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ORIGINAL PAPER

Habitat association and demographic rates for large tree species: implications for native tree species used in forestry

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Abstract Exotic tree species, though widely used in forestry and restoration projects, pose great threats to local ecosystems. They need to be replaced with native species from natural forests. We hypothesized that natural forests contain large, fast-growing, dominant native tree species that are suitable for specific topographic conditions in forestry. We tested this hypothesis using data from a 50-ha forest dynamics plot in subtropical China. We classified the plot into the ridge, slope, and valley habitats and found that 34/87 species had significant associations with at least one topographic habitat. There were 90 tree species with a maximum diameter ≥ 30 cm, and their abundances varied widely in all habitat types. In all habitat types, for most species, rate of biomass gain due to recruitment was < 1% of its original biomass, and rate of biomass gain due to tree growth was between 1 and 5% of its original biomass. For most species, biomass loss due to tree mortality was not significantly different than biomass gain due to recruitment, but the resulting net biomass increment rates did not significantly differ from zero. The time required to reach a diameter of 30 cm from 1 cm diameter for *Altingia chinensis* in the slope habitat, for *Quercus chungii* and *Morella rubra* in the ridge habitat and for *Castanopsis carlesii* in all habitats could be as short as 30 years in our simulations based on actual distributions of tree growth observed in the forest. Principal component analyses of maximum diameter, abundance and net biomass increment rates suggested several species were worthy of further tests for use in forestry. Our study provides an example for screening native tree species from natural forests for forestry. Because native tree species are better for local ecosystems, our study will also contribute to biodiversity conservation in plantations.

Keywords Native tree species · Growth simulation · Timber · Wood product · Subtropical forest

Introduction

The increasing recognition of the importance of biodiversity has led to calls for planting native tree species as an alternative to exotic monocultures (Leakey and Newton 1994; Leakey and Simons 1997; Nichols and Vanclay 2012; Almas and Conway 2016; Lu et al. 2017; Wang et al. 2022). Exotic tree species have been used in forestry in many countries for a long time (Führer 2000; Quine and Humphrey 2010; Salmón Rivera et al. 2016). They can alter local nutrient cycling, energy flow, and the species composition, diversity

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and structure of the ecosystem (Gurevitch and Padilla 2004; Dyderski and Jagodziński 2020). They can also be potentially invasive as they acclimatize easily to their environments and often outcompete native tree species (Wang et al. 2013). Compared with exotic tree species, native tree species can enhance biodiversity (reviewed by Berthon et al. 2021). For example, planting native trees rather than exotic trees in urban areas resulted in significantly higher bird species richness in Canberra, Australia and understory plant species diversity in the United Arab Emirates (Ikin et al. 2013; Slate et al. 2020). Considering the need for biodiversity conservation, native tree species should thus be prioritized in forestry (Marianov et al. 2004; Almas and Conway 2016; Cosyns et al. 2020). Even when it is not practical to entirely replace exotic species (Manetti et al. 2016; Sjöman et al. 2016), a mixture of exotic trees with native ones can also benefit the environment more than an exotic monoculture (Almas and Conway 2016).

Though native tree species are better for local environments and biodiversity conservation (Gurevitch and Padilla 2004; Ikin et al. 2013; Dyderski and Jagodziński 2020; Slate et al. 2020), the use of native tree species has been hindered by a lack of information such as their stature, abundance, distribution and demographic rates, making it difficult to choose the appropriate species for practical use in a given environment (Butterfield 1996). Hence, compiling such basic information is the first step toward their use in forestry (Lu et al. 2017).

Because tree species vary in their suitability for different habitats (Harms et al. 2001; Bin et al. 2016), they need to be selected for the specific planting site conditions to ensure the success of forestry and greening projects (McDicken 1994). Though habitat conditions are multidimensional, topography is an integrated feature associated with hydrology, soil texture, nutrient concentrations, and light availability to which trees respond (Zuleta et al. 2020; Li et al. 2022). Furthermore, topographic conditions have significant effects on tree demographic rates and distributions (Bin et al. 2016; Zuleta et al. 2020). Native tree species for such use also often need to be large and fast-growing so that within a relatively short time they can provide versatile wood products and ecological functions such as preventing soil erosion, reducing carbon dioxide and improving biodiversity (Condit et al. 1993).

Since the establishment of the first large-scale forest dynamics plot in Barro Colorado Island, Panama in 1980 (Condit 1998), 75 plots have been established all around the world, forming the ForestGEO network (https://forestgeo.si.edu/; access on 2023/3/8). Within these plots, a total of 7,000,000 trees from 12,000 species have been recorded (https://forestgeo.si.edu/, access on 2023/3/8). Tree species stature, abundance, distributions and demographic rates can be understood using these data (Harms et al. 2001; Condit et al. 2006; Bin et al. 2016; Li et al. 2022). These large-scale forest dynamics plots can serve as the basis for screening native species for forestry and restoration use (Condit et al. 1993).

Regularly censused forest plots provide a unique opportunity for understanding the distribution and growth rates of native species, and other essential information for selecting native species for forestry (Condit et al. 1993) to replace fast-growing exotic species that pose a potential threat to the composition and structure of local ecosystems (Gurevitch and Padilla 2004; Dyderski and Jagodzinski 2020).

In this study, we aimed to provide primary knowledge of species' demographic rates and habitat associations in a primary forest based on the census data obtained from a 50-ha forest dynamics plot in subtropical China. Specifically, we asked four questions: (Q1) Did native tree species show significant associations with topographic habitats? (Q2) What are the stature and abundance of the native tree species in different habitat types in the plot? (Q3) What are the demographic rates of these native tree species in different habitat types? (Q4) Are there any native tree species with potential for forestry?

