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Regional distributions of plant sexual systems in temperate forests and the differential effects of climate change

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Abstract. Variation in plant sexual systems is an important component of biodiversity. However, how the plants of different sexual systems are distributed in landscapes and how habitat conditions, particularly climates, affect the distribution is not well understood. In this study, we investigated the biogeographic distribution of species richness, biomass and productivity of three sexual systems (monoecy, dioecy and hermaphroditism) for 69 tree species in 20 families in the temperate forest of Northeast China and quantified the relative contributions of different environmental factors to these patterns. We also projected the effect of climate change on the distribution of the three sexual systems in 2100. The results showed that the majority of monoecies were originated from temperate zones and had the highest biomass, productivity and distribution in the region. This dominance of monoecies was due to that they were temperate-originated and niche-conserved. The species richness and productivity of hermaphrodites had a similar set of influencing factors as the other two sexual systems. The proportions of species richness, biomass and productivity of monoecious species were predicted to decrease by up to 43.4%, 29.0%, 25.4%, respectively, under future climate change, while the proportions of the other two sexual systems increased. Our study supports the biogeographical conservatism hypothesis under the scenario of no change of climate but predicted that temperate-originated monoecies would yield to other sexual systems under future climate change scenarios. This study contributes to understanding the regional distribution of different sexual systems in temperate forests and shows the necessity of considering geographical origins of plant sexual systems in assessing impacts of climate change on the diversity of forest flora.

Introduction

Species with different sexual systems often show a range of differences in biological traits, such as morphology and ecological traits (Harder and Barrett, 2006; Peng et al., 2014; Renner and Ricklefs, 1995). These differences affect the adaptability of plants with different sexual systems to different environments. For example, hermaphrodite plants are found to be more adaptable to harsh environments due to that their self-compatible traits, which allows establishment even with a single colonizing individual (Peng et al., 2014; Barrett and Harder, 2017; Spigler and Ashman, 2012), while dioecious plants are generally more vulnerable to environmental change given that they often exhibit spatial segregation of male and female plants (Hultine et al., 2016). Different adaptabilities of plant sexual systems to their environments affect their distribution and ecosystem functioning. This can lead to different spatial patterns in species richness, biomass and productivity of different sexual systems. It has also been shown that the different geographical origins of plants could affect these patterns (Buckley et al., 2016; Trethowan et al., 2023).

The importance of geographic origination of global flora has long been noted. For example, the tropical conservatism hypothesizes that the latitudinal diversity gradient in woody angiosperms arises from the fidelity of tropics-originated species to their native ranges (Jiang et al., 2023; Wiens et al., 2010; Wiens and Graham, 2005). Based on this niche conservatism, species tend to grow and survive favorably in the same habitats of their origin (Liu et al., 2022; Peng et al., 2014; Petitpierre et al., 2012; Wiens and Graham, 2005), resulting in sexual systems to dominate their origination region. As a consequence, different forest biomes would have different composition of plant sexual systems (Peng et al., 2014). Previous studies showed that tropical forests usually host a high number of dioecious plants (Réjou-Méchain et al., 2015; Renner and Ricklefs, 1995), while the wind-pollinated temperate forest trees are mostly monoecious (Bawa, 1974). This difference in sexual systems inevitably affects diversity patterns and functioning of forest ecosystems, including forest productivity and biomass.

The geographic variation in plant sexual systems also suggests that environmental conditions could play an important role in determining their varied distributions. It has been shown that monoecy are in general more associated with cooler temperatures, while hermaphrodites favor warmer and drier regions (Wang et al., 2021). The proportion of dioecious plants increases with humidity, whereas the proportion of hermaphrodites decreases with humidity (Wang et al., 2020). Large-scale studies show that both temperature and precipitation are influential predictors of the geographical patterns of sexual systems (Wang et al., 2021; Zhang et al., 2024). In addition to climate factors, soil and topography factors, e.g., soil moisture, can also affect the distribution of plant sexual systems (Van Etten and Chang, 2009). Further to that, it is also observed that plants of different sexual systems could respond differently to climate change, evidenced by the rapid migration of dioecious plants to higher altitudes (Etterson and Mazer, 2016). Despite of these observations, it remains poorly understood how environments may affect the spatial distributions of the diversity, productivity and biomass of different sexual systems at the regional scale.

Compared to tropical and boreal forests, temperate forests are of high heterogeneous environments and varied climates and often see a mixed flora of various origination (Qiao et al., 2023; Qiu et al., 2011). Temperate plants typically show seasonal flowering phenology and special fruiting patterns (Buonaiuto, Morales Castilla, and Wolkovich, 2021; Smith-Ramirez and Armesto, 1994). Previous studies have shown that monoecy, dioecy and hermaphrodism are well represented in temperate forests (Wang et al., 2020; Wang et al., 2021; Zhang et al., 2024). Therefore, investigating the spatial distribution of plant sexual systems in temperate regions could offer insights into the mechanisms underlying the biogeography of floral diversity and the role of sexual systems in ecosystem functioning.

