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Woody species with high wood density are more vulnerable to global change in South China

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TECHNOLOGY OF FOREST PRODUCTS

ABSTRACT

Background: To cope with global change, plants shift their distributions. Rare species tend to shift their distribution more. Over 30% of the land is covered with woody species, which because of their longevity offer unique opportunities to monitor distribution shifts. The study addresses the following questions (1) how the distribution range of eight rare woody species is changing and how effectively the plants cope with the shift; (2) whether plant traits could predict those parameters. Maxent Distribution Modelling, was carried out for this purpose, on species observation records prior to 1980 under present climatic conditions and four future (CMIP5) scenarios. To assess how effectively plants cope with migration species observations after 1980 were assessed. Relationships with plant trait data on three traits were finally assessed.

Results: The distribution ranges for four out of the eight species expanded northwards. Temperature driven (mostly through mean annual temperature which was ranked first for six out of the eight species) rather than precipitation (mean annual precipitation was ranked first only in two cases and in one case precipitation of the driest month was ranked third) driven variables described distribution shifts best. Wood density summarized well the susceptibility of those plants to climate change. There are many woody species in tropical and subtropical areas for which we have very little information available.

Conclusion: Subject to the small pool of species, a plant trait was identified, wood density, that could summarize responses to global change that could potentially be used as a tool in conservation ecology to prioritize conservation efforts.

Keywords: Biodiversity Hotspots; Extinction ecology; Species Distribution Shifts; Wood density; Wood's Economic Spectrum.

HIGHLIGHTS

Distributions of 8 species to global change were modelled.
Temperature described best distribution shifts of the eight species.
Wood density captured best the kernel distance prior to and after 1980.
Wood density captures susceptibility to global change.

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INTRODUCTION

Over 17,000 tree species are at a risk of an extinction, (Boonman et al., 2024), the vast majority of which are rare species (Vincent et al., 2020). A large proportion of plant biodiversity is found exclusively in biodiversity hotspots, which together cover less than 1.5% of the land surface (Myers et al., 2000). Plant species with narrow distributions are particularly vulnerable to extinction due to climate change (Malcolm et al., 2006; Thomas et al., 2004). As environmental conditions change, plants must shift their distribution (i.e. "migrate") either poleward or to higher elevations (Chen et al., 2011; Lenoir et al., 2008). Shifting distributions is, thus, a mechanism by which many woody plants alleviate the risk of extinction. It should be trickier for species that maintain narrow distribution ranges to take advantage of that mechanism (Tomiolo and Ward, 2018). The reason why species with narrower ranges are disadvantaged is that geographic barriers such as coastlines, lakes and altitudinal topographic gradients get more likely to block the migration of species with narrow ranges (Record et al., 2013). It is often difficult to tell which species will cope well with climate change and which ones are only found in areas where they cannot sustain long term growth and will eventually go extinct. In the latter cases, we say that the plant species are committing to an extinction dept (Halley et al., 2016; Tilman et al., 1994), which in some cases requires human intervention to get prevented (Kuussaari et al., 2009). There is therefore a consensus that distribution modelling should ideally address the distributions of those species (Lomba et al., 2010; Matern et al., 2007). Modelling the distributions of rare species, however, can be extremely difficult because in most cases there is a scarcity of available data on them. This consideration is captured through the "rare species modelling paradox", postulating that we know little on the distribution modelling of the species that we are interested in most (Lomba et al., 2010).

Climate change is not occurring uniformly across the globe (e.g. Lobell et al., 2011), meaning that each biodiversity hotspot faces unique challenges in terms of plant extinction risk (Malcolm et al., 2006). South-central China represents a plant diversity hotspot with 5.5 endemic vascular plant species per 100 km^2 (compared to a global average of about 0.2 endemic vascular plants per 100 km^2 of terrestrial habitat). Rapid scientific advances in recent years (He et al., 2010) have facilitated monitoring in the region and have opened up opportunities to map local distributions of endemic species. At the same time rapid urbanization in southern China has significantly increased the pressure on natural habitats, resulting in the fragmentation of many pristine areas (Seto et al., 2000). This may be a parameter that makes any assessment of the conservation status of the endemic flora urgent. Historical records of the occurrence of eight plant species are combined here to more recent observations from two sources of information, the Global Biodiversity Information Facility (GBIF) and the National Herbarium Collection (Chinese Virtual Herbarium) through a distributional modelling exercise to address a series of three questions.

First, the relative importance of projected global warming versus changes in precipitation frequency and intensity in structuring the distributions of our set of eight plant species (i.e. temperature versus precipitation related predictors of distribution shifts) are considered. As a subtropical climatic zone, habitats in South China, receive substantial amounts of precipitation (Trenberth, 2011), which should rarely limit plant growth. At the same time, temperature is changing rapidly in the region (Stuecker et al., 2020), which may reduce the ability of some species to persist in their former ranges. Unlike herbaceous plants which are mainly dependent on precipitation, woody species respond strongly to changes in temperature (e.g. Shi et al., 2021; Thurm et al., 2018). This could be the reason why we so often observe woody species migrating polewards and into higher altitudes (e.g. Lenoir et al., 2008). This consideration gave rise to the hypothesis that it is mainly temperature-related variables that drive the distribution of our eight species in our exercise (*Hypothesis One*).

Further questions aligned with how climate change has altered the distribution range of these eight species and whether the plant species are coping adequately with this change. All eight of the plant species in the analysis describe woody species and as a result share relatively long generation times and possess (was our selection criterion) narrow distribution ranges. It has been argued that it is the combination of these two characteristics that maximizes the likelihood that plant species have already committed to an extinction debt (e.g. Kuussaari et al., 2009), which may have been the case for all of our eight plant species. Climate change models in the Fifth Assessment Report of IPCC (i.e. Intergovernmental Panel on Climate Change), however, predict only a moderate increase by the year 2050 in temperature for the subtropical China of about 1.2^{o}C as well as increases in precipitation of about 3.4% (Fick and Hijmans, 2017). Therefore, there is a good chance that any changes in distribution will be relatively subtle and that many of these plant species, even those with small distributions, will cope better with climate change than their counterparts close to the poles. This consideration gave rise to the hypothesis that the location and the size (in square kilometres) of the distribution of several of the eight species has not changed much and that the plants have effectively caught up with these changes (*Hypothesis Two*).