Materials and methods

Study site, plot census and studied species

The study was carried out in 2011 in southern China in the 50-ha Heishiding forest plot (HSD plot; 500 m × 1000 m) in the Heishiding Nature Reserve (111.53° E, 23.27° N). The reserve is located on the tropic of cancer. It has a south subtropical monsoon climate and is covered by subtropical evergreen broad-leaved forests. The reserve has an annual mean temperature of 19.6 °C and precipitation of 1740 mm. The forest age is approximately 120 years (Chen et al. 1992; Jiang et al. 2020) and the forest height is about 60 m. The altitude of the plot ranges from 435.4 to 698.4 m a.s.l.. In the first plot census in 2011–2013, 213,969 free standing stems with DBH $\geq$ 1 cm from among 213 species, 160 genera, 71 families were recorded (Shi et al. 2018); 156 species had $\geq$ 50 individuals in the plot, and 57 species had $<$ 50 individuals (Shi et al. 2018). The vegetation was dominated by *Pinus massoniana* and *Altingia chinensis.*

For topography measurement and tree mapping, the 50-ha forest plot was divided into 1250 non-overlapping contiguous quadrats, each measuring 20 m × 20 m. The corners of every quadrat were mapped using an electronic total station. Altitudes at the four corners of each quadrat were recorded as described by Harms et al. (2001). All stems with DBH $\geq$ 1 cm in the plot were identified, mapped, tagged, and measured. In the second census in 2016, plant status (dead or living) was recorded; surviving stems were re-measured and stems that had not been recorded in the first census but reached 1-cm diameter were measured and recorded.

Data analyses

We focused on 90 species with maximum DBH ≥ 30 cm (Table S1). These species belonged to 56 genera and 37 families (Table S1). The families with the most species analyzed were Fagaceae and Lauraceae, each with 17 species in the plot (Table S1).

Because tree species are often associated with certain habitats (Bin et al. 2016; Harms et al. 2001), we first analyzed species preference for the three habitat types using torus translation tests (Harms et al. 2001). For native tree species in the different habitats, we used the maximum diameter, abundance, and biomass-related rates, and simulated the time needed for these species to reach 30-cm DBH from a starting DBH of 1 cm. For evaluating species' suitability for use in forestry in a specific topographic habitat, we first excluded those species negatively associated with that habitat and then evaluated the suitability of the remaining species based on a principal component analysis using three variables: abundance, maximum diameter measured, and net biomass increment rate. We also simulated the time needed to reach 30 cm from 1 cm in diameter (T30) as a reference of growth rate. All analyses were conducted using R 3.4.2 (R Core Team 2017). The methods to answer each question are given next.

Q1: Did native tree species show significant associations with topographic habitats?

In this analysis, we included 87 species that were represented by ≥ 50 individuals with maximum DBH ≥ 30. For the test of the association of a species with the topographic habitats using torus translation (Harms et al. 2001), the contour lines obtained using the altitudes at the corners of each 20 × 20 m^2 quadrat were used to classify each quadrat as ridge, slope, or valley (Fig. 1). For each species, we then calculated its relative observed density in each habitat type relative to its overall density in the 50-m plot (i.e., all habitat types) and compared the overall observed relative density with the distribution of relative density in this habitat type, assuming a random distribution of this species with respect to habitat types. The distribution was obtained by keeping the distribution of this species but rearranging the topographic habitat with the torus translation approach (Harms et al. 2001). Each time the map of the topographic habitat was rearranged and the distribution of the species with respect to the habitats changed accordingly. We then recalculated the relative density in this habitat type based on the new map of the topographic habitat. The species is considered to be significantly positively associated with a habitat type if the observed relative density of the species in the real habitat map is greater than the upper envelop of the 95% confidence interval of the distribution of the simulated relative densities ($\alpha = 0.05$), and vice versa.