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In this study, we aimed to analyze the distribution pattern of plants of different sexual systems and quantify the response of different sexual systems to environmental changes in the temperate forest of northeastern China. We compiled a set of detailed data on the distribution of 69 woody plant species consisting of three sexual systems (hermaphroditism, monoecy and dioecy) to analyze the distributions of their diversity, biomass and productivity and their underlying drivers in the region. Specifically, we addressed three questions: (1) Are there differences in the spatial distribution of plant species richness, biomass and productivity of the three sexual systems? (2) What factors may affect their spatial distributions and whether the factors affecting the diversity of sexual systems also affect their productivity and biomass? (3) How different sexual systems respond to future climate change? Does the niche conservatism hypothesis predict the future distribution of the sexual systems under projected climate changes?

Methods

2.1 Study area

Our study sites are located in northeastern China, comprising three provinces and an autonomous region with latitude and longitude ranging from 39°42′ to 53°19′ N and from 119°48′ to 134°01′ E. The region is characterized by a temperate continental climate and highly diverse temperate forests (Qian and Ricklefs, 2000), accounting for approximately 30% of forest land in China. The forests are mostly distributed over three forest regions, namely the Greater Khingan, the Lesser Khingan, and the Changbai. The native forest types include cold-temperate mixed broad-leaved deciduous forest, conifer-dominated forest, and cold-temperate coniferous forest. This area represents a transition zone between boreal and warm-temperate vegetation, and is sensitive to climatic change (Vetter et al., 2005). In 2017, a network of forest inventory plots, the Northeastern China Forest Inventory Network (FIN), was established (Fig. 1). The FIN consists of 456 Whittaker's 0.1 ha permanent circular plots (each with a radius of 17.85 m) and the distance between two neighboring plots ranging from 30-60 km (Fig. 1). In total, we recorded 36132 trees with diameter at breast height (DBH) ≥ 5 cm and 69 species. In each plot, increment cores for all woody stems with DBH ≥ 5 cm were collected using an increment borer with an auger diameter of 5.15 mm. Two cores were taken for each tree. In total, 72264 cores were sampled. Therefore, the DBH of each tree in 2012 and 2017 is available and the increment in DBH over a five-year period was measured. Each tree was georeferenced, and recorded by species name.

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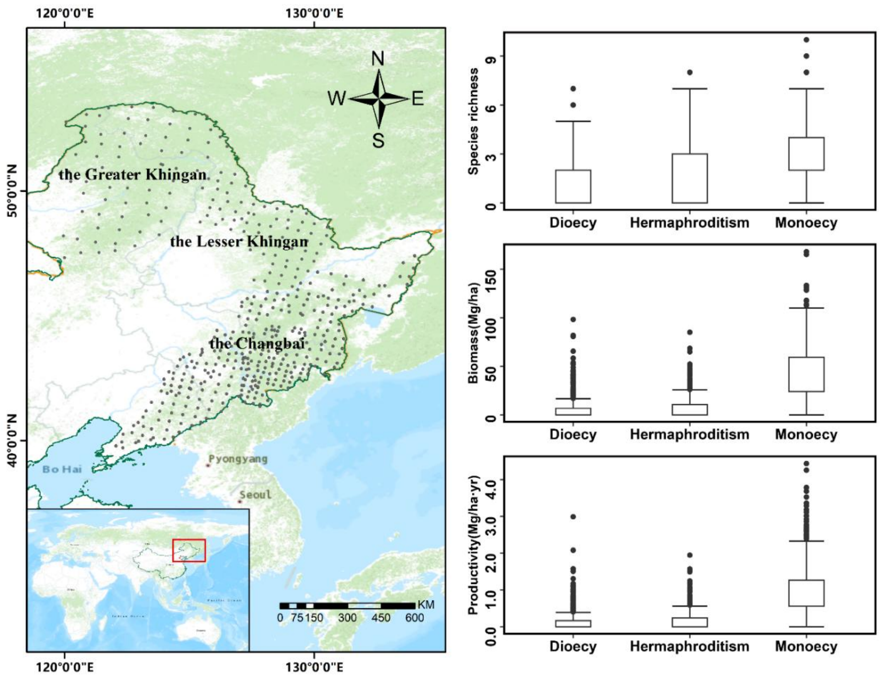

Fig. 1 Geographic distribution of the 456 forest plots in northeastern China. The three mountain ranges in the region are marked in the map: the Greater Khingan; the Lesser Khingan; the Changbai. The panels on the right column show the boxplots for woody plant species richness, biomass and productivity of the three sexual systems.