A set of three plant traits for the eight woody species was further collated to identify if there were any plant traits that could predict plant migration success in this region of the world. Migration success has been previously associated with several plant traits such as seed mass (Veresoglou and Halley, 2018), longevity (Noh et al., 2019; Vellend et al. 2006), pollination strategy and tolerance to external stresses (Saar et al., 2012). At the same time there appears to be a strong positive relationship between tree height and dispersal distances (Thomson et al., 2018), meaning that in natural forests, tree height could potentially predict the success with which trees establish to new habitats. Plant height also peaks at warmer regions (Mao et al., 2019), which could indicate a temperature dependence in woody plants. This consideration gave rise to the hypothesis (*Hypothesis Three*) that an easily collected trait, tree height, would effectively capture migration efficiency across our set of eight plant species.

MATERIALS AND METHODS

Plant Species Selection Criteria

Data was collected on eight terrestrial plant species that met the four following criteria:

1. species had been reported in Huang et al. (2017) as occurring exclusively (i.e., being endemic) to two (Geo3 and Geo4) out of the seven geographical regions of China (Liu, 1998), covering the center and south of China (15194 out of 18157 species).
2. they described woody species, either trees or shrubs (6489 out of 15194 species).
3. there was a minimum of 20 records on them in the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/).
4. the species had been reported at the Heishiding reserve (23.27° N, 111.53°E) and were thus all describing native late successional forest species (8 out of 6489 species).We integrated this latter criterion to control for the likely inclusion of invasive species or other fast growing species which could have presented idiosyncratic distributions in the area.

The final list comprised eight species. The eight species were the following: *Artocarpus hypargyreus*, *Diospyros strigosa*, *Huodendron biaristatum*, *Machilus breviflora*, *Machilus suaveolens*, *Rhaphiolepis ferruginea*, *Symplocos congesta*, and *Xanthophyllum hainanense*. Out of these species only *Artocarpus hypargyreus* is reported in the International Union for Conservation of Nature (IUCN) list as endangered. On the 15th of July 2022, all available records on the eight plant species from GBIF were extracted. Four of them had less than 80 complete (i.e. including coordinates and year of the observations) records in GBIF. To increase the number of observations for the subset of the four plants for which we retrieved from GBIF less than 80 records, there was an additional search at the Chinese Virtual Herbarium (CVH; https://www.cvh.ac.cn/) for records that had not been included in GBIF. We retrieved this way between 42 and 192 records per species (i.e. 663 observations in total). Again, only records for which coordinates were available were retained.

Environmental variables

The 19 bioclimatic variables that are described in WorldClim (https://worldclim.org/) version 1.4 (Hijmans et al., 2005) were used as predictors, presenting averages on climatic variables over the period 1960 – 1990. A complementary non-climatic predictor that can shape the distribution of plant species is altitude (Korner, 2007; Lenoir et al., 2008). The set of 19 bioclimatic variables was thus expanded with elevation data (Fick and Hijmans, 2017). All variables were extracted from raster files at a resolution of 30 seconds. To account for collinearities in our observation area which covered south-middle China (18°10′ - 36°22′ N, 97°21′ - 122°43′ E) correlations between environmental data with the R package "ENMTools" (version 1.0.6; Warren et al. 2021) were quantified. An exclusion threshold of Pearson correlations with coefficients $|r| > 0.75$ was set (Dormann et al., 2013; Merow et al., 2013). For correlations of any two climatic variables that were above the threshold, the bioclimatic variable with a higher incremental number (i.e. each bioclimatic variable has been assigned a unique ID ranging from 1 to 19) was removed from the dataset. Through this approach 12 bioclimatic variables were filtered out. The bioclimatic variables that remained after this filtering step were the following eight variables: BIO1, BIO2, BIO3, BIO7, BIO12, BIO14, BIO18 and elevation.

Plant traits

Because of the narrow distributions of the eight species, it proved hard to extract trait information on them. There were sufficient data for all eight plant species only for the following three traits:

1. *Tree height*: The plant trait summarized the ability of a plant species to intercept light in a close canopy but could also be suggestive of the rooting depth of a plant (Brando, 2018). Height values were extracted from the Encyclopedia of Life (https://eol.org/).
2. *Leaf size*: leaf size was calculated as the product between width and length of the leaf which was then multiplied with the correcting factor 2/3 (Schrader et al., 2021). Aside presenting an important trait for plant thermoregulation and photosynthetic potential (Leigh, 2022), it presents a good predictor of net primary productivity (e.g. Li et al., 2020). Leaf width and length data were extracted from the Encyclopedia of Life (https://eol.org/).
3. *Wood density* information at a genus level: The trait shows a high degree of phylogenetic conservatism (Kraft et al., 2010) and thus using data at higher taxonomic levels should pose no major issues. Less than 20% of total variance in wood density occurs within the genus level (Flores and Coomes, 2010). The median trait values reported at a genus level at ICRAF database from the World Agroforestry Center (http://db.worldagroforestry.org/) were used. Wood density represents a good proxy of mortality rates across tree species (Kraft et al., 2010) but also one of the two attributes to which we can decompose the biomass of woody plants (Phillips et al., 2019). Wood density additionally represents the core trait describing the wood economics spectrum (Chave et al., 2009), being a complementary economics spectrum to that of the leaves (Wright et al., 2006b).

The Encyclopedia of Life presents a heterogeneous dataset, with often conflicting entries. To minimize the effect of outliers, median values were preferably used for the traits with unrealistic entries being filtered out.

Species distribution models

To optimize feature classes (i.e., linear, quadratic, hinge etc.) and regularization parameters (Merow et al., 2013) for our models parsimony (AICc values) was assessed of all 60 possible combinations of 15 regularization multipliers (i.e. values 0.25, 0.5, 1, 1.25, 1.5, 1.75, 2, 2.25, 2.5, 2.75, 3, 3.25, 3.5, 3.75, and 4) and 4 feature combinations (i.e. linear, quadratic, hinge, and quadratic with hinge) per species in quintuplicates and mean AICc values of those four runs were extracted (Burnham and Anderson, 2004; Warren and Seifert, 2011). The models were evaluated with ENMeval version 2.0.3 (Muscarella et al., 2014). For maximum entropy modelling the model with the lowest AICc value in each set of species per scenario was used.