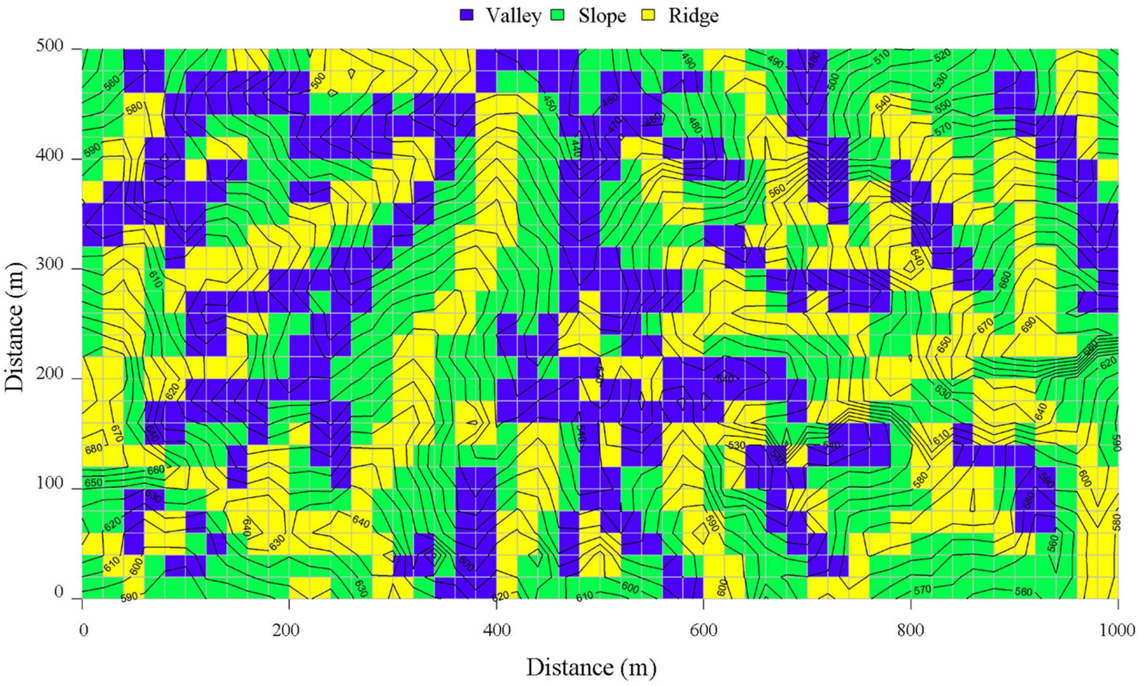


Fig. 1 Distribution of the three topographic habitats in a 50-ha plot in the southern subtropical evergreen broadleaved forest in Heishiding Nature Reserve. Each square represents a 20 m × 20 m quadrat

Q2: What are the stature and abundance of the native tree species in the different habitat types in the plot?

Maximum diameter observed in the two censuses for each species was used to represent the stature of each species. The number of stems with DBH ≥ 5 cm in each habitat type was used as the abundance of each species.

Q3: What are the biomass-related rates of these native tree species in the different habitat types?

Because the ecological functions provided by a tree and the amount of wood it produces are closely related to biomass, we estimated the aboveground biomass $\mathrm{AGB}_{\mathrm{est}}$ using the equation of Chave et al. (2014):

$$AGB_{\mathrm{est}} = \exp(-1.803 - 0.976E + 0.976\ln\rho + 2.673\ln D - 0.0299(\ln \mathrm{D})^2) \tag{1}$$

where, AGB_{est} is the estimated aboveground biomass, E is a measure of environmental stress, ρ is the wood density of the tree, and D is the DBH of the tree. E increases with temperature seasonality (Chave et al. 2014). We obtained the value of E for our study site (–0.1287045) from the web page with supporting data for Chave et al. (2014); http://chave.ups-tlse.fr/pantropical_allometry.htm. To estimate wood density, we took wood samples from a branch or trunk of at least six randomly chosen individuals for each of 75 species with maximum DBH ≥ 30 cm. An increment borer (CO400/CO500) was used to extract a 1-cm-diameter core that was 5–10 cm long at ~ 1.3-m height on the main stem for trees with DBH > 10 cm. For smaller individuals, we cut stem segments (10-cm long, 1-cm diameter) from branches. Wood sample volume (cm^3) was quantified using water displacement (Cornelissen et al. 2003), and dry mass (g) was determined after at least 48 h at 80 °C. Wood density was calculated as dry mass/volume ($\mathrm{g\ cm}^{-3}$). Wood density was fit as a function of DBH using standardized major axis regression, with species identity as a grouping factor. For species with significant size-dependent wood density variation, we predicted wood density for each individual based on the fitted functions; wood density was not predicted by extrapolation. For species without significant size-dependent wood density variation, the average wood density for the samples of this species was used for all individuals of that species.

We calculated net biomass increment rate (n), and its three components: rate of biomass gain due to recruitment (r), individual growth (g) and biomass loss due to mortality (m) using:

$$n = \frac{(Bt - Bo)/Bo}{t} \tag{2}$$

$$r = \frac{Br/Bo}{t} \tag{3}$$

$$g = \frac{Bg/Bo}{t} \tag{4}$$

$$m = \frac{Bd/Bo}{t} \tag{5}$$

where, B is aboveground biomass, B_{o} for all stems with DBH ≥ 1 cm at the first census, B_{t} for all living stems with DBH ≥ 1 cm at the second census, B_{r} for all recruits during the census interval, B_{g} for all stems that were recorded at the first census and still alive at the second census, and B_{d} for the stems that were recorded at the first census but were dead at the second census; and t is 5 years, the number of years between the two censuses. We used bootstrap sampling over the 20 m × 20 m quadrats, i.e., sampling with replacement the same number of quadrats a species was observed to occupy, for the confidence intervals of the demographic rates (Muller-Landau et al. 2006).

We also estimated the shortest amount of time that a tree species needed to reach 30 cm in diameter (T30) as a measure of tree growth. Because trees with DBH ≥ 30 cm are usually thought to be marketable for timber (Rondon et al. 2009), for each topographic habitat, we simulated the minimum number of years needed for a tree of each species to reach 30 cm in diameter so that these species can be compared in terms of the time needed for market in similar, natural environments.

In a specific habitat type, we first selected all individuals of this species within that habitat type and then categorized the sizes into four classes: (1, 5], (5, 10], (10, 15], and (15, 30]. Trees above 30 cm were excluded because simulations stopped when trees reached that size. Because tree size distributions were usually reversed-J shaped (Bin et al. 2012) and abundance for trees in large size classes decreased sharply, trees with DBH within the class (15,30] were pooled so that there were more trees for simulation in this size range. We then determined the 90th percentile of diameter increment for each size class and excluded stems below this threshold. In each simulation, diameter increment was randomly chosen from the actual diameter increment of the remaining stems within the corresponding and size class (Lieberman and Lieberman 1985; Rondon et al. 2009). Subsequently, the increment sampled was added to the original diameter to yield the new DBH. We then checked which size class the new DBH fell into and repeated the "growth" process again. Simulation stopped when the simulated tree was not < 30 cm in DBH. The time step of simulation was 5 years, which is the time interval between the two complete censuses (2011 and 2016) of the HSD plot.