2.2 Sexual systems

We compiled the sexual systems of 69 species in 20 woody plant families in the FIN network, based on the *Flora Republicae Popularis Sinicae* (http://www.iplant.cn/) (see Table S1). According to different sexual phenotypes (Cardoso et al., 2018), we classified the species into the following three sexual systems: (1) *hermaphroditic* species with both functional stamens and pistils in the same flower, (2) *monoecious* species with both staminate flowers and flowers that lack stamens occurring in the same individual but not in the same flower, and (3) *dioecious* species with male reproductive organs in one individual and female in another. The category of dioecy includes dioecious and androdioecious species, whereas monoecy includes monoecious, and andromonoecious species. In the meantime, in order to study the origin of the woody plants of different sexual systems in this area, we followed the classification system of floristic geographic origination proposed in *The Areal Types of the World Families of Seed Plants* (Wu 2003) and a recent reference (Huang et al., 2025). We divided the 69 species of the three sexual systems into five major distributional types at the family level: (1) Cosmopolitan, (2) Pantropic, (3) Tropical Asia and tropical America disjuncted, (4) North temperate, and (5) South and north temperate disjuncted (see Table 1).

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Table 1 The geographic origination and distribution of the three sexual systems of 20 families of this study.

Geographic origination/distribution	Number of families		
	Hermaphroditism (%)	Monoecy (%)	Dioecy (%)
Cosmopolitan	6 (60.0)	0	5 (62.5)
Pantropic	2 (20.0)	1 (20.0)	3 (37.5)
Tropical Asia and tropical America disjunction	1 (10.0)	0	0
North temperate	1 (10.0)	3 (60.0)	0
South and north temperate disjunction	0	1 (20.0)	0
Total	10 (100)	5 (100)	8 (100)

2.3 Species richness, biomass and productivity

Based on the data on the species' breeding systems and increment cores, we calculated species richness (*SR*), aboveground woody biomass density (*W*) and aboveground woody biomass productivity (*P*) for hermaphrodite, monoecy and dioecy, respectively, within each plot. *W* and *P* are calculated as following.

$$W = \frac{\sum_{i=1}^{N} AGB_i}{A}, \quad (1)$$

where AGB_i is the aboveground biomass for tree *i*. AGB_i was calculated by multiplying stem volumes, estimated using region-specific stem volume equations, by the wood density of each corresponding tree species (Qiao et al., 2021; Wu et al., 2019). *N* is the number of trees with DBH ≥ 5 cm in a plot and *A* is the plot area (i.e., 0.1 ha).

$$AGBP_i = \frac{W_i}{T}, \quad (2)$$

where $AGBP_i$ is the aboveground biomass productivity per tree and W_i is the change of aboveground biomass density of the tree during time *T* years (2013-2017 in this study, leading to *T*=4 years). The productivity of a plot is:

$$P = \sum_{i=1}^{N} AGBP_i. \quad (3)$$

2.4 Environmental data

In addition to species richness, biomass and productivity, we also compiled 9 environmental variables to model the effects of climate on the biogeographical patterns in species richness, biomass and productivity of the sexual systems. These 9 variables including 3 climatic variables (Fick and Hijmans, 2017), 4 soil variables (https://soilgrids.org/; FAO, 2012) and 2 topographic variables (elevation and slope) (see supplemental information in Table S2). The topographic variables were derived from our own field data. The soil data were then interpolated to locations of our 456 plots using ArcMap 10.8 (ESRI, 2019). We have also tested the collinearity of all variables using VIF<5 criterion.

To assess the effect of future climate change on the distribution of different sexual systems under two emission scenarios (SSP245 and SSP585) in 2100, we used the climate data under the Coupled Model Inter-comparison Project phase 6 (CMIP6) to represent future climate change (Eyring et al., 2016). CMIP6 provides data on regional climate under future scenarios of climate change. The two scenarios (SSP245 and SSP585) project future climates under two basic pathways of sustainable

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development. SSP245 represents a medium emission scenario with a nominal 4.5W/m^2 radiative forcing level by 2100 and SSP585 represents the highest fossil-fuel emission scenario assumed for the 21st century. We used the ordinary kriging methods in ARCGIS 10.8 to interpolate future climate data (CMIP6) to the 1 km grid. In order to reduce the uncertainty caused by the model, for each scenario we selected three available models: CanESM5, MIROC6 and NESM3, and took an average value of the projected climate of these models for year 2100 for each spatial grid point. We then used the average projected climate to predict species richness, biomass and productivity of the three sexual systems in northeastern China in 2100.

To test our hypothesis of phylogenetic niche conservatism in species' environmental niches, we calculated Pagel's λ (Pagel 1999) of all environmental variables using the R package *phytools* (see Table S3 and Fig. S3).

2.5 Random forest model calibration and evaluation

In order to predict the future species richness, biomass and productivity under the two scenarios of SSP245 and SSP585, we chose the random forest model to model and predict the distribution of the species richness, biomass and productivity of the three sexual systems. Random forest model performs better than other machine learning methods in predicting distribution and can overcome variable collinearity problem that is often a concern in traditional linear regression models (Luo et al., 2020). To facilitate model fitting, the three dependent variables: species richness (*SR*), aboveground woody biomass density (*W*) and aboveground woody biomass productivity (*P*) were log(x+1) transformed in the modeling.