Distribution models were fitted with MaxEnt 3.4.0 (Phillips et al., 2017) with 100 bootstrap replicate runs for each species and scenario (Lin et al., 2020; Wang et al., 2022). A random subset of 75% of the occurrence data for model training and the other 25% for validation was used (Garcia et al., 2013; Huberty, 1994). To parametrize the near-current prediction algorithms, the model was run exclusively on observations that were taken before the year 1980. To estimate future distribution ranges, projections for the bioclimatic variables in the year 2050 based on four global change models in the Climate Model Intercomparison Project 5 (CMIP5) were used: CCSM4, HadGEM2-AO, IPSL-CM5A-LR and MRI-CGCM3 (Yigini and Panagos, 2016) under the continue as usual climatic scenario, Representative Concentration Pathways 8.5 (RCP8.5). The data were extracted from WorldClim version 1.4 (https://www.worldclim.org/; Hijmans et al., 2005). The model estimates were kept from the original models depicting current distributions and projected them over each of the future scenarios for the year 2050. Occurrence probabilities were averaged across the four scenarios (Ding et al., 2022).

To assess the quality of our models the AUC (Area Under Curve) criterion with the threshold value of 0.7 was used, describing models with acceptable performance (Swets, 1988). Predictions on current and future projected distributions were summarized in the form of suitability values per cell ranging between 0 and 1. These values were classified into four ranks: 'high' (> 0.6), 'moderate' (0.4 - 0.6), 'low' (0.2 - 0.4) and 'unsuitable' (< 0.2) (e.g. Li et al., 2020; Yang et al., 2013; Zhang et al., 2018). Based on these thresholds, a suitable distribution described areas with suitability values above 0.2, whereas acceptable distribution with suitability values above 0.4. To infer migration the kernel (i.e. centroids; C_{cur}, C_{fut}) of the distribution ranges was estimated (Shi et al., 2021; Skov and Svenning, 2004; Thurm et al., 2018) as the arithmetic mean (i.e. centroid) of coordinates for our observations after the year 1981 (C_{obs}). The degree to which a species effectively (***effective migration ratio***) migrated to ward its new distribution range was computed as follows:

$$ef.m_i = \ln\left(\frac{\overrightarrow{C_{obs}C_{fut}}}{\overrightarrow{C_{obs}C_{cur}}}\right) \tag{1}$$

with i describing the plant species of interest and C the locations of the respective centroids.

The ***shift in the distribution range*** was assessed as follows:

$$d_i = \left|\overrightarrow{C_{fut}C_{cur}}\right| \tag{2}$$

Finally the area of the current distributions of species i, S_i was extracted.

Statistical analyses

To address whether temperature (rather than precipitation) drives the distribution of our eight species in the specific region of the world (*Hypothesis One*) the aggregate contribution scores of temperature-related and precipitation-related environmental variables across our eight individual species were quantified and got compared with a Mann-Whitney U Test.

To address the degree to which plant species have caught up with any changes of the distribution (*Hypothesis Two*) the *effective migration ratios* for all species was calculated and was used to assess whether it related (Spearman correlation) to the respective *shifts in their distribution range*. If species had already caught up with the changes in their distribution (*Hypothesis Two*) there should have been no relationship between these two variables.

To address whether tree height related with migration efficiency (*Hypothesis Three*), spearman correlations between plant height and the respective *effective migration ratios* were fitted as well as with the *shifts in the distribution range*. There were also comparable correlation tests with the other plant traits.

In all cases the analysis consisted preferably of non-parametric tests. There were complemented with respective parametric tests, even though the small pool of plant species in the analyses made testing the assumptions of parametric analyses unreliable. All statistical tests were carried on R version 4.2.2 (R core team, 2022).

RESULTS

Model performance and relationships with environmental variables

Parsimonious model settings (Table S1) across species contained a range of linear, linear quadratic or linear quadratic with hinge features settings and regularization settings varying between 0.25 and 1.75 (there were 15 regularization settings with values ranging between 0.25 and 4). In all the models the areas under receiver operating characteristic curve (AUCs) exceeded 0.88 (Figure 1). The lowest AUC value was observed for *Hyodendron biaristatum* (0.881) and the highest for *Diospyros strigosa* (0.981).

In Table S2 there is an overview on how the environmental variables contributed to the MaxEnt predictions . In all eight models the top three most important environmental variables cumulatively accounted for over 73% of the predictive power of the model. In a comparable way the permutation importance proportions of the top three most contributing variables accounted for over 70% across of the total score. The most important environmental variable was annual mean temperature (BIO1; mean contribution 34.66%) and the second most important was annual precipitation (BIO12; mean contribution: 21.54%). Results on the importance of environmental variables were relatively consistent across the different species (Table S2).

Hypothesis One: Temperature-related drive the distribution shifts

The total contribution of the temperature-related bioclimatic variables (BIO1, BIO2, BIO3 and BIO7) for the eight species varied between 35.30% and 93.97% (mean: 69.03% quartiles: 56.16%, 68.70% and 85.92%) The respective contribution estimates for the three precipitation related variables (BIO12, BIO14 and BIO18) were 2.98% - 55.85% and (mean: 27.08%, quartiles: 9.78%, 28.79% and 40.32%). The test between the overall contribution of temperature vs precipitation variables which were carried out to address *Hypothesis One* yielded the following statistics:

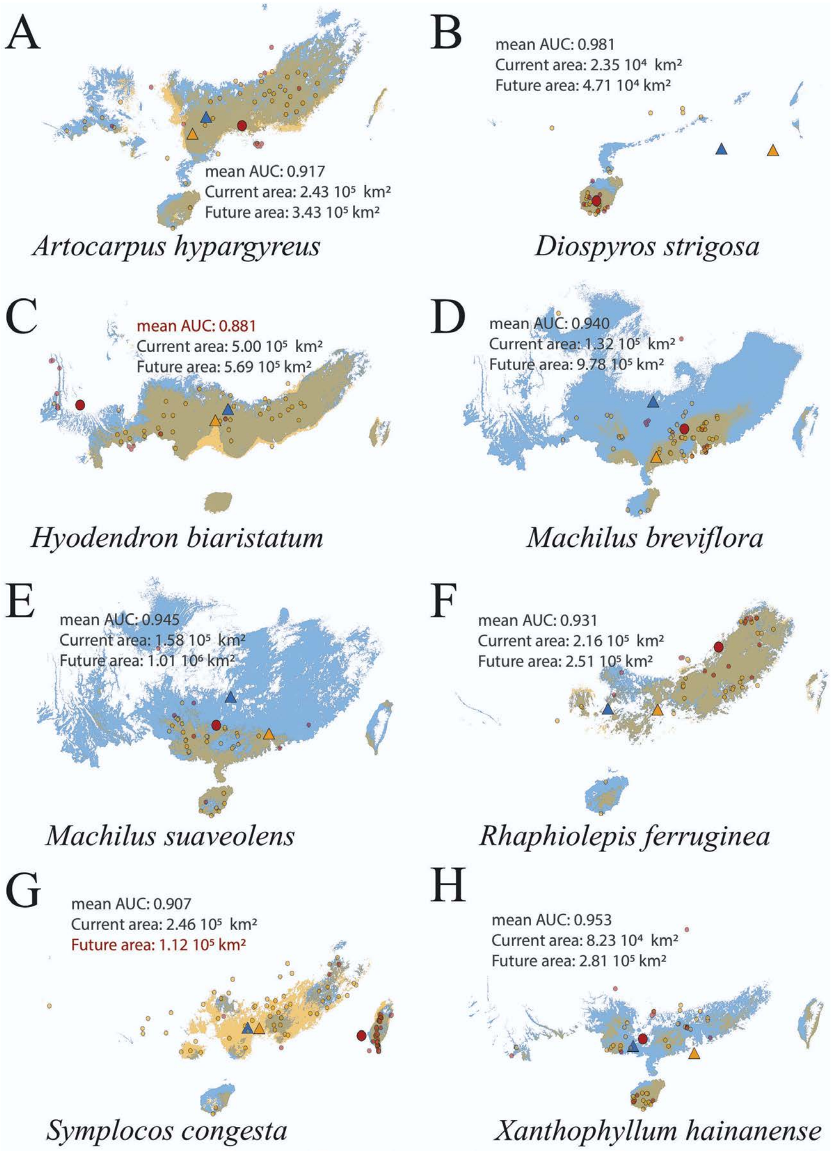

Figure 1: Acceptable (suitability values > 0.4) distributions for the eight species in our study, in relation to present (orange) and future (blue) climatic conditions. The centroids of the two distributions are marked with large (orange and blue, respectively) triangles and a large red circle is used to describe the average latitude and longitude of the species observations that were made after 1980. Pre-1980 observations are marked with smaller yellow circles, and post 1980 with red circles. Statistics on model fit and area of the two distributions are overlaid. The two statistics in red (in panels C and G) remain questionable.

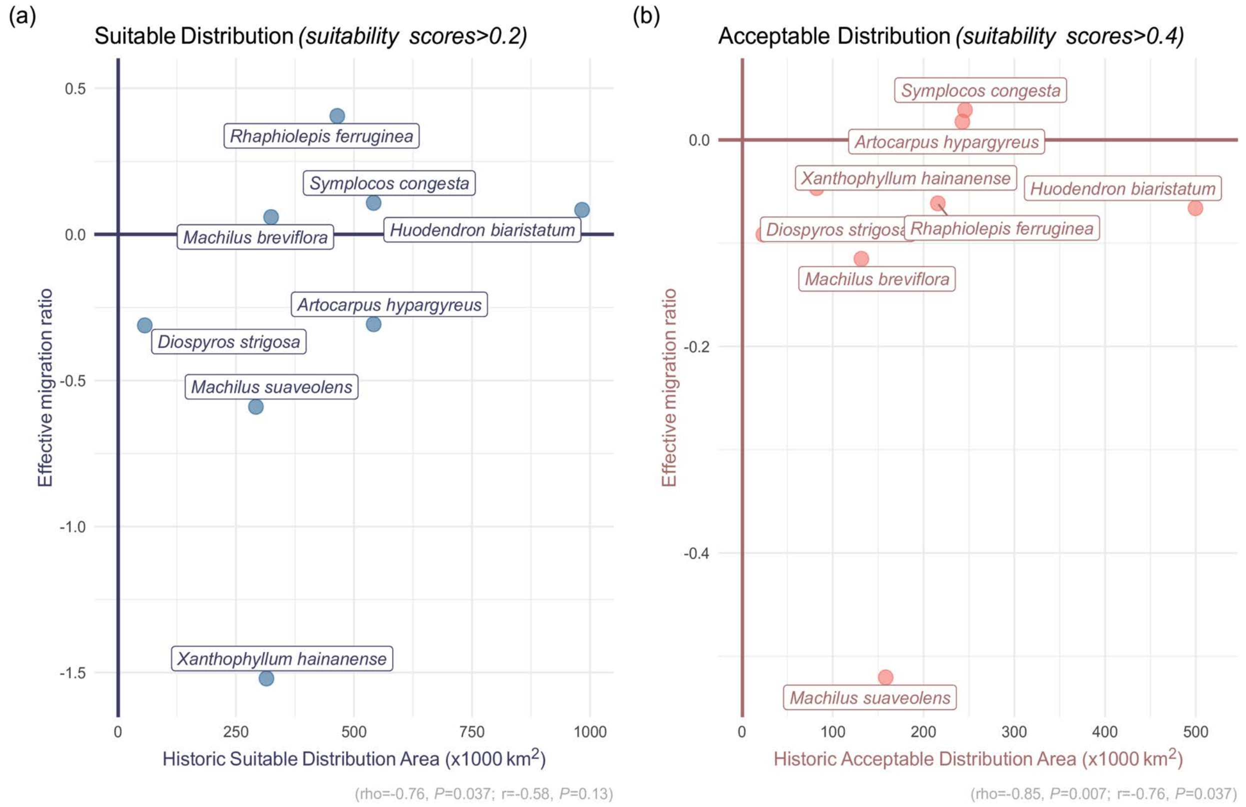

Figure 2: Relationship between the historic distribution area of the eight species and a summary static on the degree to which the most recent observations on a species manifest a high migration efficiency towards the future distribution range (i.e. effective migration ratio – higher values manifest higher efficiency). The relationships for historic (a) suitable (suitability values > 0.2) and acceptable (suitability values > 0.4) distributions are summarized. In both cases there are positive relationships (but not with parametric statistics in the case of suitable distributions). The take home message is that species that maintained smaller distributions have a harder time catching up with global change.

