremer and Farley, 2010; Brockerhoff et al., 2013; Huang et al., 2018). Besides being more resilient and less susceptible to diseases, mixed species plantings that include species with different life-history traits, e.g. fast growing vs. slow growing, shade-tolerant vs. shade-intolerant, create higher productivity and higher structural complexity that are needed to restore ecosystem functions and support local biodiversity (Menalled, Kelty and Ewel, 1998; Alexander et al., 2016; Yang et al., 2018). However, the effect of reforestation programmes on the local biodiversity is still relatively unexplored. Recent studies in China, analysing bird and arthropod communities in different types of land cover related to the GfG, found that reforestation with monocultures support the lowest diversity of both birds, bees and other arthropods, while mixed species plantations had more arthropod species in common with native forest than other land cover types (Hua et al., 2016; Wang et al., 2019). Therefore, it seems that there is a lot to gain in terms of biodiversity simply by choosing native trees planted in a mixed species setting when planning future forests restoration projects.

Species of the yew family (Taxaceae) are rarely used in reforestation. The yew family encompasses six extant genera worldwide, four of which are represented in China with eleven species where of five is endemic (Fang, Wang and Tang, 2011). Several Taxaceae genera have restricted natural distributions, e.g. most of the Chinese Taxaceae species are endemic to small regions within China or between China and neighboring countries, and many species are listed as either vulnerable or endangered (IUCN Red List). Further, many Taxaceae species are threatened especially by human factors such as collection of plant material for medicinal uses and habitat destruction, as well as climatic changes (Cope, 1998; Qin et al., 2017). Taxaceae species have flat needle-like leaves, and are mostly slow-growing, dioecious trees/shrubs (Cope, 1998). Uniquely among conifers, they produce solitary ovules surrounded by a fleshy aril, and hence have value for frugivorous animals (Cope, 1998; Li et al., 2015; Tsuji and Morimoto, 2016). Although Taxaceae species are rarely planted as part of forest restoration efforts,

several conservation projects to protect threatened populations of Taxaceae species exist worldwide (Iszkuło, 2001; Kwit, Horvitz and Platt, 2004; Shi, Bai and Lu, 2010; Qu, Wang and Zhang, 2018).

Because of their long-lived, shade-tolerant nature and low stature, Taxaceae species have the potential to provide ecosystem services in terms of adding to the structural complexity of the restored area by creating stable patches with an evergreen, middle-story layer. Structural complexity is important in controlling certain physical aspects such as soil erosion and water regulation/filtration for agricultural and urban areas, while also being an important component in supporting the native biodiversity by e.g. providing heterogeneous habitats (De Groot et al., 2010; Alexander et al., 2016). Furthermore, because of their fleshy edible seed cones, species of Taxaceae also have the potential for providing important dietary components for wildlife species as well as for local human communities (Cope, 1998; García-Nieto et al., 2013; Shackleton et al., 2017). Several Taxaceae species, especially in the *Taxus* genus, have medicinal properties with the foliage and berries having been used by native people to treat respiratory illness, rheumatism, kidney diseases etc., while recently *Taxus* foliage and bark have become important for providing a compound used in cancer treatment (Hatfield, 2004; Delong and Prange, 2010; Juyal et al., 2014). Finally, Taxaceae species have a high cultural importance in many societies related to their longevity and wood properties valued in e.g. weapon-, tool- and furniture-making and for ceremonial purposes (Delong and Prange, 2010). In this study, we chose *Taxus cuspidata* and *Torreya grandis* as our study species, as they represent important species in terms of rarity, culture and economy in China. Both species play roles in sustaining local communities – *To. grandis* is cultivated widely in the Zhejiang province and there is a big industry connected to the nuts of this species (Chen and Jin, 2019), while the berries of *Ta. cuspidata* are used on a smaller scale as local farmers will collect/cultivate and sell them for human consumption (Kou et al., 2017, info on *Ta. cuspidata* berries from authors own experience).

Here, we present a species distribution modelling (SDM) framework for assessing the potential use and integration of native species into local forest restoration projects. We chose two species from the Taxaceae family for our case study since they represent species that are usually under-used in reforestation, but that can potentially bring both ecologically and culturally important functions to a restored ecosystem. We address the following questions in the assessment: 1) Which areas of China are climatically suitable and available for reforestation using *Torreya grandis* and *Taxus cuspidata*? 2) How is the local-scale natural occurrence of these species affected by environmental factors, and what are the implications for their use in restoration?

## 2. Materials and methods

### 2.1. Species descriptions

*Torreya grandis* is an evergreen conifer tree species native to the subtropical monsoon regions of east-central China. It grows most often as an understorey tree at elevations between 200 and 1400 m a.s.l. reaching up to 25 m tall and producing fleshy, edible seed cones (Flora of China). A variant of the species, *To. grandis* cv. Merrilli, is cultivated on a large scale and the aril and seeds are used for making essential oil and for human consumption (Feng et al., 2011; He et al., 2016; Yu et al., 2016; Chen and Jin, 2019).

*Taxus cuspidata* is a small evergreen conifer tree native to northeast China, east Russia, Korea and Japan. The species often grows in cold, humid forests at elevations of 500–1000 m a.s.l. as an understorey tree that reaches a maximum height of 20 m (Flora of China). It produces red, fleshy seed cones that are edible (aril only), while the foliage, bark and seeds contain the poisonous alkaloids called taxines (like all members of the *Taxus* genus) (Russin et al., 1995; Thomas and Polwart, 2003). The wood is used for manufacturing of furniture and as carving material, while the heartwood yields a red dye (Flora of China).

### 2.2. National scale analyses

#### 2.2.1. Data

We obtained occurrence data for *Taxus cuspidata* and *Torreya grandis* from the *Chinese Vascular Plant Distribution Database,* assembled by the Biodiversity and Biosafety Group at the Institute of Botany, Chinese Academy of Sciences (Huang et al., 2011). The data consists of county-level occurrence records collected in the period 1900 – current time with most records collected after 1950.

As *To. grandis* is native to the subtropical monsoon regions of east-central China, we expect its distribution to be limited by precipitation. Therefore, we chose seasonal climatic variables that relate to precipitation for use in the species distribution models (Table A1). As we wanted to keep the same methodology for both species, we made sure that the same climatic variables were sensible for describing the climatic limitations of *Ta. cuspidata* in temperate north-eastern China. We found that the wet/warm and dry/cold quarters (bio8/bio18, bio9/bio19) correspond well to summer and winter seasons in this region.

#### 2.2.2. Species distribution modelling

##### 2.2.2.1. Ensemble modelling.
We modelled the potential distributions of *Ta. cuspidata* and *To. grandis* using the ensemble forecasting methods from the R-package 'biomod2' (vs. 3.3 – 7.1) (Thuiller et al., 2016). In order to standardized the data, we converted the species occurrence data from county polygons to a raster using the *fasterize* function of the 'fasterize' package in R, to a resulting grid cell size of 20 km × 20 km. The resulting raster consisted of grid cells containing 1's (grid cells located inside the species occurrence polygon), and 0's (grid cells located outside of the species occurrence polygon) (Fig. A1).

As only presences are recorded in the species datasets, we created pseudo-absence (PA) datasets for use in modelling instead of assuming that a non-presence equals a true absence. The method of creating pseudo-absence data was adopted from Barbet-Massin et al. (2012), and hence we created the pseudo-absences by randomly drawing points from within the entire China, so-called background points. We balanced the number of pseudo-absence points to those of the presence points, and a total number of 708 and 245 pseudo-absence points were chosen, for *To. grandis* and *Ta. cuspidata* respectively, for each pseudo-absence dataset.

The algorithms that we chose for modelling are all commonly used in SDM studies and comprise a mix of simple and complex ones (Table A2) (Marmion et al., 2009). All individual models with TSS and AUC values above a threshold of 0.7 were chosen for the ensemble modelling. We performed the ensemble modelling using the *'EMmeanByTSS'* and *'EMcaByTSS'* algorithms. The *'EMmean'* algorithm combines all the individual models into an ensemble model containing the mean prediction for all individual models. The *'EMca'* algorithm computes the committee average of all model predictions, meaning that the output will describe model agreement (on predicting either presence or absence) where high values mean high agreement on predicting presence and low values (close to zero) mean high agreement on predicting absence, hence this algorithm also quantifies the uncertainty of the mean predictions.