To calibrate the models, each of them was trained using a subset of data randomly sampled 90% from the full dataset. The robustness of the random forest models was assessed using 20 iterations of cross-validation. The performance of the calibrated RF algorithms was evaluated using the remaining 10% data using three measures: coefficient of determination (R^2), root mean square error (*RMSE*) and mean absolute error (*MAE*). For random forest model, the parameters were set as follows: *ntree* = 1500, *mtry* = 3, *nodesize* = 3. These parameter values are set based on prior knowledge and preliminary experiments. The averaged R^2, *RMSE* and *MAE* were used to evaluate the performance of the method (Fig. S1).

The relative importance of the variables for predicting the three sexual systems were assessed based on the increased mean error of the random forest algorithm. Spearman rank coefficients were calculated to assess the strength of correlation (and consistence) between the variables responsible for the distribution of different sexual systems. This analysis answers Question (2) of our objectives: whether the factors affecting the diversity of sexual systems also affect their productivity and biomass?

Because spatial autocorrelation can bias the estimation of the random forest models, thus their predictions, we used Moran's I to test if there was autocorrelation in the residuals of the trained random forests models (see Fig. S4-S6).

2.6 Interpolation and mapping

To map the distributions of the current (2017) and future (2100 under SSP245 and SSP585) species richness, biomass and

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productivity of the three sexual systems for the region of northeast China, we divided the area into a grid of 1 km pixels and assumed each pixel represented a relatively homogeneous landscape. From the 456 FIN sample plots, we used the best-performed random forest model and future climate data obtained from CMIP6 to estimate and map the current (2017) and predict the future (2100) distributions of species richness, biomass and productivity for at 1 km pixel resolution. In order to compare the dominance of different sexual systems, we calculated the mean proportions of species richness of hermaphroditic, monoecious and dioecious species across 456 plots, as well as the mean proportions of biomass and productivity (Fig. 2). To compare the future change of each sexual system, we compared its current (2017) and future (SSP245 and SSP585) proportions across the same 456 plots using the Wilcoxon signed-rank test (Table S4).

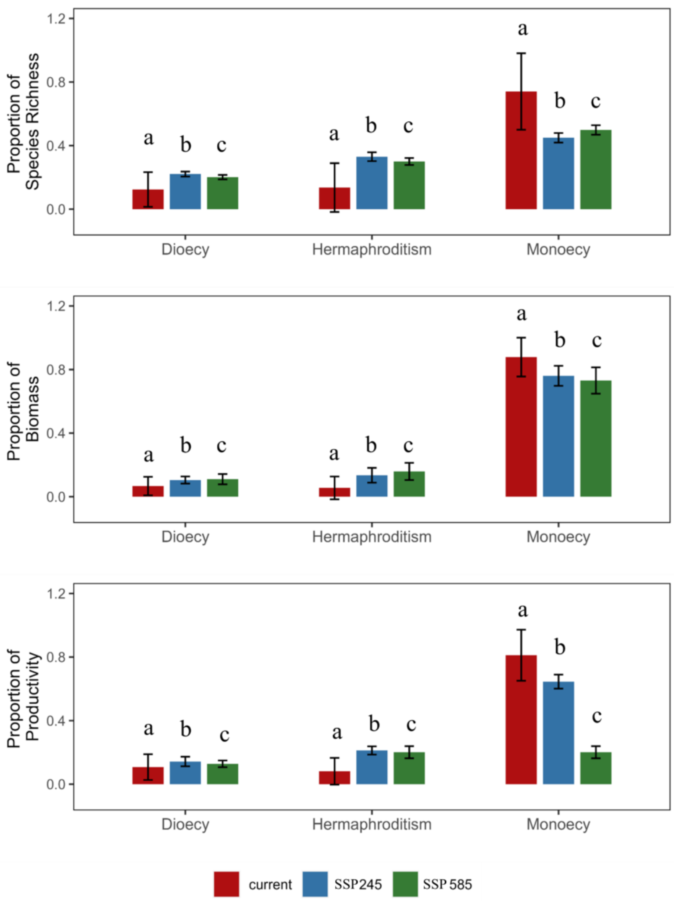

Fig. 2 Bar plots of current and future (2100) mean proportions of species richness, biomass and productivity of hermaphroditic, monoecious and dioecious species across 456 plots of the temperate forest of northeastern China (error bars indicate the standard deviation of 456 plots). SSP245 and SSP585 represent the projected climates scenarios (see Methods of the main text). Different lowercase letters on bars indicate significant differences ($P < 0.001$) in species richness, biomass and productivity of the three sexual systems.

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Results

3.1 Biogeographic origination of different sexual systems in northeastern China

Following the classification of Wu et al. (2003), results in Table 1 show the 69 species of the three sexual systems had a diverse biogeographic origination, with the majority of monoecies (80.0%) originated from temperate region. More than half of the hermaphrodites (60.0%) belonged to the Cosmopolitan type, followed by 20.0% belonging to the Pantropic type. 62.5% of dioecies belonged to cosmopolitan and nearly 40% of dioecies originated from the Pantropic regions (Table 1).

Our results also show that significant phylogenetic signal was observed in the environmental variables to which species adapted (see Table S3). For example, for PDQ, $\lambda = 0.879$ ($p = 0.0012$), and for MAT, $\lambda = 0.690$ ($p = 0.0012$).