Hypothesis Two: There are only subtle shifts in the ranges of the eight species

The areas of suitable habitat were calculated at different suitability levels for the eight species (Table S3). *Diospyros strigosa* had the smallest distribution range, while *Huodendron biaristatum* had the largest range (Table S3). 73.8% of the suitable area for *Xanthophyllum hainanense* described occurrence probabilities between 0.2 and 0.4 (i.e. described low suitability area). This proportion was significantly higher than for the other seven species averaging 53.8% of their suitability areas. The projections to the year 2050 indicate that the suitable area of *Xanthophyllum hainanense* will increase by 59.6%. With the exception of *Symplocos congesta*, for which a decrease of 2.9% was found (and a correspondent decrease in the acceptable areas of 54.4%), an increase in the distribution areas of species for all species was predicted. These ranged for the acceptable distributions between 13.9% for *Huodendron biaristatum* and 643.3% for *M. breviflora* (Figure 1).

The largest northward shift in the distribution range of a species was predicted for *Machilus breviflora* at 3.35 degrees of latitude, while the corresponding value for the congeneric *Machilus suaveolis* was 2.23 degrees of latitude. At the other extreme, the smallest northwards swift was predicted for *Symplocos congesta* by 0.39 degrees of latitude. *Artocarpus hypargyreus* and *Huodendron biaristatum* could also move eastwards, while the other six species would move westwards. *Xanthophyllum hainanense* showed the highest westward tendency of centroid movement with 4.19 degrees of longitude (Table S4).

Hypothesis Three: Wood density and not tree height predicts migration lag best

Post 1980 observations for trees of species for which there were above-average changes in their distributions (historical vs future; here change is captured through the distance to which their distributions changed: variable *shift in the distribution range*) were closer to the historical distribution than to the future distribution (variable *effective migration ratio*: rho=-0.76, P=0.037; the observation was robust to the considering acceptable distributions in which case rho=-0.76, *P*=0.037).

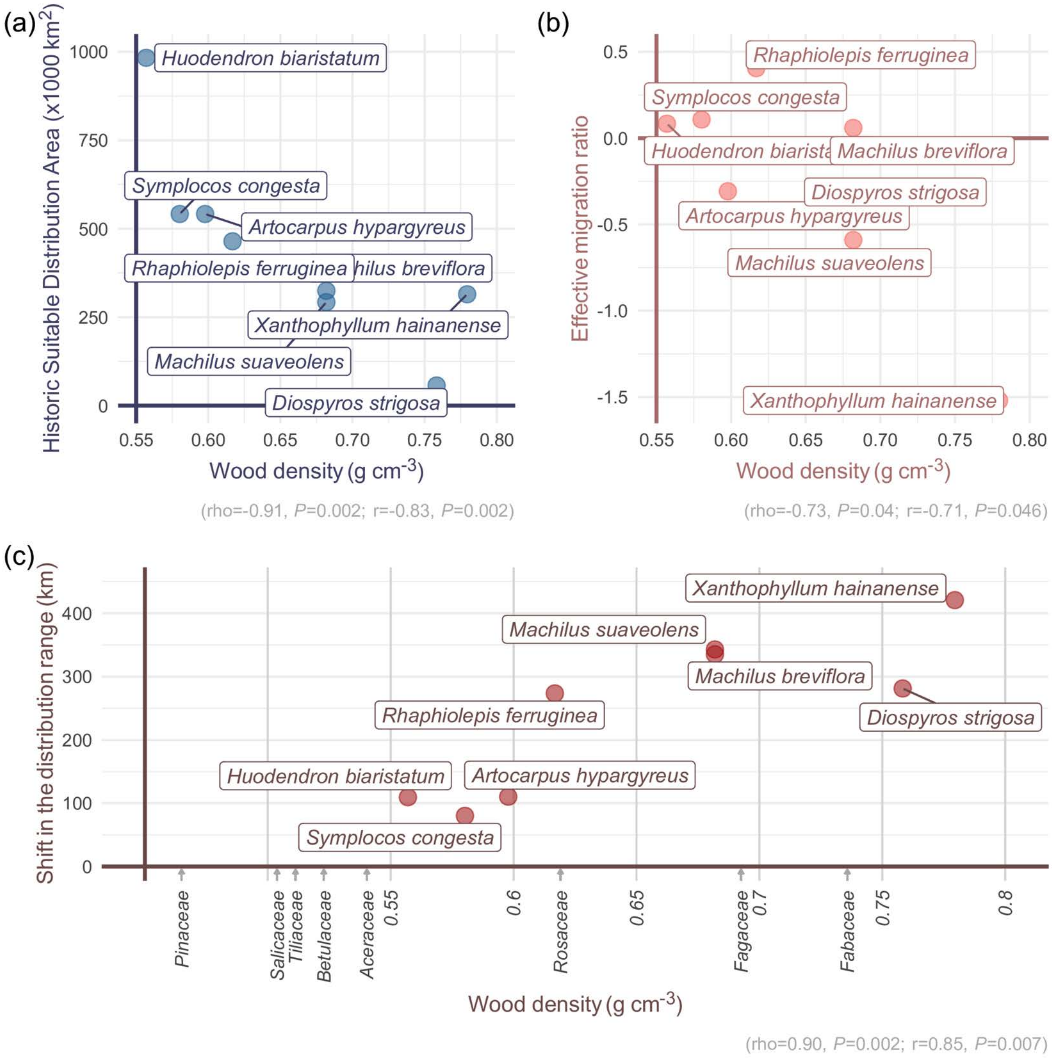

Figure 3: Relationships between wood density (*x*-axis) and (a) historic distribution area; (b) effective migration ratio; (c) the distance between the centroids of future vs historic distributions for the eight plant species. In panel (c) median wood density data for some characteristic families of woody plants are overlaid, implying that the plant species in the study had above average wood density. In all cases there were strong relationships suggesting that wood density is a plant trait that can effectively predict migration efficiency across woody plant species.