For validating our models, we chose the block cross validation method (blockCV) as described in Roberts et al. (2017) and Valavi et al. (2019), instead of 'biomod2''s default strategy of repeatedly and randomly resampling data into a calibration set and a validation set (Hao et al., 2019). BlockCV increases independence by dividing data into units based on e.g. geographic space. This means that when performing the cross validation, evaluation data are spatially separated from training data, helping overcome the issue of overestimation of model evaluations from using spatially similar training and evaluation data, i.e. helping to test whether the model predicts equally well on close as well as distant locations (Roberts et al., 2017; Valavi et al., 2019). In order to have both presences and pseudo-absences in all folds, the best blockCV method was the systematic assignment of spatial blocks to the
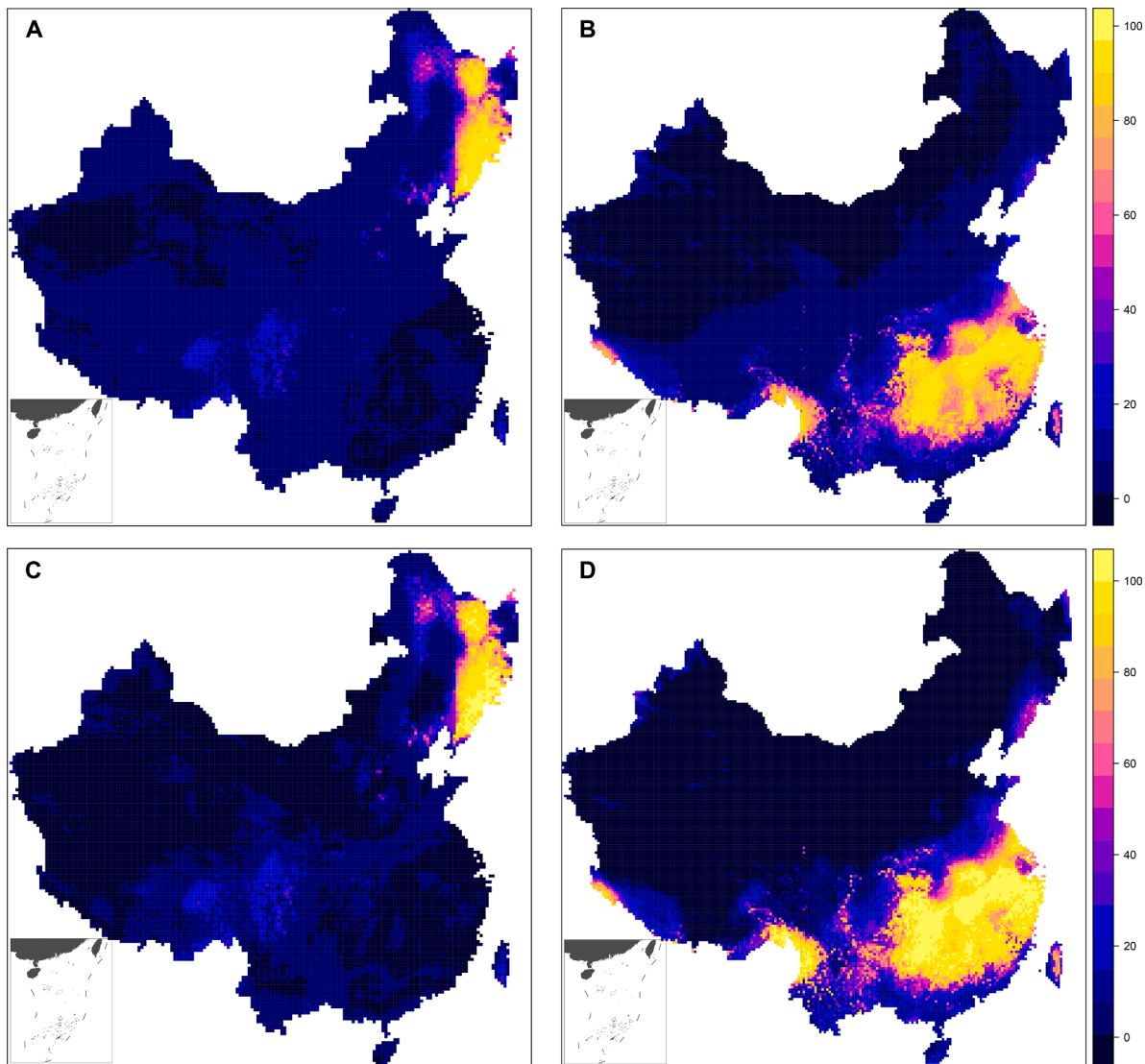
**Fig. 1.** Model predictions from Ensemble modelling. A: Taxus cuspidata mean predictions across the 10 PA datasets, B: Torreya grandis mean predictions across the 10 PA datasets, C: Ta. cuspidata mean of the committee average of predictions across the 10 PA datasets, and D: To. grandis mean of the committee average of predictions across the 10 PA datasets. Inserts show the South China Sea, but no predictions are shown here as it contains no species data. The map projection used here is the Albers Equal Area Conic projection.

environmental data, the so-called checkerboard pattern method (Roberts et al., 2017). The resulting block sizes were species specific, since all blocks need to contain species presences in order to use them in the SDMs, and presences varied in both number and spatial structure between the two species (Fig. A2). For *To. grandis* the size of each block was 8°E × 6.66°N (WGS84) and divided into two training datasets (~2/3 of the data) and two testing datasets (~1/3 of the data). For *Ta. cuspidata*, block size was 5.7°E × 4°N (WGS84) organized similarly into training and testing datasets.

*2.2.2.2. Bioclimatic envelope modelling.* In order to assess the realism of the predicted distributions from the ensemble models, we supplemented them with simple models of the bioclimatic envelope of each species and compared their predicted species distributions respectively. A bioclimatic envelope model ('SRE' algorithm in 'biomod2') uses presence only data to produce a multidimensional environmental space for the species, so we did not produce presence-absence datasets for these models. We chose to do 10 evaluation runs to reduce random effects on the model performance, and the final model results are based on an ensemble of the evaluation runs ('EMmean' and 'EMca').

*2.2.2.3. Model evaluation.* We averaged the evaluation statistics, TSS, AUC, Sensitivity and Specificity, across all pseudo-absence datasets for the final ensemble models and across all evaluation runs for bioclimatic envelope models (Table A3). We averaged variable importance estimates across all individual algorithms and evaluation runs for the ensemble models and across all evaluation runs for the bioclimatic envelope models, resulting in one mean value for each explanatory variable. We present the ensemble model projections as the mean predictions across all pseudo-absence datasets within each ensemble algorithm ('*EMmeanByTSS*' and '*EMcaByTSS*') for the ensemble models and across all evaluation runs for the bioclimatic envelope models (Fig. 1 and Fig. A3).

*2.2.3. National scale reforestation potential*

In order to assess the potential for using the two Taxaceae species in reforestation in China, we estimated the area that the species do not currently occupy and that has potential for reforestation. To do this, for each species we converted the predicted species distribution (*EMmeanByTSS*) to binary format using 0.5 as a threshold, meaning that all values below 0.5 were considered species absences and all values above 0.5
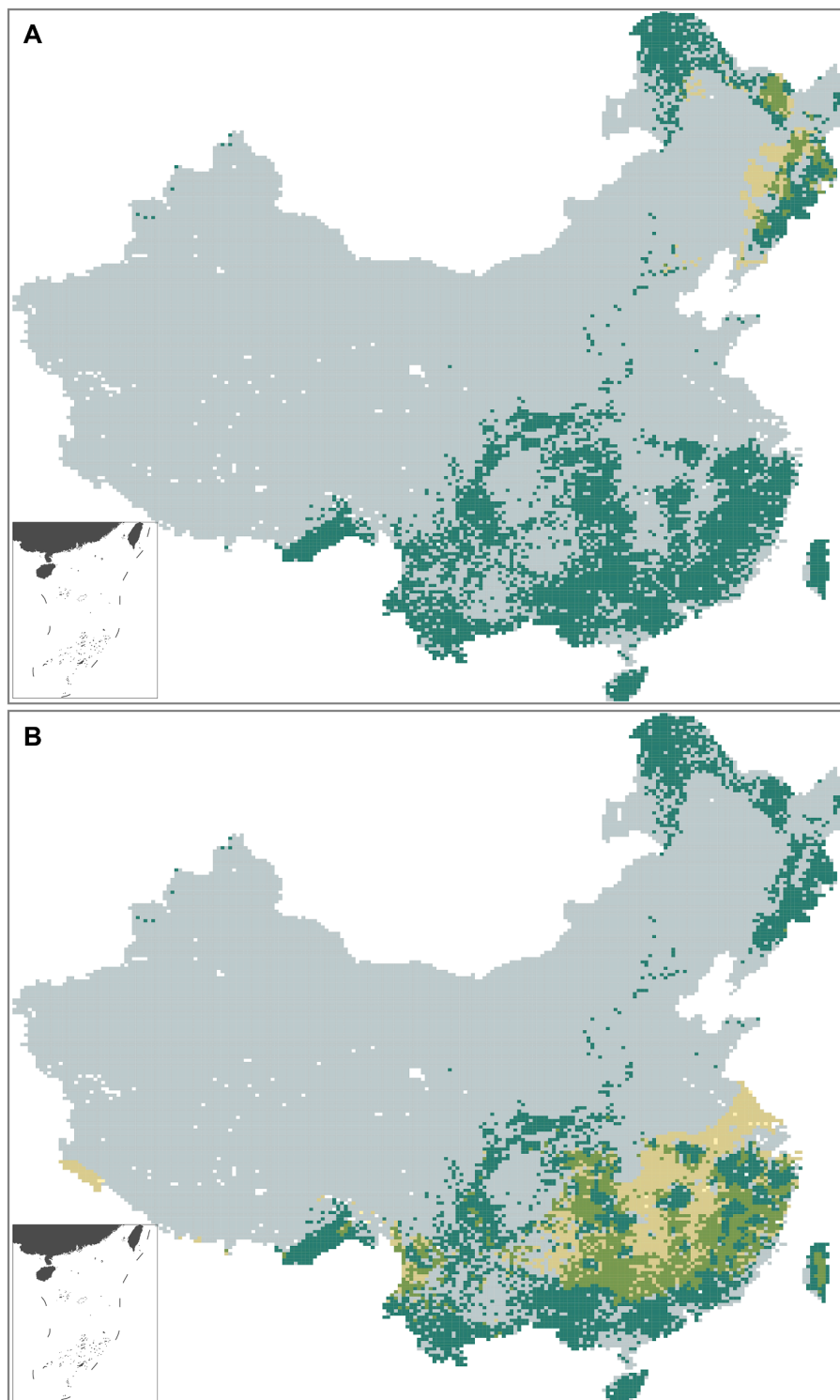
**Fig. 2.** Potential areas for reforestation using Taxus cuspidata and Torreya grandis obtained from subtracting current species ranges from the Ensemble model predictions and intersecting this with 'The tree restoration potential' map. A: Potential areas for reforestation using Ta. cuspidata, B: Potential areas for reforestation using To. grandis. Yellow colour denotes species suitable ranges (outside current range), dark green colour denotes the 'Tree restoration potential' from Bastin et al. (2019) and areas of overlapping colour represent the estimated potential reforestation area. Inserts show the South China Sea, but it contains no species data. The map projection used here is the Albers Equal Area Conic projection. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were considered species presences. We obtained this threshold value by running the '*find.Optim.Stat*' function from the 'biomod2' package, which searches for the optimal threshold value for converting the continuous predictions into binary predictions. The computed optimal threshold corresponded well with the average cut-off values obtained from the evaluation summaries from the ensemble model results. Afterwards, we subtracted the known area of species occurrence to get the areas that are climatically suitable for the species but where the species is currently absent (*SuitAbs*). To identify the areas that are realistically