Stems with ≥ 4 cm of shrinkage in DBH or ≥ 20 cm increment in DBH between the two censuses were excluded because these records were likely due to measurement error. After excluding these stems, only species with ≥ 10 stems in each size classes were included in this analysis.

Q4: Are there any native tree species with potential for forestry?

We expect species with potential for forestry to be large, adaptive to local climate, and fast to accumulate biomass, which are often the selection criteria in other forestry projects (Meli et al. 2014). Therefore, candidates to test further were identified using a principal component analysis of three variables: abundance, maximum diameter observed, and net biomass increment rate. The time to reach 30 cm in DBH was not included because many species did not have enough trees in all size classes for simulation.

Results

Q1: Did native tree species show significant associations with topographic habitats?

The slope habitat was the largest habitat type, occupying 480 20 m × 20 m quadrats, followed by the ridge habitat (418 quadrats), then the valley habitat (352 quadrats). Of the 87 species included in this analysis, 34 had either a positive or negative association with at least one habitat type. A small fraction of tree species had positive associations with the ridge habitat (16/87), and most of these were negatively associated with the valley habitat (14/16, 87.5%) (Table S1). Similarly, 16 tree species were positively associated with the valley habitat, and 93.8% of these (15/16) were negatively associated with the ridge habitat (Table S1). Nine species were positively associated with the slope habitat (Table S1); most of these nine were neutral to the ridge (77.8%) and to the valley habitat (66.7%) (Table S1).

Q2: What are the stature and abundance of the native tree species in the different habitat types in the plot?

Neolitsea phanerophlebia Merr. was the most abundant species (5636 ind., 337.08 ha^{-2}; Table S2) in the ridge habitat. *Cryptocarya concinna* Hance was the most abundant species in both the slope (11,227 ind., 587.74 ha^{-2}; Table S2) and the valley (9837 ind., 698.65 ha^{-2}; Table S2) habitats. Abundance in the ridge habitat ranged from 2 (0.12 ha^{-2}) to 5636 (337.08 ha^{-2}) among the species we tested (Table S2), with a mean density of 48.29 ha^{-2}. Though species abundance in the slope and valley habitats had wider ranges (slope: 33–11,227 species; valley: 13–9837 species) than in the ridge habitat, the mean density did not differ significantly among the three habitat types (ridge: 48.29 ha^{-2}; slope: 47.46 ha^{-2}; valley: 50.56 ha^{-2}).

The observed maximum diameter of the studied species in each habitat ranged from several centimeters to above 130 cm (Table S2). In the slope habitat, the maximum DBH was 136.94 cm for *Castanopsis nigrescens* Chun et C. C. Huang, which was also the largest among all species in the whole plot (Table S2). In the ridge habitat, the maximum diameter was 135.25 cm for *Castanopsis carlesii* (Hemsl.) Hay., and 130.58 cm in the valley plot also for *C. carlesii* (Table S2). For the entire plot, five species had maximum diameters larger than 100 cm (Table S2): *Altingia chinensis* (Champ.) Oliver ex Hance, *C. nigrescens, Exbucklandia tonkinensis* (Lec.) Steenis, *Cinnamomum validinerve* Hance and *Mytilaria laosensis* Lecomte.

Q3: What are the demographic rates of these native tree species in the different habitat types?

Excluding 10 species without data available for wood density, the majority of species tested had $r < 0.01$(upper CI < 0.01) and g between 0.01 and 0.05 (lower CI $> 0.01$and upper CI < 0.05) in all habitat types (for ridge, slope and valley, respectively, r: 91.3%, 86.3%, 85.0%; g: 58.8%, 60.0%, 55.0% of species; Table S3). For about 90% of the species tested, m was not significantly different from r (Table S3, overlapping CI). Adding r up with g and subtracting m, the resulting net biomass increment rates did not differ significantly from zero for over 90% of the species in the ridge (93.8%), slope (95.0%) and valley (96.3%) habitats (Table S3, zero not included in CI). A total of nine species had significant net biomass increment rates in the three habitat types (Table 1). No species tested had a negative net biomass increment rate.

In the 1000 simulations, the average time for *C. carlesii* in all habitat types and *Engelhardia roxburghiana* Wall in the ridge habitat to reach 30 cm in diameter was shorter than 50 years (Fig. 2). *Elaeocarpus decipiens*, *C. nigrescens*, *Lindera metcalfiana* Allen, *Lithocarpus calophyllus* Chun ex C. C. Huang et Y. T. Chang, and *Morella rubra* Lour. in the ridge habitat, *Cinnamomum austrosinense* H. T. Chang and *L. metcalfiana* in the slope habitat and *M. laosensis* in the valley habitat needed slightly longer time, but were all < 55 years. The lowest T30 could be as short as 30 years for *C. carlesii* in all habitats (Fig. 3), *A. chinensis* in the slope habitat, *Quercus chungii* F. P. Metcalf and *M. rubra* in the ridge habitat in our simulations. The longest time to reach 30 cm in our simulation ranged from 55 to 290 years, depending on species and habitat type. The shortest time to

Table 1 Species with significant net biomass increment rate in at least one topographic habitat