There was no relationship between leaf size or tree height and any of the distribution related variables. Species with a high wood density maintained, however, a smaller distribution area than species with a lighter wood (rho=-0.91, *P*=0.002, Figure 3a) and were relatively closer to their historical distributions than their future distributions (relationship with the variable *effective migration ratio*: rho=-0.73, P=0.040, Figure 3b). The mean wood density across our eight species was 0.657 (interquartile range: 0.59, 0.70), above the community weighted value of 0.619 that was reported for tropical systems (Phillips et al., 2019) and above means reported for many common tree families (Figure 3c). it was the species with higher wood density that also showed the greatest distance change in distribution ranges (relationship with the variable *shift in distribution range*: rho=0.90, *P*=0.002).

DISCUSSION

This distribution modelling exercise concerned the distribution ranges of eight plant species in southern China under past and future climate scenarios to assess how they may respond to anticipated global change. Based on *Hypothesis One*, the distribution ranges would be mainly shaped by temperature-related parameters rather than precipitation-related parameters which was the case (Table S2). *Hypothesis Two* further postulated that the distribution range of most of the species would be resilient to climate change. There were universal northward shifts in agreement with many other empirical studies (Kumar and Rawat, 2022; Lu et al., 2021; Mueller et al., 2022; Yang et al., 2022) and the distribution ranges of most species expanded (Figure

1). *Hypothesis Three*, finally, predicted that plant traits could capture migration efficiency and in agreement to it species with a higher wood density maintained a smaller range, a higher range shift and greater difficulty in coping with climate change among the eight species (Figure 3).

Many of the animals that went extinct had distinctive features – traits. For example, the dodo had evolved in an environment without natural predators, making it an easy target for human hunters (Roberts and Solow, 2003), while the thunderbird (*Genyornis newtoni*), another flightless bird in Australia, evolved an island gigantism (Miller et al., 2016). In addition to small body size, animals that effectively disperse over greater distances may also be more resilient to climate change (Nadeau and Fuller, 2016). It is unclear whether comparable traits exist for plants that can summarise their vulnerability to global change. Some studies have observed correlations between life history traits such as flux phenology, seed size, stress tolerance, dispersal mode and plant height with extinction risk in plants (Fréville et al., 2007), but these have not been consistent across ecosystems (e.g. Matteodo et al., 2013). O'Rourke et al. (2022) assessed the extent to which the extinction risk status of the Irish flora could be predicted by a set of fourteen leaf traits and concluded that any such correlation should be weak in magnitude. It might be easier, to predict extinction risk, instead, which relates in the case of woody plants to their migration efficiency. Several studies have already linked extinction risk to plant traits, such as migration efficiency (Liao et al., 2020), longevity (Noh et al., 2019; Vellend et al., 2006), pollination strategy and tolerance to external stress caused by changes (Saar et al., 2012).

This study focused on three plant traits for which data collection was possible for all eight plant species, leaf size, tree height and wood density. There were only correlations of the migration variables with wood density. The wood economics spectrum has recently been proposed as an extension of the leaf economics spectrum (Chave et al., 2009). Trees with a low wood density should maintain, based on the spectrum, higher relative growth rates but experience a higher mortality (Chave et al., 2009). The likely relationships with growth and mortality rates may be precisely why wood density could in our study predict migration parameters. The wood economics spectrum may not be completely independent from the respective leaf's spectrum (Reich et al., 2003; Zhao et al., 2017), meaning that high wood and leaf densities could compromize growth rates but secure tissue longevity (Wright et al., 2006a). The focus on woody species may explain why a variable from the wood economics spectrum, wood density outperformed in predicting migration respective variables from the leaf economics spectrum such as leaf size.

Although each of the biodiversity hotspots faces unique challenges in terms of plant extinction risk, such as the degree of endemism and the biome specificity of the plant species (Malcolm et al., 2006), the results may be generalisable across natural systems and biodiversity hotspots. First, because rare plant species that are likely endemic to this biodiversity hotspot were specifically targeted, and thus experience a high degree of genetic isolation. This should make the analysis descriptive for most rare plant species across all biodiversity hotspots. Second, migration parameters were assessed in relation to three crude plant traits, that capture three common life history syndromes (i.e. wood -wood density- and leaves -leaf size-economic spectrum but also body mass – tree height, for the three traits, respectively) across plant species and should be generalizable across habitats. Plant rarity tends to increase vulnerability to environmental variability (Malcolm et al., 2006; Thomas et al., 2004). This means that the analysis specifically targeted species that may experience large changes in distributions in the face of global change.

A limitation of this study is that it consists of the distribution of just eight plant species. Nevertheless, these were the only eight woody species that met the filtering criteria. Could, thereby, the relationships that were observed been due to idiosyncrasies of the species considered? There were clear relationships between the variables and the analyses were paired with conservative and robust to likely outliers non-parametric Spearman rho tests. Furthermore, many of the relationships were consistent with the original expectations. For example, species with larger distributions migrated more effectively (Figure 2), which is consisent with Malcolm et al. (2006) postulating that such species are less susceptible to climate change. It may, nevertheless, be difficult to generalize the findings for other regions. For example, most European woody plant species have much larger ranges. There is, nevertheless, a good chance that an important driver of vulnerability of woody plants to climate change in the specific region, was captured through this study.

Notwithstanding the likely generality of the findings there were additional reasons why it was important to focus on this particular region. THis is a region where global change models predict strong changes in precipitation frequency and intensity (e.g. Trenberth, 2011), and through the analysis it was possible to question whether these would overwhelm the expected importance of temperature-related parameters in relation to vulnerability risk. Furthermore, many plants in the region remain undocumented and up to 794 new plant species are discovered each year (http://sp2000.org.cn/). This means that assessing extinction risk in the region for these less well-documented plant species may only be possible through general predictive models that integrate plant traits (McGill et al., 2006).