available for reforestation, we took into account the human infrastructure, land-use and other human activity in China obtained from the 'tree restoration potential' map from Bastin et al. (2019). This map shows the areas that have the space and need for tree restoration, expressed as low to high potential (0–1000). First, we converted the 'tree restoration potential' map into binary format using a conservative threshold of 500, as we were interested in the areas having a relatively high potential. Then, in order to estimate the final reforestation potential for each of our focal species we identified the overlapping areas of the binary 'tree

restoration potential' map with the before mentioned species *SuitAbs* maps. We overlaid the species *SuitAbs* maps with the binary 'tree restoration potential' maps to locate the areas within the climatically suitable ranges that have high potential for tree restoration. The final result for each species therefore represent the areas of the species potential distributions where the species are currently absent and that have a high potential for reforestation (Fig. 2). Subsequently, we identified all counties and provinces located within each estimated potential reforestation area, as well as calculated the size of the reforestation areas (using ArcMap version 10.5.1).

### 2.3. Local scale analyses

#### 2.3.1. Data and field work methods

*2.3.1.1. Torreya grandis.* We collected data on *To. grandis* in Tianmu Mountain National Nature Reserve in July and August 2018. We chose Tianmu Mountain as the habitat here is representative for the most common habitat where this species is found, namely mountains and valleys by streams at elevations from 200 to 1400 m (Flora of China). Tianmu Mountain National Nature Reserve is located in the northwestern part of Zhejiang Province. The area became a national nature reserve in 1986 and the forests have been protected from logging since then. The mean annual temperature in Tianmu Mountain ranges from 14.5 °C near the base (350 m a.s.l.) to 9.0 °C near the top (1,506 m a.s.l.) and the annual precipitation ranges from 1739 mm at the base to 1751 mm at the top (Da et al., 2009). The Tianmu mountain area is a species-rich region with around 2160 vascular plant species and is further known for harbouring large trees of species such as *Cryptomeria japonica, Ginkgo biloba,* and *Torreya grandis* (López-Pujol, Zhang and Ge, 2006). Data collection was performed by laying out transects within the main distribution of *To. grandis* along the centrally located stream. Along each transect we set up 5 m × 5 m subplots covering the entire elevational gradient within the species distribution area (400–900 m a.s.l.). For each subplot, we collected data on diameter at breast height (DBH) and height of all *To. grandis* individuals as well as DBHs of co-occurring tree species above a DBH of 3 cm. Further, we collected GPS-location (using Haglöfs VL5), altitude, slope, distance to water and light availability (canopy openness) for each subplot (Table A1). We recorded all these environmental variables at the midpoint of the subplot. The distance to the nearest stream was recorded as a proxy for water availability, as this has been shown to work well for other species of the Taxaceae family (Sanz et al., 2009). We recorded the light availability as the proportion of open canopy using a densiometer (Baudry et al., 2014). The final light availability value is an average of four readings in each compass direction, to obtain an average canopy openness un-affected by slope or other obstructions, and expressed as a percentage (https://www.forestry-suppliers.com/Documents/1450_msds.pdf).

*2.3.1.2. Taxus cuspidata.* We collected data on *Taxus cuspidata* in Muling *Taxus cuspidata* National Nature Reserve. The area was approved as a national-level nature reserve in 2009 to protect the natural populations of *Taxus cuspidata,* and the environment here therefore should represent common natural habitat for this species. The reserve is located in Heilongjiang province and the annual mean temperature in the reserve is −2 °C, annual precipitation is 450–510 mm, and the elevation ranges from 500 to 900 m a.s.l. Data on *Ta. cuspidata* were collected in a 25-ha forest plot that was established in 2013 as part of the Chinese Forest Biodiversity Monitoring Network (CForBio, https://geobon.org/downloads/PDF/2016-CForBio-EN.pdf) and ForestGeo network (https://www.forestgeo.si.edu/). The forest plot is covered by a grid with grid cells measuring 20 m × 20 m each, and we collected grid-based data by measuring GPS-coordinates, elevation, canopy height, soil temperature, soil volumetric water content and soil electric conductivity at a number of selected grid-cell intersections (Table A1). Further, we

used information from the CForBio inventory data to easily locate each individual adult *Ta. cuspidata* tree and record GPS location, elevation and slope (using Haglöfs VL5), aspect, DBH and height. For collecting data on *Ta. cuspidata* seedlings, we randomly selected 78 grid cells, 40 from a list of all grid cells and 38 from a list of grid cells with known seedling locations provided by the CForBio inventory data. In each of the 78 randomly chosen grid cells, we set up a 10 m × 10 m subplot where we recorded GPS location, elevation, slope, aspect, DB (diameter at base), height and light (canopy gap, measured by densiometer, same method as for *To. grandis*) for each individual seedling.

In order to compare presence locations with absence locations, we created pseudo-absences by randomly selecting points from the grid cells that did not contain *Ta. cuspidata* individuals. We chose to balance the number of pseudo-absences to the number of collected presence records, so the final number of pseudo-absence points is 200. To include the impacts of competition in the analyses, we made three competition variables. First, we located all the neighbouring trees in a 10-m radius from each presence/pseudo-absence of *Ta. cuspidata*, and then we organized those neighbours into functional groups based on whether they are deciduous (BA_DEC) or evergreen. We further divided the evergreen tree group into two groups based on the type of foliage: *Abies* and *Picea* have dense shade-providing foliage (BA_PA) while *Pinus* has more sparse foliage (BA_PINUS). Finally, we summarized the basal areas of the trees of each functional group resulting in one measure of competition for each functional group for each observation of *Ta. cuspidata* (Table A1).

We created several environmental raster layers by interpolating grid-based field data (canopy height, soil temperature, soil water, soil electric conductivity and elevation) to the whole area using the Kriging method in ArcGIS. Further, we created a raster of topographic wetness index (TWI) based on the newly created elevation raster and the ArcGIS tools *flow direction* and *flow accumulation*. Finally, we extracted values from all environmental raster layers to each presence and pseudo-absence point. We used ArcMap version 10.5.1 to create the above variables, and these and other variables used for the analyses are described in Table A1.

#### 2.3.2. Analyses

Because of highly zero-inflated data, we used a two-step approach in the analyses (Welsh et al., 1996). First, we analysed the presence-absences of each species (PA analysis) in order to find the important abiotic and biotic factors that influence the local distribution. Secondly, we analysed the non-zero data with basal area of the focal species as the response (BA_1 analysis), representing size and indirectly age. With this analysis, we are able to describe in detail what influences the growth of the species, specifically which roles environment and competition play here. To complement the basal-area-data analysis, we did another analysis using only the basal-area-data for the smaller individuals (BA_2 analysis). For *To. grandis,* we labelled all subplots containing at least one individual with a DBH < 5 cm as *Juvenile,* and conducted a separate GLM analysis on these. For *Ta. cuspidata*, seedlings were recorded separately from adults (seedling DBH < 5 cm) and we similarly did a final analysis on just the seedling data. The results from these complementary analyses (BA_2) will serve to test the patterns that we see in the basal-area analyses on all individuals (BA_1). We chose a mix of environmental- and competition predictor variables for the analyses on both species, but the variable composition varied across analyses (Table A1). The Pearson correlations among the predictors in each analysis were always ≤ 0.65.

We started the analyses by running several algorithms on our data, ranging from simple linear regression models to more complex machine-learning algorithms (Table A4) in order to choose the algorithm that was best suited to the specific data ('caret' package). For the *To. grandis* data, all algorithms performed equally well on the data (Table A4), so we chose to use GLMs for the analyses since they are simpler and therefor easier to interpret. For the *Ta. cuspidata* data, random forest (RF) and boosted regression trees (GBM) outperformed the other algorithms (Table A4), but we chose to use the random forest algorithm for all *Ta.*

**Table 1**

Variable importance (VarImp) values were averaged across all individual algorithms and evaluation runs for the Ensemble model and the bioclimatic envelope model for both species. VarImp values are presented as the mean (±SD).

| Variable name | Variable Importance, mean (SD) | | | |
| --- | --- | --- | --- | --- |
| | *Torreya grandis* | | *Taxus cuspidata* | |
| | Ensemble | Bioclim | Ensemble | Bioclim |
| Summer temperature | 0.123 (0.0504) | 0.156 (0.016) | 0.187 (0.074) | 0.621 (0.017) |
| Winter temperature | 0.174 (0.077) | 0.314 (0.015) | 0.384 (0.061) | 0.569 (0.013) |
| Summer precipitation | 0.279 (0.085) | 0.507 (0.0081) | 0.508 (0.097) | 0.660 (0.013) |
| Winter precipitation | 0.622 (0.098) | 0.601 (0.0058) | 0.146 (0.057) | 0.517 (0.009) |

*cuspidata* datasets, since RF is increasingly used in ecological modelling, and is easily implemented and interpreted as well (Cutler et al., 2007).