Significant net biomass increment rate		Species
The ridge habitat	Positive	*Elaeocarpus decipiens*, *Xanthophyllum hainanense*, *Ilex rotunda*, *Symplocos wikstroemiifolia*, *Neolitsea phanerophlebia*
	Negative	–
The slope habitat	Positive	*Cryptocarya concinna*, *Nyssa sinensis*, *Ilex rotunda*, *Neolitsea phanerophlebia*
	Negative	–
The valley habitat	Positive	*Cryptocarya concinna*, *Symplocos pseudobarberina*, *Ixonanthes reticulata*
	Negative	–

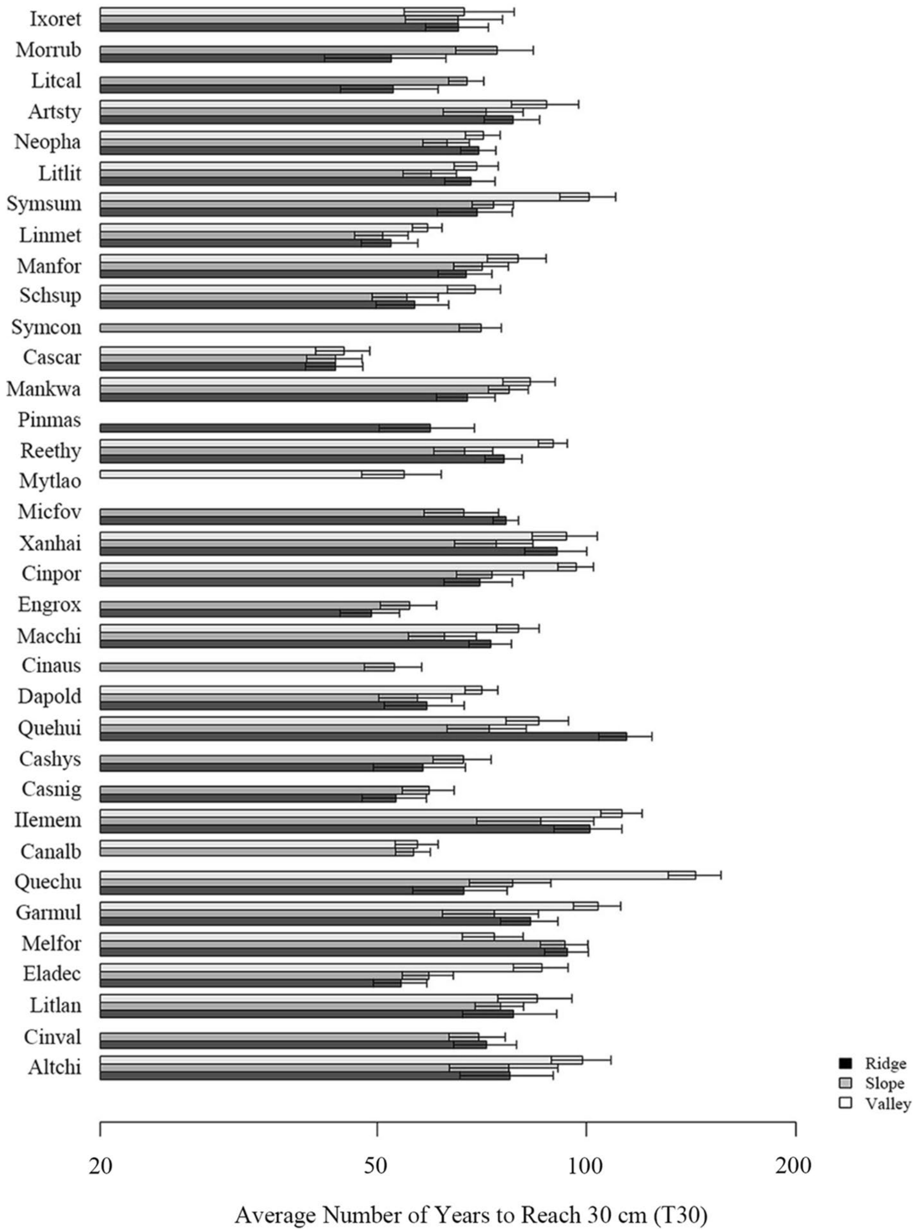


Fig. 2 Simulated mean (± SD) number of years to reach 30 cm DBH for species that reached 30 cm within 50 years in at least one of the 1000 simulations of tree growth in at least one habitat type in the 50-ha plot in Heishiding. Altchi: *Altingia chinensis*; Cinval: *Cinnamomum validinerve*; Litlan: *Litsea lancilimba*; Eladec: *Elaeocarpus decipiens*; Melfor: *Meliosma fordii*; Garmul: *Garcinia multiflora*; Quechu: *Quercus chungii*; Canalb: *Canarium album*; Ilemem: *Ilex memecylifolia*; Casnig: *Castanopsis nigrescens*; Cashys: *Castanopsis hystrix*; Quehui: Quercus *hui*; Dapold: *Daphniphyllum oldhami*; Cinaus: *Cinnamomum austrosinense*; Macchi: *Machilus chinensis*; Engrox: *Engelhardia roxburghiana*; Cinpor: *Cinnamomum porrectum*; Xanhai: *Xanthophyllum hainanense*; Micfov: *Michelia foveolata*; Mytlao: *Mytilaria laosensis*; Reethy: *Reevesia thyrsoidea*; Pinmas: *Pinus massoniana*; Mankwa: *Manglietia kwangtungensis*; Cascar: *Castanopsis carlesii*; Symcon: *Symplocos congesta*; Schsup: *Schima superba*; Manfor: *Manglietia fordiana*; Linmet: *Lindera metcalfiana*; Symsum: *Symplocos sumuntia*; Litlit: *Lithocarpus litseifolius*; Neopha: *Neolitsea phanerophlebia*; Artsty: *Artocarpus styracifolius*; Litcal: *Lithocarpus calophyllus*; Morrub: *Morella rubra*; Ixoret: *Ixonanthes reticulata*