A major challenge in conservation biology is identifying species facing a risk of extinction. This facilitates an early intervention and can render conservation more cost-effective (Dominoni et al., 2020). Trait ecology presents a recently developped tool in conservation biology to assess vulnerability of species for which there are insufficient distribution data available (Ribeiro et al., 2016; Gallagher et al., 2021). The challenge in those cases is to choose relevant traits to be used for conservation purposes (Gallagher et al., 2021). The analysis here presents evidence that wood density may qualify as a particularly good and easy to assay proxy of vulnerability of woody plants to extinction. Conservation science is an interdisciplinary science, which requires the coordination of numerous stakeholders, comprising indigenous people, policy makers and researchers from diverse disciplines (Wheeler and Root-Bernstein, 2020), necessitating raising awareness, which is hopefully done through this study.

CONCLUSION

This is a distribution modeling exercise that supports that high wood density in rare plant species contributes to relatively smaller geographic distribution ranges and more pronounced range shifts. Wood density may thus represent an inconspicuous component of plant physiology that links plant growth components to range shifts and susceptibility to environmental change, thus opening opportunities for larger syntheses in plant biogeography. A remaining open question is the extent to which our observations can be generalised across habitats and biomes. At the same time, it remains unclear whether collating information on additional traits could lead to better predictors of migration potential across plant species. Regardless of these two perspectives, replicating the analysis across biodiversity hotspots could contribute immensely to the synthesis of trait and extinction ecology.

DATA AVAILABILITY

The datasets supporting the conclusions are included in the article.

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SUPPLEMENTARY MATERIALS

Contents:

- Appendix 1:Detailed Materials and Methods
- Supplementary Tables 1 - 5

Appendix 1: Detailed Materials and Methods

We gathered from GBIF and the Chinese Virtual Herbarium (CVH) a total of 420 observations (Table S5). We classified them into the classes of historic observations (prior to 1980) which we modelled with historic climatic settings and recent observations (post 1980) which we used to assess the efficiency with which the plant species catch up with climate change.

To fit our models we used the Java version (MaxEnt.jar) of Maxent v3.4.2. Our models were as follows:

1. Predictors

To address over-fitting, in our models, we excluded collinear environmental variables (Dormann et al. 2013; Merow et al. 2013). Dormann et al. 2013 suggested an absolute threshold of Pearson correlation coefficient 0.70 to exterminate collinearity in most situations. Variance inflation factor (VIF) test is alterative (Naimi et al. 2014). However, if a study has aims, for example, on which variables drive species distribution, Merow et al. 2013 suggested not to prescreen the predictors too excessively. In this study, we set an exclusion threshold of Pearson correlation coefficient $|r| > 0.75$ to necessarily and not excessively prescreen predictors. Attached to this step, we used the variance inflation factor (VIF) to check collinearity (VIF < 5 for no collinearity, and VIF >10 for significant collinearity), and using this threshold the VIF was still 52. We faced a trade-off on prescreening and remaining variables. Since thresholds from 0.7 to 0.8 were largely used in this field, we considered this level of collinearity acceptable, because we would select relatively best settings to avoid overfitting afterwards.

2. Size of the modelling area

To increase the accuracy of the predictions we restricted the size of the modelling area to tropical, subtropical and a few temperate regions in China. The exact window was as follows: 18°10’ - 36°22’ N, 97°21’ - 122°43’ E.

3. Test set

We consistently, across our models, used a regular set of 75% of observations for training and 25% of observations for validation by randomly sampling in agreement with recommendations in the literature (Garcia et al. 2013; Phillips 2008).

4. Settings of the two parameters

We experimented with the following feature settings: appropriate feature classes (i.e. linear, quadrat and hinge), regularization parameters and (we used 15 different parameters ranging from 0.25 to 4) and nonspatial partitioning techniques (optimal nonspatial partitioning techniques were decided based on the number of observations) (Merow et al. 2013). We decided on optimal models (Table S1) based on parsimony – AICc values.

5. Representative of plant species pool (maxent modelling).

Our pool of wight species presented all eight woody species that met the four species inclusion criteria (main manuscript). We understand that our finding on wood density may be difficult to get generalized across other ecoregions, globally. As an example, most European wood plant species maintain considerably larger distribution areas. We are, nevertheless, confident that we captured a major driver of susceptibility of woody plants to climate change in the specific region.

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Table S1: Parsimonious model settings across species contained a range of linear, quadratic, hinge or quadratic with hinge features settings and regularization settings varying between 0.25 and 1.75 (which was decided after testing 15 regularization settings ranging between 0.25 and 4) were selected based on non-duplicate coordinate data.

Species	partitioning[1]	independent runs[2]	final decision[3]
Artocarpus hypargyreus	random K-fold	fc.LQ_rm.0.5 fc.LQH_rm.1 fc.LQH_rm.1.25 fc.LQH_rm.1 fc.LQH_rm.1	fc.LQH_rm.1
Diospyros strigosa	Jack knife	fc.LQ_rm.0.5 fc.L_rm.0.5 fc.L_rm.0.5 fc.L_rm.0.5 fc.L_rm.0.5	fc.L_rm.0.5
Huodendron biaristatum	Jack knife	fc.LQH_rm.1 fc.H_rm.0.25 fc.LQH_rm.1 fc.LQH_rm.1.25 fc.LQH_rm.1.5	fc.H_rm.1.75
Machilus breviflora	random K-fold	fc.LQ_rm.0.5 fc.LQ_rm.0.5 fc.LQ_rm.0.5 fc.LQ_rm.0.5 fc.LQ_rm.0.25	fc.LQ_rm.0.5
Machilus suaveolens	Jack knife	fc.LQH_rm.1.75 fc.H_rm.2 fc.LQH_rm.2 fc.LQ_rm.0.5 fc.H_rm.1.75	fc.L_rm.0.25
Rhaphiolepis ferruginea	Jack knife	fc.LQH_rm.1 fc.LQH_rm.1 fc.LQH_rm.1.25 fc.LQH_rm.1 fc.LQH_rm.1.5	fc.LQH_rm.1
Symplocos congesta	random K-fold	fc.H_rm.1 fc.LQH_rm.1.5 fc.LQH_rm.1.5 fc.LQH_rm.1 fc.LQ_rm.0.25	fc.LQH_rm.1
Xanthophyllum hainanense	Jack knife	fc.LQH_rm.1.75 fc.H_rm.1.5 fc.LQH_rm.1 fc.LQH_rm.1 fc.LQH_rm.1.25	fc.LQH_rm.1.5

[1] The nonspatial partitioning techniques were chosen for each species based on the amounts of coordinates (random K-fold for those less than 50 and Jack knife for those more than 50). [2] We ran five independent times for each species. fc indicates feature characters, rm indicates regularization multipliers, L indicates linear, Q indicates quadradic, and H indicates hinge. [3] We averaged the AICs of independent runs and selected parameter settings with the lowest AICs for each species.