For the GLM analyses, we used a forward stepwise selection method (*qselection*, 'FWDselect' package) to find the final variable subsets that minimised Akaike's Information Criterion (AIC) for each of the three response variables of the *To. grandis* data. We log-transformed the BA response and BA predictor variables prior to modelling, to meet the assumptions of the linear regression algorithm (e.g. make them conform to a normal distribution).

Prior to fitting the random forest models on the *Ta. cuspidata* data, we tuned the parameter 'mtry' by systematically fitting models with different values of the 'mtry' parameter in order to get the lowest OOB error (Out-Of-Bag error) (*tuneRF* function, 'randomForest' package). The 'mtry' parameter is the number of randomly selected variables at each split in the classification/regression tree. RF models were all run with the optimal 'mtry' values and with the parameter 'ntree' = 501, while all other parameters were set to their default values. We excluded highly correlated variables (Pearson's correlation coefficient > 0.7) prior to modelling.

We evaluated the GLM models based on Accuracy for the classification analysis and pseudo-$R^2$ for the regression analyses. For evaluating the importance and effect of the predictor variables on the response variable, we report variable estimates, standard errors and p-values for all predictor variables as well as response plots for the predictor variables in each analysis (Table 2 Fig. 3).

We evaluated the RF models in a similar manner to the GLM models, based on Accuracy for the classification analysis and $R^2$ for the regression analyses. For the classification analysis, we evaluated variable importance as the permuted variable mean decrease in accuracy. A high mean decrease in accuracy means that the variable is important for predicting the model outcome. For the regression analyses, we evaluated variable importance as the permuted variable percent increase in mean square error. A high increase in mean square error means that the variable is important in predicting the model outcome (Genuer, Poggi and Tuleau-Malot, 2010). We report importance estimates, p-values and partial dependence plots for the three most important variables for all

RF models (Table 3, Fig. 4).

When not otherwise stated, we did all processing and analyses using R version 3.6.1

## 3. Results

### 3.1. National scale analyses

#### 3.1.1. SDM model evaluations

Evaluation statistics show that the ensemble models generally performed better than the bioclimatic envelope models (Table A2). Mean TSS and AUC values for the ensemble models were above 0.88 for both species, while mean TSS and AUC values for the bioclimatic envelope models were all above 0.7.

Precipitation (especially winter precipitation) is generally more important than temperature for describing the distribution of *Torreya grandis*, while the most important factors for *Taxus cuspidata* were summer temperature and precipitation (Table 1).

#### 3.1.2. SDM model projections

The ensemble forecasts generally show that there are many areas with suitable environmental conditions outside of the counties where the species are currently observed (Fig. A1 & Fig. 1A,B). The committee average predictions show that there is a high agreement among the individual models in the ensemble in the core area of species occurrences (Fig. 1C,D). The mean predictions from the bioclimatic envelope model show a similar area of suitable habitat for both species, albeit this is considerable broader for *To. grandis* (Fig. A3). Again, the committee average predictions are similar to the mean predictions (Fig. A3).

#### 3.1.3. Reforestation potential

The maps of the estimated potential reforestation areas show that a substantial area is available for restoration including both tree species (Fig. 2). An area of 72,800 km$^2$ is available for reforestation including *Ta. cuspidata*, constituting 5 provinces and 64 counties. The area for potential reforestation including *To. grandis* is substantially larger at 499,600 km$^2$ spanning 18 provinces and 608 counties including the provinces of Taiwan and Yunnan where currently only few or no *To. grandis* are present.

### 3.2. Local scale analyses

#### 3.2.1. Torreya grandis

From the PA data analysis, we found that altitude and basal area of all trees are the most important variables for explaining the presence of *To. grandis* at this local scale (Table 2). Response plots show that *To. grandis* is mainly present at high altitudes (maximum altitude 865 m.a.s. l.) and with a low amount and/or small size of co-occurring trees (DBH > 3 cm) (Fig. 3A-B). From the analysis on basal area of all *To. grandis* individuals, we found that the most important variables are light and the basal area of evergreen angiosperm trees (Table 2). Response plots show

**Table 2**

Results from the regression analyses on Torreya grandis. Variable estimates, standard errors (S.E.) and p-values are reported for all three analyses: PA = analysis done on Torreya occurrence data, BA_1 = analysis on Torreya BA data for all individuals, BA_2 = analysis on Torreya BA data for only smaller individuals (DBH < 5 cm). Model summary for the PA model: Pseudo-$R^2$ (Tjur) = 0.10, p = 0.000, Null deviance = 215.48 on 169 degrees of freedom, Residual deviance = 198.03 on 167 degrees of freedom and AIC = 204.03. Model summary for the BA_1 model: Pseudo-$R^2$ (Nagelkerke) = 0.28, p = 0.009, Null deviance: 298.03 on 89 degrees of freedom, Residual deviance: 269.10 on 87 degrees of freedom, AIC: 361.98. Model summary for the BA_2 model: Pseudo-$R^2$ (Nagelkerke) = 0.22, p = 0.098, Null deviance: 123.03 on 49 degrees of freedom, Residual deviance: 111.97 on 47 degrees of freedom, AIC: 190.2. Significance codes: '***' $p < 0.001$, '**' $p < 0.01$, '*' $p < 0.05$, '.' $p < 0.1$, ' ' $p < 1.0$.

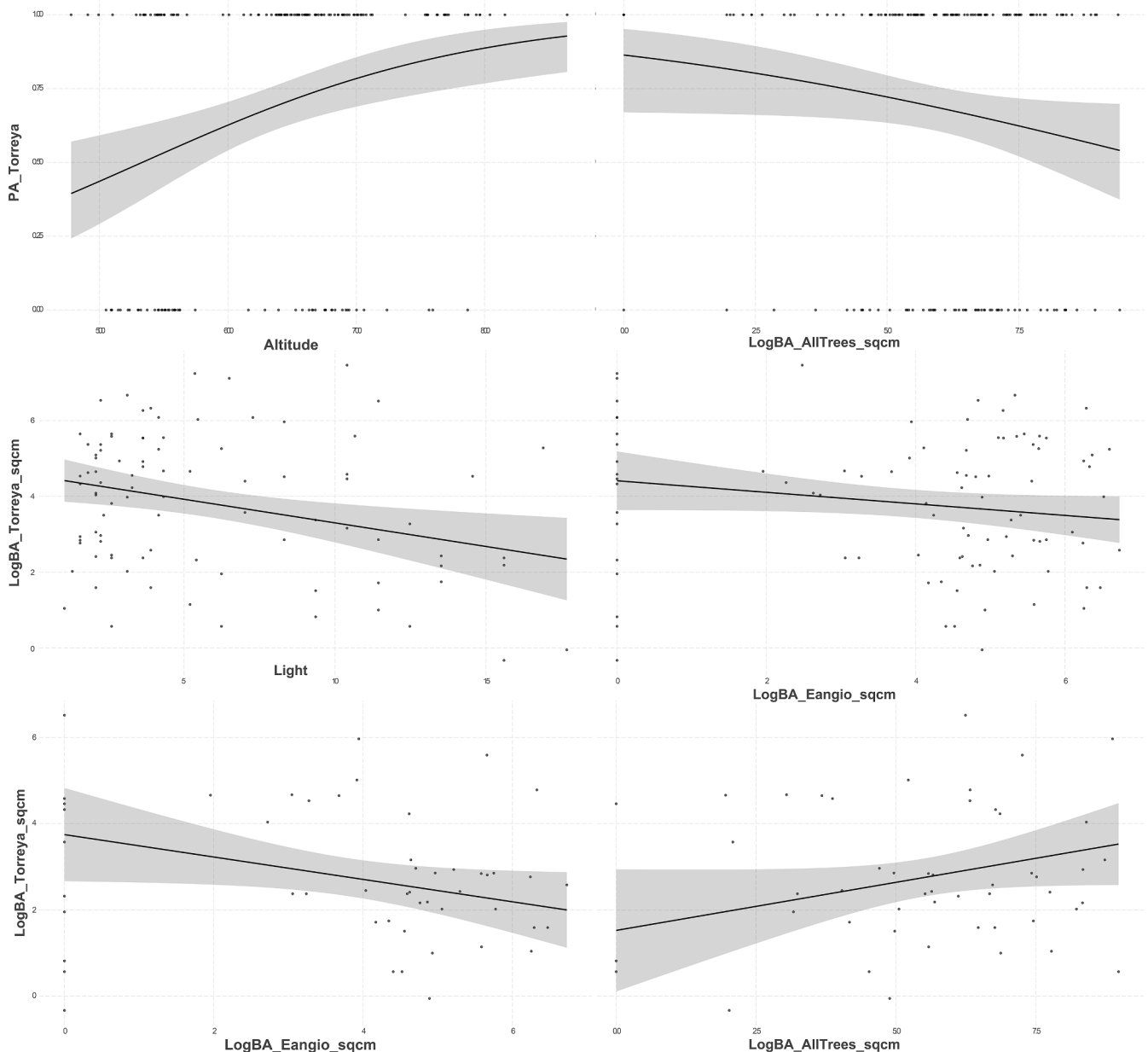| | Estimate | | | S.E. | | | p-value | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | PA | BA_1 | BA_2 | PA | BA_1 | BA_2 | PA | BA_1 | BA_2 |
| All trees | −0.393 | – | 0.514 | 0.197 | – | 0.279 | 0.046 * | – | 0.072 . |
| Altitude | 0.653 | – | – | 0.188 | – | – | 0.001 *** | – | – |
| Evergreen angiosperms | – | −0.334 | −0.561 | – | 0.192 | 0.279 | – | 0.086 . | 0.05 * |
| Light | – | −0.55 | – | – | 0.192 | – | – | 0.005 ** | – |