3.2 Regional distributions of species richness, biomass and productivity

Monoecious plants dominated the region in species richness, biomass and productivity (Fig. 2 and 3). Hermaphrodites and dioecies were mainly concentrated in the Changbai region locating in the southeastern part of the region (Fig. 3). Under both SSP245 and SSP585 scenarios, all three sexual systems show an overall northward shift in distribution in the future (2100) (Fig. 4 and Fig. S2). The Wilcoxon test showed the proportion of species richness, biomass, and productivity of monoecious plants would decrease in the future (p<0.001), while the proportions of the other two sexual systems would increase (p<0.001) (Fig. 2).

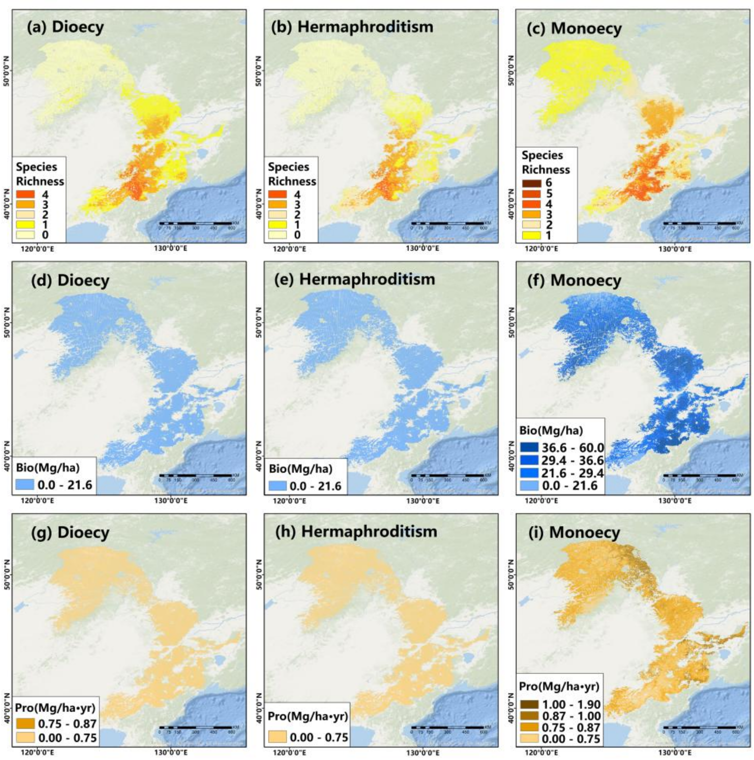

Fig. 3 Current distributions of species richness, biomass and productivity of hermaphrodites, monoecies and dioecies in the forested regions of northeastern China. (For biomass and productivity maps, we divided the biomass and productivity of monoecy into four classes using the default breakpoints of ArcGIS and forced other two systems to follow the same classes of monoecy; this same map scale applies to Fig. 4 and Fig. S2.)

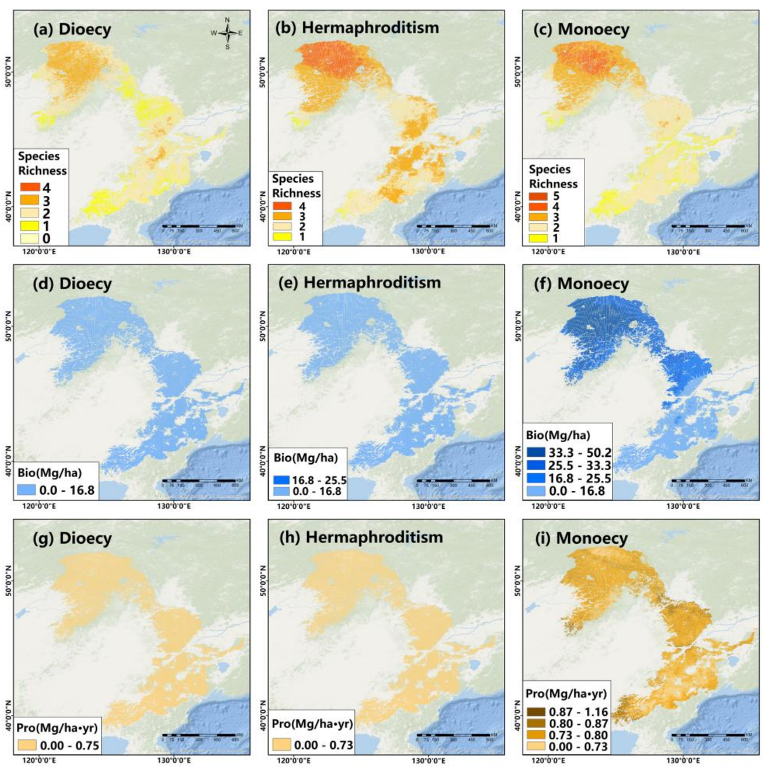

Fig. 4 Future (2100) distributions of species richness, biomass and productivity of hermaphrodites, monoecies and dioecies in the forested regions of northeastern China under SSP245 scenario.