Table S2: Contribution of environmental variables[1] to optimal models for the eight species.

Species		BIO1	BIO2	BIO3	BIO7	BIO12	BIO14	BIO18	elev
Artocarpus hypargyreus tree	C[2]	27.87		28.16		28.99			
	PI[3]	39.68		15.20		28.42			
	JR[4]	I		II		III			
Diospyros strigosa shrub	C	28.37			64.92			3.12	
	PI	36.41			23.72	15.87			
	JR	I	III		II				
Huodendron biaristatum shrub	C	17.54		31.82		30.73			
	PI		40.72	17.08	16.32				
	JR	I		II		III			
Machilus breviflora tree	C	56.73		7.37		17.30			
	PI	43.62		11.77		20.98			
	JR	I				II		III	
Machilus suaveolens tree	C	75.33			18.23				1.62
	PI	72.08	6.24						14.38
	JR	I			II				III
Rhaphiolepis ferruginea shrub	C	10.91		20.71		41.99			
	PI		23.09			29.67			10.62
	JR	III		II		I			
Symplocos congesta tree	C			15.84	22.39	38.94			
	PI			12.99	25.03	32.34			
	JR	II			III	I			
Xanthophyllum hainanense tree	C	49.73			15.32	12.41			
	PI	37.28				14.68			17.47
	JR	I		III	II				

[1] The top three contributing variables for each species were displayed. [2] C: contribution (%). [3] PI: permutation importance (%). [4] JR: Jackknife of regularized training gain, and roman numerals indicate the contribution ranks.

Table S3: Areas of the suitable habitats in different suitability levels.

Areas (10000 km^2)	Year	low	moderate	high	acceptable	suitable
Artocarpus hypargyreus	1980	29.88597	18.21396	6.068194	24.28215	54.16812
Diospyros strigosa	1980	3.330417	1.432431	0.923125	2.355556	5.685972
Huodendron biaristatum	1980	48.35299	31.97	17.99056	49.96056	98.31354
Machilus breviflora	1980	19.29625	8.495278	4.6575	13.15278	32.44903
Machilus suaveolens	1980	13.38785	10.20396	5.632708	15.83667	29.22451
Rhaphiolepis ferruginea	1980	24.89111	16.87493	4.702292	21.57722	46.46833
Symplocos congesta	1980	29.59187	21.14285	3.434097	24.57694	54.16882
Xanthophyllum hainanense	1980	23.23222	6.135903	2.093542	8.229444	31.46167
Artocarpus hypargyreus	2050	42.31951	27.56458	6.705625	34.27021	76.58972
Diospyros strigosa	2050	10.65146	3.212222	1.496319	4.708542	15.36
Huodendron biaristatum	2050	67.83431	51.97979	4.946528	56.92632	124.7606
Machilus breviflora	2050	42.275	33.88174	63.88701	97.76875	140.0437
Machilus suaveolens	2050	46.87972	35.27931	66.02396	101.3033	148.183
Rhaphiolepis ferruginea	2050	24.97562	19.15986	5.983958	25.14382	50.11944
Symplocos congesta	2050	41.42312	8.859792	2.338125	11.19792	52.62104
Xanthophyllum hainanense	2050	22.08646	17.76285	10.36667	28.12951	50.21597

Table S4: Geographic coordinates of the distribution centroids in near-current predictions and future projections.

Species	1980 predictions		after 1980		2050 projections	
	longitudes	latitudes	longitudes	latitudes	longitudes	latitudes
Artocarpus hypargyreus	110.57	22.859	113.2948	23.23373	111.3198	23.66754
Diospyros strigosa	119.2115	21.38312	109.5565	18.88741	116.3994	21.43851
Huodendron biaristatum	109.5419	24.10164	100.2931	25.01755	110.3949	24.78714
Machilus breviflora	110.768	22.00353	112.7116	23.67576	110.5679	25.3497
Machilus suaveolens	113.4465	23.26277	109.8554	23.73984	110.8393	25.49018
Rhaphiolepis ferruginea	112.607	23.30669	115.9551	26.33625	109.8727	23.36253
Symplocos congesta	112.6681	23.45628	119.6794	22.99352	111.8691	23.49478
Xanthophyllum hainanense	113.0054	21.66383	109.491	22.51431	108.8197	22.09638

Table S5: Analytical statistics on the observations we gathered per species.

Species	GBIF	CVH	all_obs	before1980		after1981	
				collected	used	collected	used
Artocarpus hypargyreus Hance	85		85	67	56	18	17
Diospyros strigosa Hemsl.	25	17	42	35	27	7	7
Huodendron biaristatum Rehder	82		82	61	42	21	21
Machilus breviflora (Benth.) Hemsl.	52	38	90	74	67	16	12
Machilus suaveolens S.K.Lee	22	24	46	38	36	8	7
Rhaphiolepis ferruginea Metcalf	32	18	50	34	30	16	16
Symplocos congesta Benth.	192		192	34	72	98	95
Xanthophyllum hainanense Hu	36	40	76	59	43	17	14

Appendix 2: Sources of data on the distribution of the eight species

1. *Artocarpus hypargyreus*

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2. *Diospyros strigosa*

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6. *Machilus suaveolens*

Ramirez J, Watson K, McMillin L, Gjieli E (2022). The New York Botanical Garden Herbarium (NY). Version 1.49. The New York Botanical Garden. Occurrence dataset https://doi.org/10.15468/6e8nje accessed via GBIF.org on 2022-09-06.

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