**Fig. 3.** Response plots of the two most important variables from the logistic regression analyses on Torreya grandis local data. A-B: Occurrence data analysis (PA), Altitude (p-value = 0.001), BA all trees (p-value = 0.046). The probability of presence of To. grandis seems to increase with increasing altitude and decrease with increasing basal area of all trees (increasing competition). C-D: basal area analysis of all individuals (BA_1), Light (p-value = 0.005), basal area of evergreen angiosperms (p-value = 0.086). The size (BA) of To. grandis seems to decrease with increasing light and amount of evergreen angiosperms present (increasing competition). E-F: basal area analysis of small individuals (BA_2), Basal area of evergreen angiosperms (p-value = 0.05), basal area of all trees (p-value = 0.072). The size (BA) of To. grandis seems to decrease with increasing amount of evergreen angiosperms present (increasing competition) while the size of To. grandis seems to increase with increasing amount of trees in general (all trees).

that we mainly find the large sized *To. grandis* in plots with low levels of light (closed canopy) and a low amount of and/or with small sized co-occurring evergreen angiosperm trees, suggesting an avoidance of the most shaded conditions (Fig. 3C-D). From the analysis on basal area of only the small individuals of *To. grandis*, we found that the most important variables are basal area of evergreen angiosperms and basal area of all trees, suggesting that competition from woody neighbours is increasingly important with smaller size. (Table 2, Fig. 3E-F).

### 3.2.2. Taxus cuspidata

From the PA data analysis, we found that soil temperature, elevation and soil electric conductivity are the most important variables for pre-dicting species presences and absences (Table 3). Partial dependence

plots show that soil temperature positively influences predicting the presence of the species at values below ~ 14 °C, elevation has a positive influence at values below ~ 760 m and soil electric conductivity has a positive influence at values below ~ 0.06 dS/m (Fig. 4A-B). From the analysis on basal area of all individuals of *Ta. cuspidata* we found that the most important variables are soil water content, soil temperature and canopy height (Table 3). Partial dependence plots show that higher values of both soil water content and soil temperature result in higher predicted values of *Taxus* basal area, while canopy height displays the opposite effect with higher predicted basal area values at smaller values of canopy height (Fig. 4C-D). From the analysis on basal area of only the small individuals of *Ta. cuspidata*, we found the most important vari-ables to be soil water content, canopy gap and northness (Table 3).

**Table 3**

Results from the random forest analysis on Taxus cuspidata. Here we report variable importance values alongside p-values for the three most important variables in each analysis. PA = analysis done on Taxus occurrence data, BA_1 = analysis on Taxus BA data for all individuals, BA_2 = analysis on Taxus BA data for only smaller individuals. Model summary for the PA model: Accuracy = 0.83, Sensitivity = 0.86 and Specificity = 0.86. Model summary for the BA_1 model: Variance explained (training data) = 37.53%, mean of squared residuals = 528997.6, pseudo $R^2$ (correlation between predicted ~ observed (test data)) = 0.45. Model summary for the BA_1 model: Variance explained (training data) = 21.76%, mean of squared residuals = 0.1362342. Variable importance for the PA data analysis is the mean increase in accuracy, while for BA data analyses it is the percent increase in mean square error (MSE). P-value significance codes: '***' p < 0.001, '**' p < 0.01, '*' p < 0.05, '.' p < 0.1, ' ' p < 1.0.

| Variable | Variable importance | | | p-value | | |
|---|---|---|---|---|---|---|
| | PA | BA_1 | BA_2 | PA | BA_1 | BA_2 |
| Canopy Gap | – | – | 7.01 | – | – | 0.024 * |
| Northness | – | – | 5.69 | – | – | 0.99 |
| SoilT | 30.76 | 15.77 | – | $2.14 \times 10^{-12}$ *** | 0.1184 | – |
| SoilC | 21.12 | – | – | 0.00156 *** | – | – |
| SoilW | – | 18.79 | 7.56 | – | $2.78 \times 10^{-10}$ *** | $5.09 \times 10^{-15}$*** |
| Canopy Height | – | 11.91 | – | – | $1.09 \times 10^{-6}$ *** | – |
| Elevation | 24.96 | – | – | $7.14 \times 10^{-8}$ *** | – | – |

Partial dependence plots show that low values of both northness and soil water content result in higher predicted values of *Taxus* basal area. Oppositely, high values of canopy gap result in higher predicted basal area values, suggesting that large individuals of *Ta. cuspidata* juveniles are especially limited by light availability (Fig. 4E-F).

## 4. Discussion

In this study, we investigated the potential of using two rare, native tree species, from the reforestation-wise largely overlooked yew family, for reforestation in China. We analysed species occurrence data on two spatial scales in order to assess the national potential area of reintroduction of the species in reforestation projects, as well as examine the environmental drivers of species occurrence and growth on a local scale. We found that generally the species have a larger potential range in terms of suitable climate compared to the present range of occurrences, and the species share preferences for low levels of competition from woody species and moderately shaded to fairly open canopy conditions at the local scale.

### 4.1. Reforestation potential of Taxaceae species

Our results show that there is a large area available for reforestation using both of the Taxaceae species (Fig. 2). Consistent with *To. grandis* being more widespread than *Ta. cuspidata*, the potential suitable range for this species is larger, covering 18 provinces compared to five provinces for *Ta. cuspidata*. As we took into account human activity, i.e. land-use, infrastructure, cities etc. by calibrating the species potential distribution maps with the 'tree restoration potential' map by Bastin et al. (2019), we expect the final reforestation potential for each species to reflect areas that are truly suitable for growing forests. However, since the current species distributions are affected by human activity (at least within the past 100 years) (Jensen et al., 2020) and thus their true climatic limitations are possibly different/wider than we see today, the potential distribution of each species is probably larger than the ones we estimate here, making our potential reforestation areas conservative estimates. Furthermore, as the 'tree restoration potential' was estimated under current climate and land use, the potential areas of reforestation

using *Ta. cuspidata* and *To. grandis* will therefore change with future climate and societal changes. Additionally, even though the potential reforestation area for each species represent suitable habitat, it is important to identify current threats facing each species, in order to minimize the effects of these when selecting suitable areas within the species potential reforestation area for performing forest restoration (Maschinski and Albrecht, 2017).

### 4.2. Implications of using Taxaceae species in reforestation

#### 4.2.1. The case study

Results from the analyses on local species data show that for both species light and competition from woody species are important factors driving the spatial distribution and size of individuals. Low levels of competition and high light availability is most important for the small/young individuals (Figs. 3 and 4). Experimental studies on the effect of light on *Taxus baccata* seedlings/saplings show a similar association of young individuals with light, where the youngest individuals tolerate deep shade, while light becomes increasingly important for the older seedlings and saplings (Iszkuło, 2001, 2010; Iszkuło and Boratyński, 2005, 2006; Peragón, Matías and Simón, 2015). Indeed, the ability of the young *Ta. cuspidata* seedlings in our study to tolerate low light levels, might reflect a lack of competitive ability of these smallest individuals against herbs and grasses that become more dominant at higher light levels (Iszkuło and Boratyński, 2006). Similarly, Tang et al. (2015) experimentally determined 75% shade as the optimal light conditions for *To. grandis* seedling growth, corresponding well to light conditions in our study site in Tianmu, where most *To. grandis* individuals were found under close to full shade (mean canopy openness = ~5%). *To. grandis* in our study was, like *Ta. cuspidata*, affected by light so that the smaller individuals were generally found under higher levels of light as well as lower levels of competition from co-occurring species, probably reflecting some form of light competition as well (Table 2, Fig. 3). Another well-known factor affecting regeneration and survival of Taxaceae individuals is browsing on seeds and seedlings. Several studies have found that *Taxus* sp. seedlings are at risk of damage by browsing animals such as deer, and that fencing out deer results in higher survival and growth compared to unfenced individuals (Holmes et al., 2009; Iszkuło, Nowak-Dyjeta and Sekiewicz, 2014). *Taxus* is however, known to be quite resistant to browsing and combined with the protection from spiny shrubs such as *Rubus* spp., seedling survival rates are reported to be unexpectedly high in some cases (Thomas and Polwart, 2003; Iszkuło, Nowak-Dyjeta and Sekiewicz, 2014). Additionally, growing in spiny fruit-producing scrub by species such as *Rubus* spp., has another advantage of attracting frugivorous birds that can help regeneration of *Taxus* sp. by dispersing their seeds to suitable habitats (Thomas and Polwart, 2003). Although we did not see any signs of animal browsing on *To. grandis* and *Ta. cuspidata* or shrubs/trees acting as nurse trees in our study sites, it is worth taking into consideration when planning forest restoration in areas of dense deer - or rodent populations (Iszkuło, 2011; Feng et al., 2018). A factor concerning mostly Taxaceae species with a north-temperate distribution or growing at high elevations is the risk of damage caused by frost (Thomas and Polwart, 2003). Our results showed that the young *Ta. cuspidata* individuals were dependent on light with the larger individuals found under larger canopy openings (Table 3, Fig. 4). Theoretically, these individuals are more protected from frost by a potentially higher snow cover in winter resulting from a higher exposure to open sky and thus have better chances of survival (Drescher and Thomas, 2013). Therefore, it seems that it is worth considering the frost exposure of seedlings and saplings when performing reforestation of north-temperate or high-elevation sites.