3.3 The drivers of species richness, biomass and productivity

For hermaphrodites, the environmental factors driving species richness, biomass and productivity were highly correlated (p<0.01), suggesting that drivers that influence species richness of hermaphroditism also influence its biomass and productivity. Of these factors, MAT was most important for hermaphroditic plants' species richness, biomass and productivity (see Table S5 for more information). For monoecies, species richness and biomass were not significantly correlated with productivity (Fig. 6), neither was the correlation between biomass and productivity of dioecy (ρ=0.67; Fig. 6).

Spearman's rank correlations showed species richness of hermaphroditism and the other two sexual systems shared a highly correlated, common set of environmental variables (Fig. 6), suggesting that factors affecting hermaphroditic richness also affected the richness of other two, and the species richness of the three sexual systems was mainly driven by climate

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variables of temperature and precipitation. All variables except SOIL significantly affected the species richness of the three sexual systems (Fig. 5). Similarly, the productivity of the monoecy and dioecy also shared a highly correlated set of environmental variables.

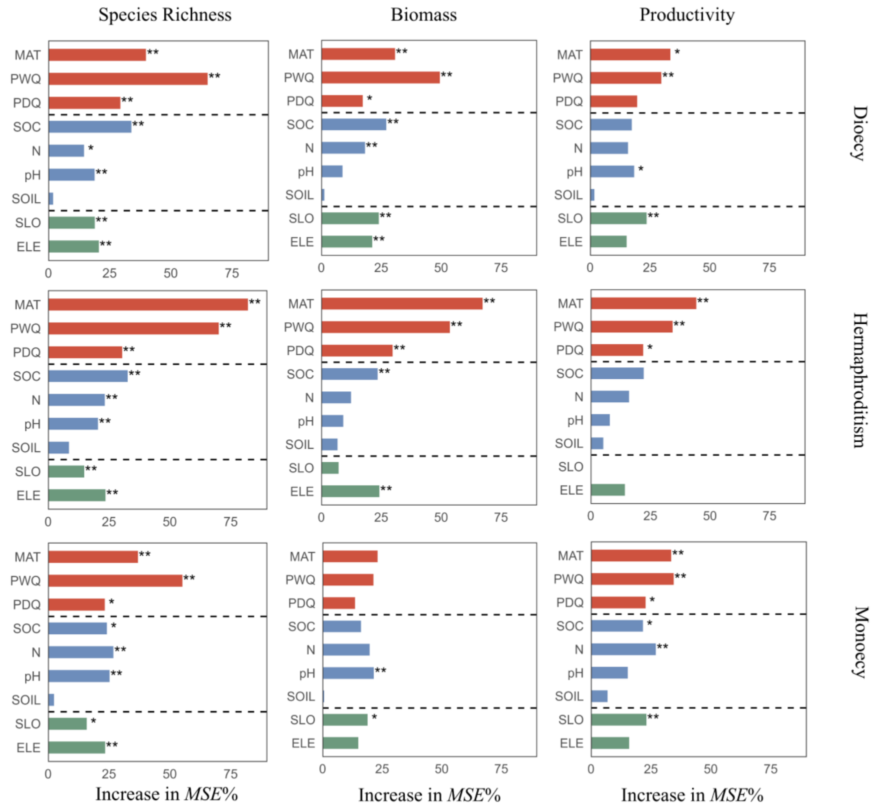

Fig. 5 Relative importance of the variables predicting the three sexual systems determined by random forest algorithm. The variables were ranked by their contributions to increasing the mean square error of the random forest classification. The variables are: MAT (annual mean temperature), PWQ (precipitation of wettest quarter), PDQ (precipitation of driest quarter), SOC (soil organic carbon), N (nitrogen), pH (water pH), SOIL (soil depth), ELE (elevation), SLO (slope). See Table S2 for the full descriptions of all variables. The red bars represent climate variables, the blue bars soil, and the green bars topography.

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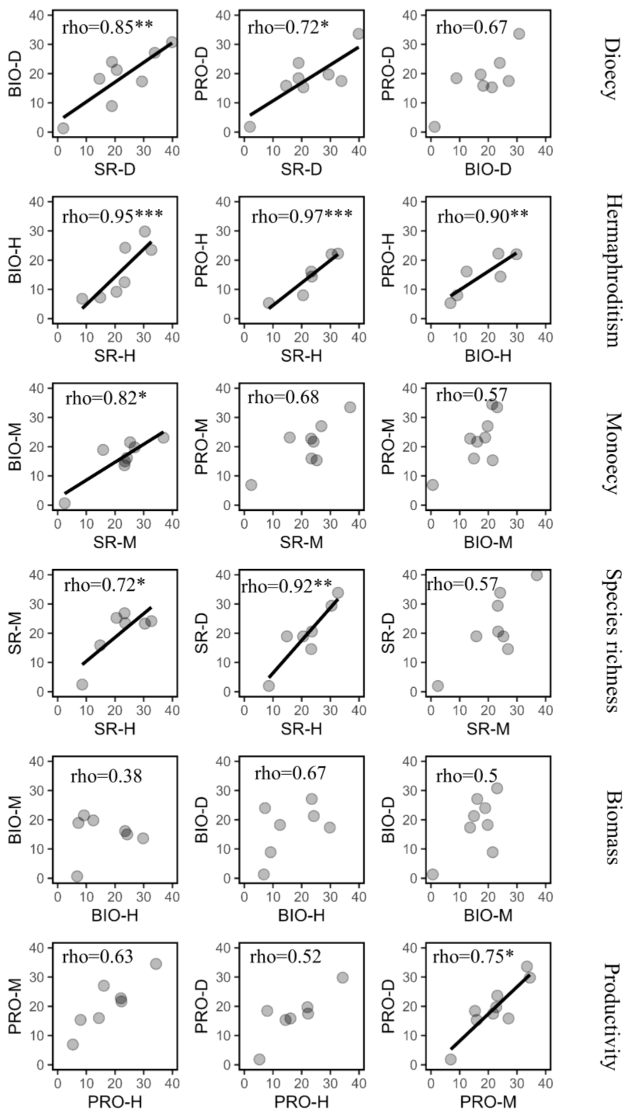