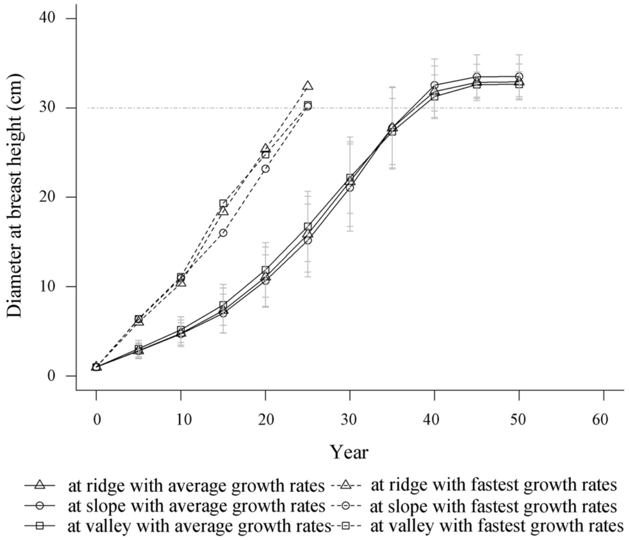


Fig. 3 Mean ± SD simulated growth curves in 1000 simulations for *Castanopsis carlesii* in the three habitat types based on random sampling of actual diameter increments from stems with diameter increments above the 90th percentile of diameter increments of all stems within the corresponding size classes. The curves for the fastest growth rates are the DBH trajectories for the tree that reached 30 cm in the shortest time in 1000 simulations

reach 30 cm in our 1000 simulations was only 71.6% (SD 9.9%) of the average T30.

For species whose T30 were available in all habitat types, a longer time was needed for trees to reach 30 cm in DBH in the valley habitat than the ridge and slope habitats (ridge: $t = 2.042$, $P = 0.045$; slope: $t = 2.9072$, $P = 0.005$; Table S2). No significant difference in T30 was detected between the slope and ridge habitats ($t = -0.833$, $P = 0.408$).

Q4: Are there any native tree species with potential for forestry?

In the ridge and valley habitats, loadings for abundance (ridge: 0.642; valley: 0.663) and maximum diameter (ridge: 0.678; valley: 0.617) on PC1 were positive and large; on PC2, the net biomass increment rate had heavy loadings (ridge: –0.919; valley: –0.883). In the slope habitat, loadings of abundance and net biomass increment rate were relatively large (> 0.5) on PC1, and on PC2, maximum diameter had a heavy loading (0.799). Thus, species in the lower half of the first quadrant and the upper half of the second quadrant were relatively suitable for the selection purpose compared with other species (Fig. 4), such as *A. chinensis* (species 1 in Fig. 4, hereafter listing only the species number), *C. carlesii* (51), *N. phanerophlebia* (73), *Schima superba,* (53), *Ixonanthes reticulata* (88), *Manglietia kwangtungensis* (48) in the ridge habitat, *Schima superba* (53), *Symplocos pseudobarberina* (67), *C. concinna* (34), *N. phanerophlebia* (73), *Litsea lancilimba* (7), *Machilus breviflora* (9) in the slope habitat and *N. phanerophlebia* (73), *Ardisia elegans* (50), *Xanthophyllum hainanense* (37), *Ixonanthes reticulata* (88) and *Cryptocarya chinensis* (27) in the valley habitat.

Discussion

Our study made use of two consecutive censuses of a 50-ha forest plot and found native species that could be valuable for domestication trials for forestry use under different topographic conditions in subtropical China. Our results will inform efforts for conserving species diversity in subtropical China and other areas with similar climatic conditions.