From our study, it seems that light and competition are driving the establishment and growth of the two Taxaceae species, especially the young individuals. Therefore, in a reforestation setting it is important to create moderately shaded conditions allowing the smallest individuals to escape competition from herbs, while at the same time providing
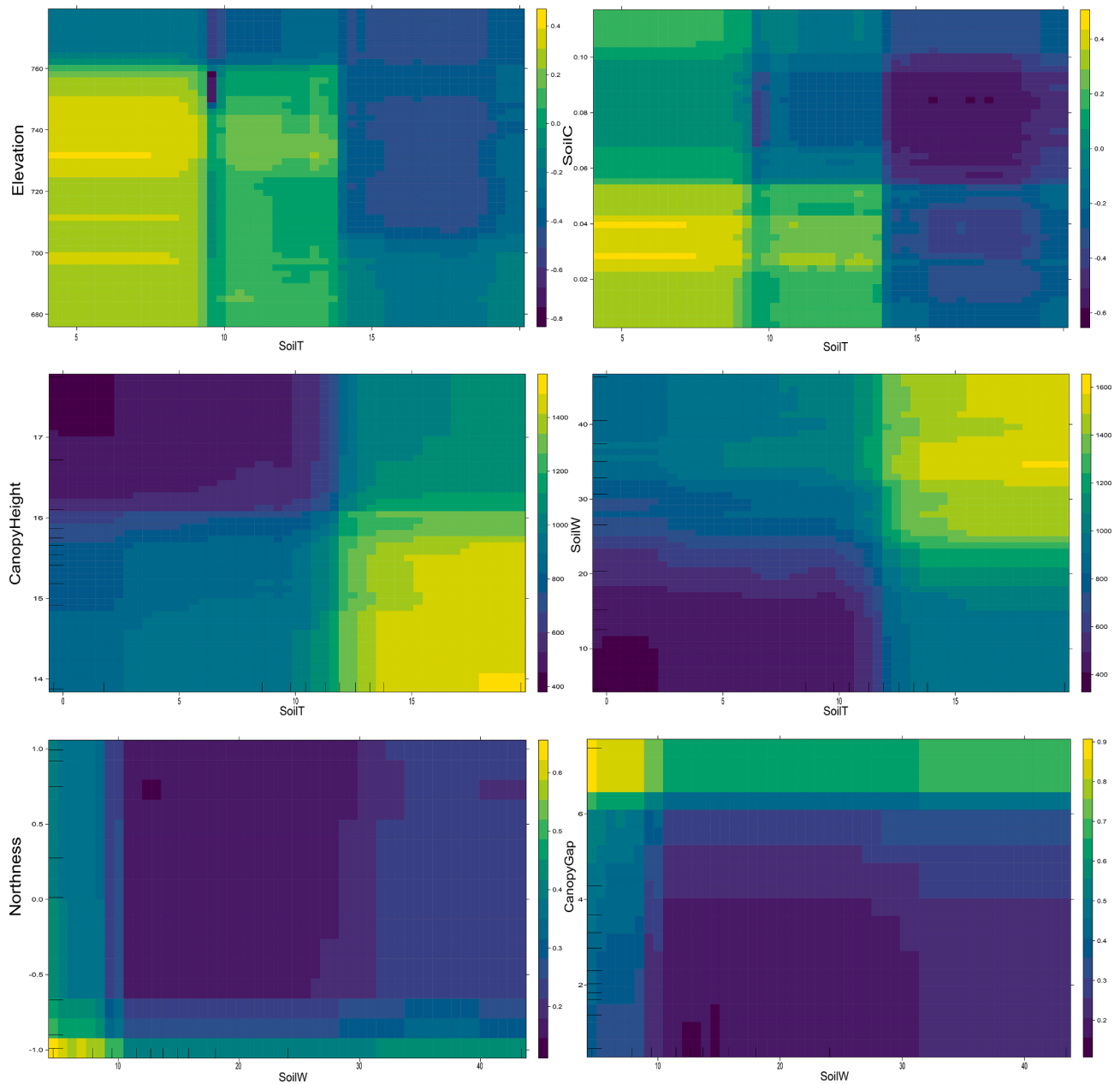
**Fig. 4.** Partial dependence plots from the Random Forest analyses on Taxus cuspidata local data. A-B: occurrence data analysis (PA), soil temperature (p-value = $2.14 \times 10^{-12}$), soil electric conductivity (p-value = 0.00156), elevation (p-value = $7.14 \times 10^{-8}$). Probability of occurrence of Ta. cuspidata increases at low elevation, low soil electric conductivity and low soil temperature values. C-D: basal area analysis on all individuals (BA_1), soil temperature (p-value = 0.1184), soil water content (p-value = $2.78 \times 10^{-10}$), canopy height (p-value = $1.09 \times 10^{-6}$). The size of Ta. cuspidata increases at high soil temperatures, low canopy height and high soil water values. E-F: basal area analysis on only the small Taxus individuals (BA_2), soil water content (p-value = $5.09 \times 10^{-15}$), northness (p-value = 0.024), canopy gap (p-value = 0.99). The size of Ta. cuspidata increases at low soil water content, low northness values and high canopy gap values.

enough light for the growth of larger individuals. These conditions could be created simply by planting the species in a mix with other woody species that can provide the needed shade, or even by using nurse trees/shrubs (Yelenik, Dimanno and D'Antonio, 2015). At the same time, planting seedlings and saplings under a nurse shrub could potentially protect them from browsing by deer and thus enhance their chances of survival. When protection from the nurse trees/shrubs is no longer needed, they could potentially be harvested, thus providing an economical benefit as well (Nord-Larsen and Meilby, 2016). Another approach could be to plant several focal species – such as Taxaceae species – in small groups while allowing for natural regeneration of woody and herbaceous species between the groups (Corbin and Holl, 2012; Jacobs et al., 2015). This strategy is more time- and cost-efficient, and at the same time provides a more natural setting for the development of a multi-layered, heterogeneous and diverse forest that is able to sustain local biodiversity and ecosystem service requirements (Corbin and Holl, 2012; Thers, Bøcher and Svenning, 2019). The choice of focal species should depend on the availability of local natural seed sources, where species that have a low abundance or are locally absent should be planted to support and enhance species diversity of the reforested site through colonization of native woody species (Lee, Hau and Corlett, 2005). Additionally, the inclusion of large herbivores to the reforested system could restore some missing dynamics in terms of natural disturbances that will further enhance the complexity, and therefore diversity, of the new forest (Perino et al., 2019).

As rare species often have limited geographical ranges, either naturally or because of human influences (Schoener, 1987), and they often occupy very specific habitats and have low competitive abilities (Harrison et al., 2008), they may have lower chances of survival in a newly established natural forest compared to more common species. Therefore, the survival of such species in a restored forest might depend on the management approaches that are undertaken during and after planting (Yang et al., 2013; Maschinski and Albrecht, 2017). To maximise the chances of a rare species surviving in a forest where natural dynamics govern the survival of individuals, choosing seedlings/saplings with a large genetic diversity for planting, using >50 individuals to establish the population and providing the basic species-specific ecological requirements is key to success (Maschinski and Albrecht, 2017).

We acknowledge that there is some uncertainty in translating our local scale results to the national scale potential reforestation areas, but we believe that since our results agree with the literature on related species in terms of limiting ecological factors, they can be used to guide reforestation in a wider range of habitats.

### 4.2.2. General ecosystem benefits

Being long-lived, Taxaceae species have a high potential for increasing the structural complexity of a reforested site, leading to a higher heterogeneity of available habitats for supporting local biodiversity, if planted alongside other species with different life-history traits (Alexander et al., 2016). Further, as all Taxaceae species produce fleshy seed cones, their presence attracts frugivorous birds and mammals, leading to increases in local biodiversity as well (Lu, Zhu and Deng, 2008; Duan, Goodale and Quan, 2014). Other ecological benefits include limiting soil erosion and water pollution as is reported in a recent review on *Torreya* forests (Chen and Jin, 2019). This review reports that old-growth *Torreya* forests (*To. grandis* cv. Merrilli) have the lowest soil erosion of 10 forest types in Zhuji County in Zhejiang Province, conserving 3–4 times more water than Chinese fir (*Cunninghamia lanceolata*) forests, while young *Torreya* plantations oppositely are direct causes of soil erosion and water pollution (Chen and Jin, 2019). Therefore, planting slow-growing, long-lived Taxaceae species such as *To. grandis* and *Ta. cuspidata*, along with other species with different life-strategies, will help provide the functions needed to mitigate environmental issues such as water pollution and soil erosion, without contributing the negative effects of planting monocultures. Therefore, we argue that because of Taxaceae species being long-lived, understorey

trees, they bring unique ecological functions to ecosystems that might ensure long-term quality and resilience of reforested lands.