Fig. 6 Scatter plot showing the correlation of variable importance, measured by the increase in *MSE* (%) of the RF algorithm, between different sexual systems of the same variable and comparison between different variables of the same sexual system. Spearman's correlation coefficient, rho, is presented. The notations are: SR = species richness, BIO = biomass, PRO = productivity, H = hermaphroditism, M = monoecy, and D = dioecy.

Discussion

The documented dominance of temperate-originated monoecious species in our study supports the biogeographical conservatism hypothesis, highlighting the role of evolutionary history in shaping community structure. However, under future climate change, the dominance of monoecious species was predicted to decrease, challenging the predictability of the

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hypothesis under rapid environmental shifts. The variations in the environmental factors among sexual systems reveal the nuanced differences of different reproductive systems in response to environmental changes. These results underscore that sexual systems are important for understanding and predicting the impact of global change on forest diversity and dynamics.

4.1 Current distributions of species richness, biomass and productivity of different sexual systems

Our finding that the proportion of monoecy was higher in the region than that of dioecy and hermaphrodite is consistent with previous studies that show monoecious species are more common in temperate forests than other sexual systems (Renner and Ricklefs, 1995; Chen and Li, 2008). According to the hypothesis of niche conservatism, climate prevents temperate-originated monoecies from migrating to other regions (Pyron and Burbrink, 2009; Wiens et al., 2010; Wiens and Donoghue, 2004). These species are best adapted to temperate climate and their distributions are mostly restricted to the temperate zone as our study has shown. Besides, the dominance of sexual systems is also closely related to their adaptation to the region. For example, hermaphroditic plants dominate temperate forests in Europe (Smith et al., 2020), while monoecious plants dominate temperate forests in northeastern China. This may be because European temperate forests are affected by a maritime climate with more even precipitation, which is conducive to self-pollination of hermaphroditic plants. In contrast, northeastern China's temperate forests have cold and dry winters, and anemophilous pollination of monoecious conifers is more adaptable to this environment.

For the three sexual systems, their diversity, biomass and productivity are all high in the Changbai region, the southeastern part of the study area (Fig. 3), where the higher precipitation and warmer temperature are favorable to forest growth, as also observed by others (Luo et al., 2020; Tan et al., 2007). For monoecy, their biomass and productivity also dominate the Greater Khingan (Fig. 3f and Fig. 3i) where the climate is cold with little precipitation and the forest is conifers dominated (Tan et al., 2007). Conifers are typically single-stemmed, evergreen monoecious trees (Gernandt et al., 2011; Neale and Wheeler, 2019). The conifer-dominated forest is responsible for the high biomass of monoecious plants in the Greater Khingan, although the diversity in this region is not as high as in the Changbai region (Fig. 3 b-c).

4.2 The environmental factors driving the distributions of different sexual systems

For hermaphroditism, the environmental factors driving species richness, biomass and productivity are highly correlated (Fig. 6). This suggests factors influencing species richness of hermaphrodites also influence their biomass and productivity, and vice versa. Of the factors affecting hermaphrodites, MAT stands out to be the most important, followed by precipitation-related variables (PWQ and PDQ; Fig. 5). This result is consistent to some studies showing that climate factors (e.g., MAP and MAT) that affect species richness also affect biomass and productivity (Chen et al., 2018; Chen et al., 2023; Liu et al., 2022).

But for the other two sexual systems, the factors driving their diversity, biomass and productivity were not as closely correlated as for hermaphrodites (Fig. 6). This inconsistence between monoecious and dioecious species could be driven by a number of reasons. First, different from hermaphrodites, the male and female sex organs of both monoecious and dioecious

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plants are separated to a varied degree (male and female flowers/cones separated on the same plant for monoecy, and separate on distinct individuals for dioecy). These sex segregations may lead to certain physiological and morphological specialization of each sex and result in sex-specific adaptations to different microhabitats (Harder and Barrett, 2006; Hultine et al., 2016; Van Etten and Chang, 2009). For instance, in dioecious species, females often incur higher reproductive costs through fruiting and seed production, at the expense of their growth and biomass accumulation. Males, focused on pollen production, invest heavily during flowering. Consequently, the alternating growth patterns dissociate aggregate biomass from instantaneous productivity, thereby decoupling population productivity from biomass (Hultine et al., 2016; Obeso, 2002).