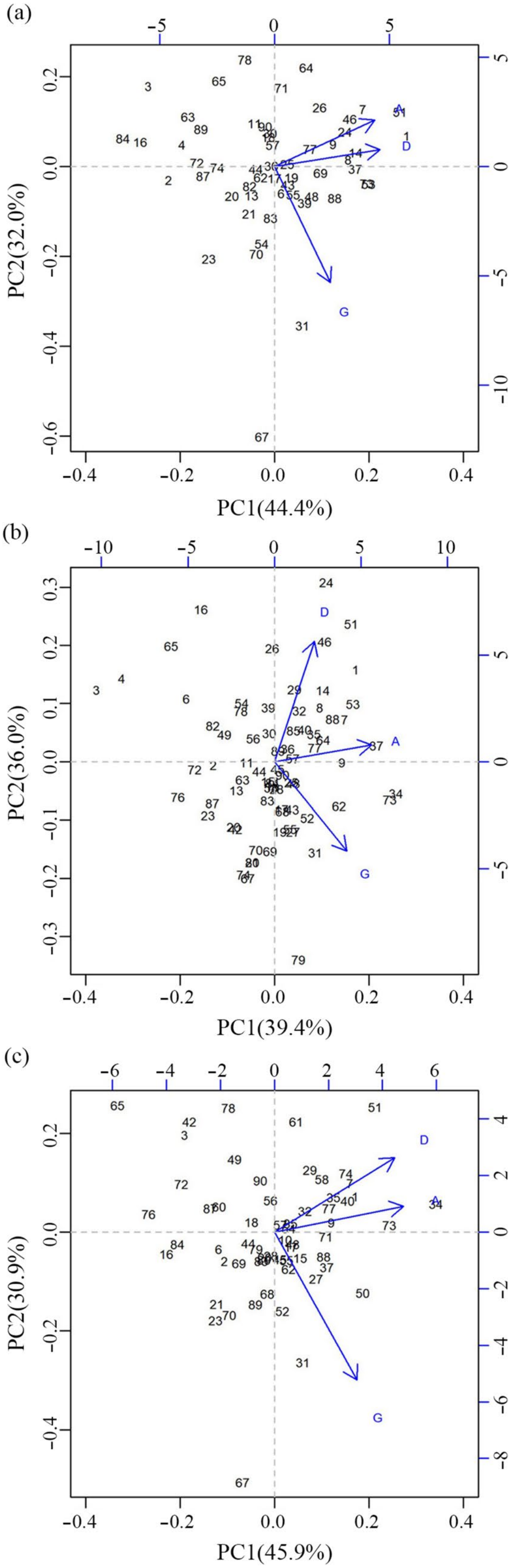
Using the torus translation test to evaluate species' associations with topographic habitats (Harms et al. 2001; Bin et al. 2016; Li et al. 2022), we identified 16 species associated positively with the ridge and the valley habitats, respectively, and nine species with the slope habitats, suggesting that a considerable proportion of species had a preferred habitat, and thus habitat preference needs to be taken into account when establishing plantations.

In natural forests, a high abundance of a species within a habitat is often an indicator of suitability (Harms et al. 2001; Naimi and Araujo 2016; Noce et al. 2017; Ajene et al. 2020) because it is the result of long-term species interactions with the given environments (Harms et al. 2001). In our study, the wide variation in abundance among species in topographic habitats suggests that species differ in their suitability to given habitats, which must also be considered when choosing species for economic use.

Though both of our methods indicated species' habitat preference, the torus translation test compared a species' density in a habitat type with the density in the whole plot while census data for the habitats can be used to compare the abundance of the focal species with those of coexisting species in the plot. As such, a species can be less abundant relative to other species in a habitat but still be positively associated with that habitat.

Because fast-growing species enable rapid economic and ecological returns for forestry and restoration projects (Guo et al. 2016), we assessed growth rates of these native tree species using the data from the two censuses of this plot. Not surprisingly, the native species all grew relatively slowly compared with the exotic tree species. Annual rate of biomass gain due to individual growth of our species centered around 0.02–0.03, regardless of the habitat type. Additionally, in the fastest simulation of our simulation tests, only 21 species reached 30 cm in diameter within 40 years, which is about the harvesting cycle of some plantations (Rondon et al. 2009). However, *Eucalyptus* species only need about 10 years for an economic return (Ouyang et al. 2021). It is important to note that besides species identity, habitat condition, and tree size, which we considered here, many other factors such as climate

Fig. 4 Biplots obtained from principal component analyses of species' abundance (A), maximum diameter at breast height (D), and net biomass increment rate (G) when growing in the ridge **a**, slope,**b** and valley, **c** habitats. Numbers in each panel denote species. 1: *Altingia chinensis*; 2: *Artocarpus hypargyreus*; 3: *Styrax faberi*; 4: *Alniphyllum fortunei*; 6: *Exbucklandia tonkinensis*; 7: *Litsea lancilimba*; 8: *Elaeocarpus decipiens*; 9: *Machilus breviflora*; 10: *Meliosma fordii*; 11: *Garcinia multiflora*; 13: *Ormosia fordiana*; 14: *Quercus chungii*; 15: *Canarium album*; 16: *Diplospora dubia*; 17: *Ilex memecylifolia*; 18: *Ormosia glaberrima*; 19: *Syzygium kwangtungense*; 20: *Beilschmiedia fordii*; 21: *Camellia semiserrata*; 23: *Madhuca hainanensis*; 24: *Castanopsis nigrescens*; 25: *Craibiodendron stellatum*; 26: *Castanopsis hystrix*; 27: *Cryptocarya chinensis*; 28: *Ternstroemia gymnanthera*; 29: *Quercus hui*; 30: *Daphniphyllum oldhami*; 31: *Cinnamomum austrosinense*; 32: *Machilus chinensis*; 34: *Cryptocarya concinna*; 35: *Engelhardia roxburghiana*; 36: *Cinnamomum porrectum*; 37: *Xanthophyllum hainanense*; 39: *Michelia foveolata*; 40: *Mytilaria laosensis*; 42: *Castanopsis fissa*; 43: *Reevesia thyrsoidea*; 44: *Acer tutcheri*; 45: *Castanopsis faberi*; 46: *Pinus massoniana*; 48: *Manglietia kwangtungensis*; 49: *Castanopsis fordii*; 50: *Ardisia elegans*; 51: *Castanopsis carlesii*; 52: *Symplocos congesta*; 53: *Schima superba*; 54: *Machilus litseifolia*; 55: *Manglietia fordiana*; 56: *Choerospondias axillaris*; 57: *Ormosia pachycarpa*; 58: *Lindera metcalfiana*; 60: *Vitex quinata*; 61: *Engelhardia fenzlii*; 62: *Antidesma venosum*; 63: *Photinia prunifolia*; 64: *Lithocarpus litseifolius*; 65: *Castanopsis eyrei;* 67: *Symplocos pseudobarberina*; 68: *Beilschmiedia tsangii*; 69: *Eurya hebeclados*; 70: *Symplocos wikstroemiifolia*; 71: *Distylium racemosum*; 72: *Pentaphylax euryoides*; 73: *Neolitsea phanerophlebia*; 74: *Laurocerasus phaeosticta*; 76: *Helicia cochinchinensis*; 77: *Artocarpus styracifolius*; 78: *Lithocarpus calophyllus*; 79: *Neolitsea chui*; 80: *Schefflera octophylla*; 82: *Morella rubra*; 83: *Olea dioica*; 84: *Rhododendron simsii*; *85: Lithocarpus crassifolius*; 87: *Meliosma rigida*; 88: *Ixonanthes reticulata*; 89: *Meliosma squamulata*; 90: *Quercus neglecta*