In many cultures across continents, *Taxus* species have previously been valuable for making different artefacts such as weapons and tools and have held a special religious importance as is seen from the many plantings of *Taxus* species near churches, town squares, manor houses etc. (Piovesan et al., 2009; Uzquiano et al., 2014). Today, species of this genus are mostly known for containing the cancer-treatment compound taxol, extracted from bark and foliage (Russin et al., 1995; Thomas and Polwart, 2003; Juyal et al., 2014; Miao et al., 2014). Furthermore, the fleshy seed cones of some Taxaceae species are popularly consumed by humans, such as *Torreya grandis* (cv. Merrilli) and *Torreya nucifera*, and in certain regions of China, *To. grandis* plantations are an economically important industry (Zhang et al., 2017; Chen and Jin, 2019). On the other hand, fruits from *Taxus* species are currently not popular for human consumption despite prehistoric evidence showing that *Taxus* fruits used to be consumed by humans (Uzquiano et al., 2014). If used in reforestation, Taxaceae species such as *Ta. cuspidata* and *To. grandis* that produce edible fruits could potentially provide a basis for sustainable foraging by local people (Shackleton et al., 2017; Landor-yamagata and Kowarik, 2018). In China, where old *Torreya* plantations exist, there is a high cultural importance of this species in local societies, where the slow growth and manor of fruit production of the tree symbolize 'longevity, happiness and reunion' (Chen and Jin, 2019). Therefore, it seems that Taxaceae species can potentially bring both cultural and aesthetic benefits, such as foraging for fruits and recreational activities, to a reforested site.

### 4.3. Conclusions

In this study, we show that there is substantial quantitative potential of using *Taxus cuspidata, Torreya grandis*, as well as likely other native Taxaceae species, in reforestation in China. Based on our results and on findings from the scientific literature, we argue that Taxaceae species can contribute to generate structurally complex stands of increased value for biodiversity and increased stability, hereby also contributing to climate change mitigation as well as other important ecosystem services. Further, using rare Taxaceae species in reforestation will also help conserve these rare species in a changing future.

**CRediT authorship contribution statement**

**Ditte Arp Jensen:** Conceptualization, Formal analysis, Investigation, Writing - original draft. **Mide Rao:** Investigation, Writing - review & editing. **Jian Zhang:** Resources, Writing - review & editing. **Mette Grøn:** Investigation. **Songyan Tian:** Resources. **Keping Ma:** Data curation. **Jens-Christian Svenning:** Conceptualization, Funding acquisition, Supervision, Writing - review & editing.

**Declaration of Competing Interest**

The authors declared that there is no conflict of interest.

Heilongjiang Province (2014-2018), and The National Natural Science Foundation of Province (QC2018025). JCS also considers this work a contribution to his VILLUM Investigator project "Biodiversity Dynamics in a Changing World" funded by VILLUM FONDEN (Grant 16549) and his Independent Research Fund Denmark/Natural Sciences TREE-CHANGE project (Grant 6108-00078B).

**Appendix**

This appendix contains figures and tables that are not vital for the understanding of the main story of the paper, but add supporting information .
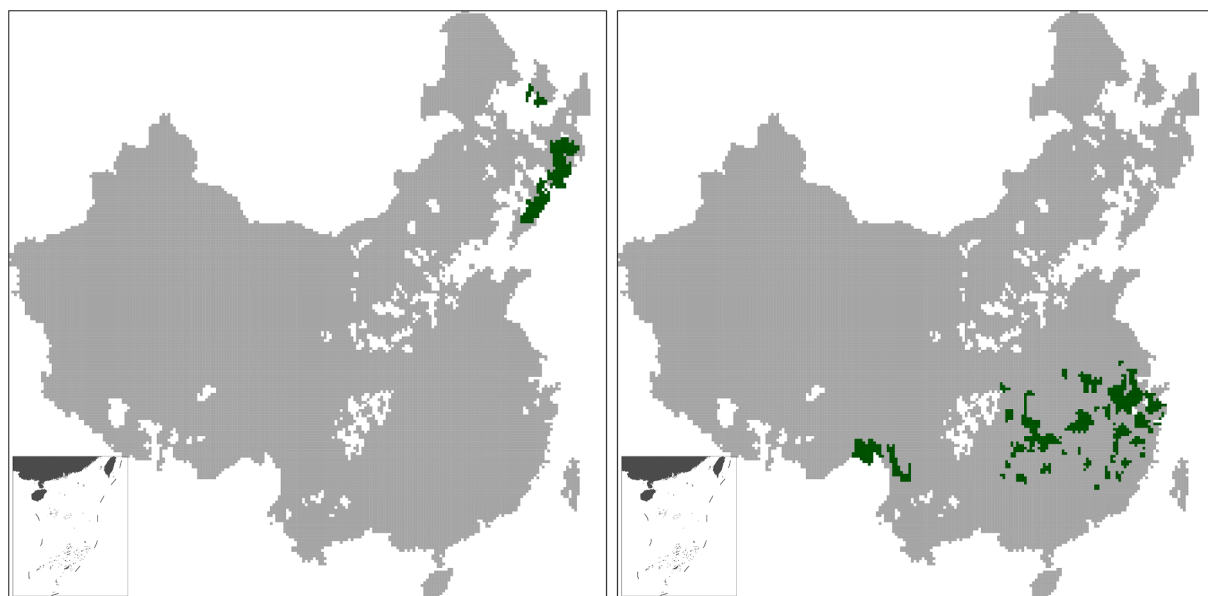
.



**Fig. A1.** Rasterized occurrence data for Taxus cuspidata (left) and Torreya grandis (right). The resolution is 20 km × 20 km. Green colour = species presence. Grey colour = background data. White colour = no data. Inserts show the South China Sea, but it contains no species data. The map projection used here is the Albers Equal Area Conic projection.
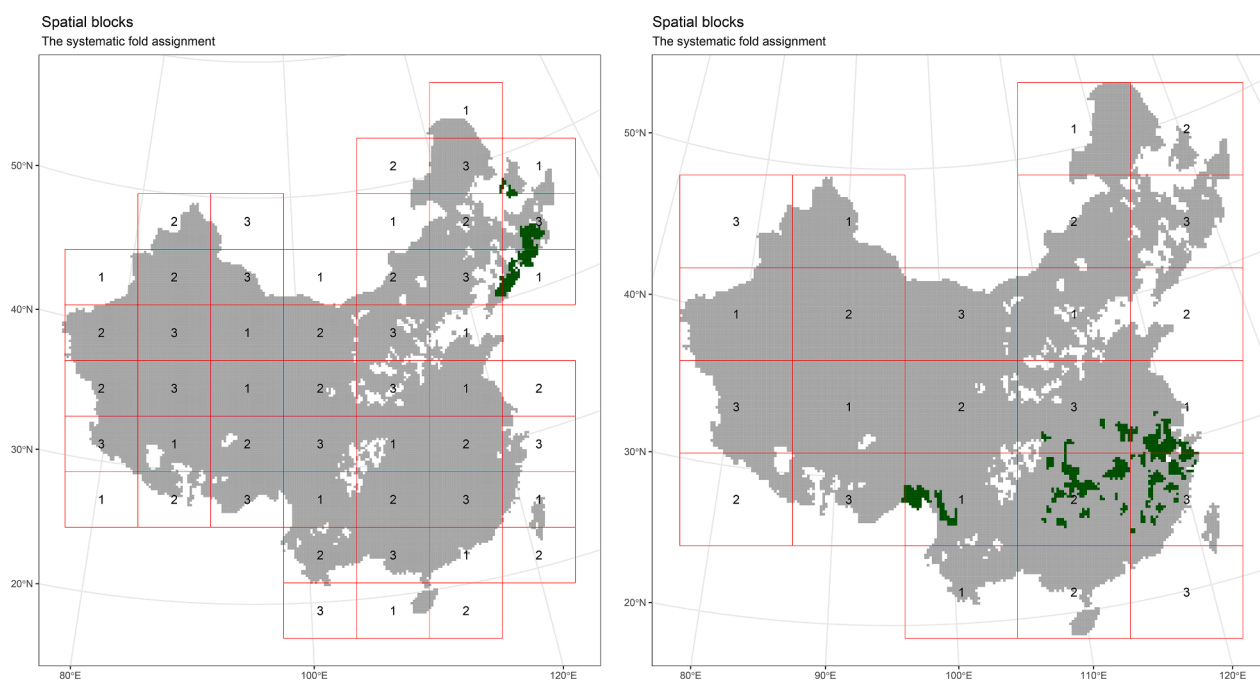