Second, demographic processes might be disrupted by habitat fragmentation. Most monoecious species in our study, such as Betulaceae, Fagaceae, Aceraceae and Juglandaceae, are self-incompatible. Although Pinaceae species are generally self-compatible, they rely predominantly on wind pollination (Williams, 2007). Therefore, the spatial segregation of the sexes in monoecy requires effective pollen transfer among individuals. If habitat fragmentation or other barriers of dispersal can differentially affect the establishment or survival of one sex than the other (Ghazoul, 2005), this can limit reproductive success and productivity without immediately reducing species richness at the plot scale. Therefore, unlike hermaphrodites, the spatial segregation of monoecious and dioecious plants could allow their diversity, biomass and productivity to respond differently to environmental factors.

Spearman's rank correlations reveal that factors affecting species richness of hermaphroditism and the other two sexual systems were highly correlated (Fig. 6), indicating the diversity of hermaphroditism and the other two sexual systems shared a similar set of determining factors. Three climatic factors including MAT, PWQ and PDQ significantly affected the species richness of the three systems (Fig. 5). Our results are consistent with other studies showing climates are the most important factors in determining woody-plant species richness in China (Wang et al., 2011; Wang et al., 2012), particularly in northeast China (Wang et al., 2009). Together with temperature, we found that precipitation factors are among the most important factors in determining species richness of the three sexual systems, thus supporting the energy hypothesis (Currie et al., 2004; Hawkins et al., 2003). Climate is clearly more important than topographic and soil variables in modeling regional distribution of species diversity of different sexual systems. Similarly, monoecy and dioecy also share a set of common factors determining their productivities (Fig. 5 and 6), although the strength was more varied. For example, the productivity of dioecious plants showed relatively weak environmental determination compared to monoecy (Fig. 5), suggesting that dioecious plants be less sensitive to changes in environmental conditions. This is because that at the population level, environmental factors may have different effects on female and male individuals, thus adjusting the population sex ratio, thereby helping dioecy to adapt to climatic changes (Etterson et al., 2016; Moutouama et al., 2025).

4.3 Future distributions of species richness, biomass and productivity of different sexual systems

Despite that the projected future distributions of the three sexual systems show an overall increase in the north and a decrease

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in the south (Fig. 4), a main result of our study is that the proportion of monoecious species in diversity, biomass and productivity is predicted to decrease under future climate change, while the proportions of the other two sexual systems increase (Fig. 2). Most monoecious species in our study area were originated from the northern temperate zone and are presumably best adapted to the temperate environment (Liu et al., 2022; Petitpierre et al., 2012). Under the niche conservatism hypothesis, the monoecious plants are unlikely able to track climate change and adapt to new environments (Peterson et al., 1999; Wiens et al., 2010; Wiens and Graham, 2005). Therefore, future climate change will make the region less suitable for monoecious species, upsetting the niche conservatism, which leads to a decline in species diversity and productivity of monoecious plants in the region. In contrast, hermaphrodites and dioecious plants are predicted to increase their richness, biomass and productivity in 2100 (Fig. 2 and 4). These increases are due to the fact that both hermaphrodite and dioicous plants are predominantly widespread and pantropical with broader ecological niches that are flexible to adapt to changing environments (Sheth et al., 2020; Slatyer et al., 2013). These projected future distributions confirm that species' geographical origination can influence their distribution and adaptation to the future environments (Dupin and Smith, 2019; Wang et al., 2020).

In summary, our study found that the forests of northeast China are dominated by temperate-originated monoecious species in diversity, biomass and productivity, supporting the biogeographical conservatism hypothesis. However, this conservatism hypothesis breaks down under future climate change, as the dominance of monoecious species is predicted to reduce, while the importance of the other two sexual systems increases under climate change scenarios. The distributions of species richness, biomass and productivity of hermaphrodites showed a highly correlated set of environmental variables, while monoecious and dioecious plants shared weaker correlated environmental factors, likely due to the separation of male and female flowers/cones of the latter two groups. Here, we would like to note that our study does not consider species dispersal, nor human-disturbance factors, which could affect the distributions of different groups of species. Nevertheless, the overall finding is that all the three sexual systems share a good degree of common environmental factors influencing the distributions of their diversity and productivity. Our study suggests the necessity to consider sexual systems and their geographical origination in studying forest biodiversity and ecosystem functioning and the potentials of species of different reproductive systems in adapting to the change of future environments.

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Data availability

The data that support the findings of this study can be found:

http://datadryad.org/share/LINK_NOT_FOR_PUBLICATION/3UkdQYUR719GoqzO1ZMnkr0s4KEfbN3fpU_wKLf-21s

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Competing Interests

The authors have no competing interests to declare.

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