and biotic interactions influence the observed growth rate (Peters 2003; Zuidema et al. 2022). We had only considered those factors for which data were available.

The growth rates simulated in our study were chosen from the top 10% fastest observed in this forest. In natural forests, trees are under intensive competition from neighboring plants (Uriarte et al. 2012; Bin et al. 2019), resources are less available than in managed plantations that are fertilized and watered (Samuelson et al. 2001; Uriarte et al. 2012; Bin et al. 2019). The time to reach 30 cm in the fastest simulation was only about 70% of average T30, suggesting that the growth of most individuals of these species was suppressed. Many tree species grow faster in plantations than in natural forests (Lawson 1994; Burns et al. 1996; Samuelson et al. 2001; Dickens et al. 2003; Guo et al. 2016). For example, mean DBH was 40.20 cm and tree height was 19.50 m for a 99-year-old *Parakmeria lotungensis* (Chun et C. Tsoong) Law trees in a natural forest, but 18.30 cm and 16.20 m, respectively, for 29-years old trees in plantations (Lin 2013). *Lindera communis* Hemsl. also grows faster in plantations than in natural forests (Liu 2006). Thus, it is likely that our simulations did not reveal the fastest growth our native tree species can potentially achieve.

These native tree species will likely grow faster when planted in habitats that match their preferences, especially with optimal spacing, thinning, and fertilization (Lawson 1994; Burns et al. 1996; Samuelson et al. 2001; Dickens et al. 2003; Guo et al. 2016). For example, most of our tree species needed longer to reach 30 cm in diameter in the valley habitat than in the slope and ridge habitats. Soil fertility and water availability, in general, increase from ridge to valley habitats, but light availability had an opposite trend (Scholten et al. 2017). Therefore, slower growth rates in the valley might be due to limited light availability in this habitat type. In this case, species that favor low light such as *Ardisia elegans* and *Cryptocarya chinensis* should be prioritized, and species such as *Schima superba* and *Quercus chungii* should be avoided. Thinning can also improve light availability and increase growth rates (Burns et al. 1996; Samuelson et al. 2001).

Temperature, light and moisture availability, and biotic interactions can also differ greatly between natural forests and plantations (Taki et al. 2011). Therefore, domestication and small-scale experiments are essential for selecting the best species for the conditions in forestry and restoration projects.

Besides information from our analytical results, the international timber market also provides information on the economic potential of tree species. In the international market, 1713 species from 108 families were used for commercial timber (Mark et al. 2014), including three species in our study that had maximum DBH ≥ 30: *Engelhardia roxburghiana*, *Cinnamomum porrectum* (Roxb.) Kosterm., and *Vitex quinata* (Lour.) Will. Among them, *Engelhardia roxburghiana* also had a relatively short T30 in our study. About half (48.8%) of the species with maximum DBH ≥ 30 in our study were in genera with at least one commercial timber tree species (Mark et al. 2014), suggesting that a considerable proportion of these species could potentially be used in forestry given that growth rate can be increased under proper management.

Native tree species establish close associations with the local biome during their evolution and are thus especially important for biodiversity conservation (Marianov et al. 2004; Cosyns et al. 2020). With regard to conservation, planting exotic tree species with native tree species may be an alternative to solely planting native species when native species cannot meet the need for wood products (Amazonas et al. 2018). When planted with native tree species, *Eucalyptus* trees grew larger and produced about 75% of the basal area yielded by *Eucalyptus* monocultures even though they accounted for only 50% of the seedlings in the mixtures (Amazonas et al. 2018). In addition, the productivity of four of five plantation species was on average 55% higher when planted in mixtures than in monocultures (Erskine et al. 2006), and mixtures can also increase biodiversity because native tree species are more friendly to the environment than exotic monocultures (Liu et al. 2018; Schuldt et al. 2022). However, exotic tree species, however, are often supplied by nurseries at relatively low prices and with detailed planting techniques that enhance their survival in plantations.

As we mentioned earlier, some native tree species grow slower than the exotics. Their wood can also be very dense. For example, in our study, the wood density of *Syzygium kwangtungense*, *Olea dioica* and *Distylium racemosum* was over 1 g cm^{-3}. Although they are probably suitable for fine furniture and musical instruments and have commercial potential, they are not fast-growers, which was the focus of this study.

Conclusion

In conclusion, based on two complete censuses of a forest dynamics plot, we identified native tree species with a relatively large stature, high abundance and fast growth rate that are worth testing further in domestication trials. If they grow well in these trials, their use in this region and regions with similar climatic conditions will help achieve sustainable forestry goals.

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