**Fig. A2.** Spatial blocks constructed using the blockCV method. Left-hand plot shows the blocks used for the Taxus cuspidata analyses, right-hand plot shows the blocks used for Torreya grandis analyses. The South China Sea is not included since it is not part of the dataset.
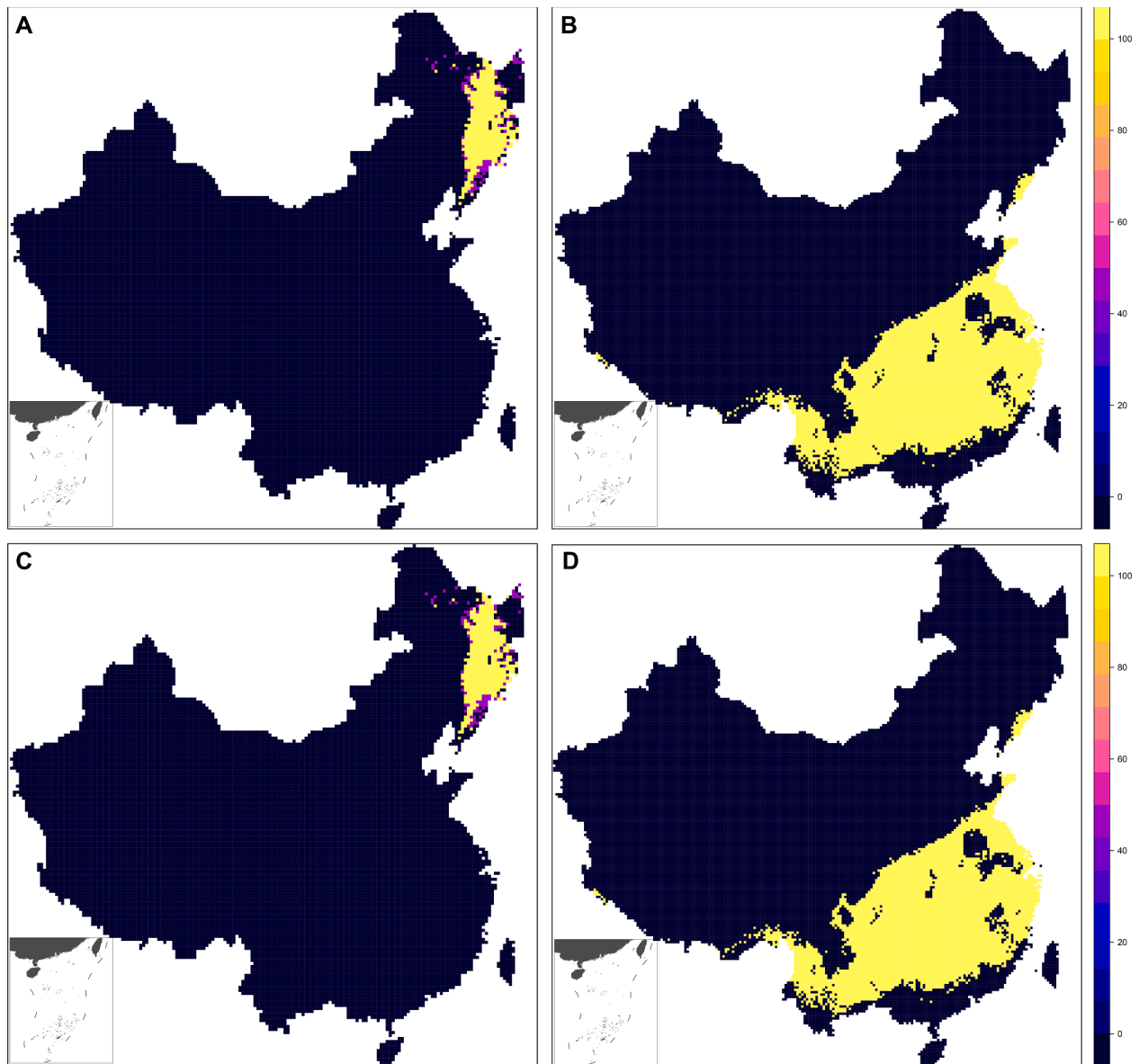
**Fig. A3.** Model predictions from the bioclimatic envelope (SRE) modelling. A: Taxus cuspidata mean predictions across 10 evaluation runs, B: Torreya grandis mean predictions across 10 evaluation runs, C: Taxus cuspidata mean of the committee average of predictions across 10 evaluation runs, and D: Torreya grandis mean of the committee average of predictions across 10 evaluation runs. Inserts show the South China Sea, but no predictions are shown here as it contains no species data. The map projection used here is the Albers Equal Area Conic projection.

**Table A1**

Environmental variables chosen for the national and local scale analyses. ANALYSIS = which analyses are the local scale predictors used in: PA = presence-absence analysis, BA_1 = basal area analysis on all individuals, BA_2 = basal area analysis on only small individuals. The Analysis column reports the specific analyses that each predictor was used in. For the National analyses, all predictors were used.

| Species | Environmental variable | Explanation | Analysis |
|---|---|---|---|
| | *National data* | | |
| *Torreya grandis & Taxus cuspidata* | BIO8 | Mean Temperature of Wettest Quarter (°C) / Summer temperature | |
| | BIO9 | Mean Temperature of Driest Quarter (°C) /Winter temperature | |
| | BIO18 | Precipitation of Warmest Quarter (mm) / Summer precipitation | |
| | BIO19 | Precipitation of Coldest Quarter (mm) / winter precipitation | |
| | *Local data* | | |
| *Torreya grandis* | Alt | Elevation at midpoint of subplot (m a.s.l.) | PA,BA_1, BA_2 |
| | slope | Mean slope of the subplot (%) | PA,BA_1, BA_2 |
| | water | Distance to water from the subplot (m) | PA,BA_1, BA_2 |
| | Light | Density of canopy, average of four readings (%) | PA,BA_1, BA_2 |
| | BA_Dec | Basal area of all deciduous trees in the subplot (cm$^2$) | PA,BA_1, BA_2 |
| | BA_Eangio | Basal area of all evergreen angiosperms in the subplot (cm$^2$) | PA,BA_1, BA_2 |
| | BA_Egym | Basal area of all evergreen gymnosperms in the subplot (cm$^2$) | PA,BA_1, BA_2 |
| | BA_All | Basal area of all trees in the subplot (cm$^2$) | PA,BA_1, BA_2 |
| *Taxus cuspidata* | Alt | Elevation at species presence/ absence point (m.a.s.l.) | PA,BA_1, BA_2 |
| | slope | Slope at species presence/ absence point (%) | BA_1, BA_2 |
| | SoilW | Volumetric water content at species presence/absence point (%) | PA,BA_1, BA_2 |
| | SoilT | Soil temperature at species presence/absence point (°C) | PA,BA_1, BA_2 |
| | SoilC | Soil electrical Conductivity at species presence/absence point (dS/m) | PA,BA_1, BA_2 |
| | CanopyHeight | Canopy height at species presence/absence point (m) | PA,BA_1, BA_2 |
| | TWI | Topographic wetness index at species presence/absence point | PA,BA_1, BA_2 |
| | CanopyGap | Amount of open sky at species presence/absence point (%) | BA_2 |
| | Northness | A corrected measure of the Aspect of the slope at species presence/absence point | BA_1, BA_2 |
| | BA_Dec | Sum of basal area of all deciduous trees in a 10-meter radius from species presence/ absence point (cm$^2$) | PA,BA_1, BA_2 |
| | BA_AP | Sum of basal area of all individuals of the genus *Abies* and *Picea* in a 10-meter radius from species presence/absence point (cm$^2$) | PA,BA_1, BA_2 |
| | BA_Pinus | Sum of basal area of all individuals of the genus *Pinus* in a 10-meter radius from species presence/absence point (cm$^2$) | PA,BA_1, BA_2 |

**Table A2**

List of the algorithms used in the biomod2 ensemble modelling.

| Algorithm name in biomod2 | Full names |
|---|---|
| GLM | Generalized linear models |
| GAM | Generalized additive models |
| MARS | Multivariate adaptive regression splines |
| ANN | Artificial neural networks |
| GBM | Gradient boosting machines/boosted regression trees |
| RF | Random forest |
| CTA | Collaborative tracking algorithms |
| SRE | Surface range envelope / 'bioclim' |

**Table A3**

Summary statistics of the Ensemble SDM and the bioclimatic envelope SDM for both species. Summary statistics were computed on blockCV test datasets, and here we present the mean (±SD) of evaluation scores across 10 pseudo-absence datasets/models. The bioclimatic envelope model summary statistics are the mean evaluation scores (±SD) across 10 runs of one BIOCLIM (SRE) model.

| Summary statistic | Summary statistic value, mean (SD) | | | |
|---|---|---|---|---|
| | *Torreya grandis* | | *Taxus cuspidata* | |
| | Ensemble | Bioclim | Ensemble | Bioclim |
| TSS | 0.881 (0.0092) | 0.704 (0.00) | 0.980 (0.0079) | 0.833 (0.00) |
| AUC | 0.979 (0.0018) | 0.859 (0.00) | 0.998 (0.0009) | 0.917 (0.00) |
| Sensitivity | 97.8 (0.71) | 86.7 (0.00) | 99.8 (0.47) | 84.9 (0.00) |
| Specificity | 90.3 (0.94) | 83.7 (0.00) | 98.2 (0.77) | 98.4 (0.00) |

**Table A4**

Performance of algorithm on PA data and BA data respectively. All algorithms perform relatively similar and unrelated to their complexity. Abbreviations: glmboost = boosted generalized linear model, glm = generalized linear model, rf = random forest, nnet = neural networks, gbm = gradient boosting machine (boosted regression trees), bayesglm = bayesian generalized linear model.

| | ALGORITHM PERFORMANCE | | | |
|---|---|---|---|---|
| | *Torreya grandis* | | *Taxus cuspidata* | |
| | PA data | BA data | PA data | BA data |
| **Algorithm** | *Mean Accuracy* | *Mean R$^2$* | *Mean Accuracy* | *Mean R$^2$* |
| **glmboost** | 0.612 | 0.0334 | 0.705 | 0.359 |
| **glm** | 0.619 | 0.0266 | 0.698 | 0.338 |
| **rf** | 0.635 | 0.0627 | 0.817 | 0.388 |
| **nnet** | 0.649 | – | 0.643 | – |
| **gbm** | 0.643 | 0.0274 | 0.810 | 0.392 |
| **bayesglm** | 0.626 | 0.0266 | 0.697 | 0.338 |

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