The role of breeding system in community dynamics: Growth and mortality in forests of different successional stages

Yunyun Wang1,2,3 | Robert P. Freckleton2 | Bojian Wang1,4 | Xu Kuang5 | Zuoqiang Yuan1 | Fei Lin1 | Ji Ye1 | Xugao Wang1 | Zhanqing Hao1

Abstract

Plant sexual systems appear to play an important role in community assembly: Dioecious species are found to tend to have a higher propensity to colonize communities in early successional stages. Here, we test two demographic hypotheses to explain this pattern in temperate forests. First, we test demographic differences between hermaphrodite and dioecious species in stressful younger successional stages: Previous theory predicts that hermaphrodite seed production is more harmed in stressful environments than that of dioecious populations leading to an advantage for females of dioecious species. Second, in primary forest, we hypothesized that dioecious species would show demographic advantage over monomorphic ones. We used data from two temperate forest plots in Northeast China surveyed over 10 years to compare the rates of growth and mortality of tree species with contrasting breeding systems in both secondary and primary forests. We assessed the effect of breeding system on the growth-mortality trade-off, while controlling for other traits usually considered as correlates of growth and mortality rates. We show that in the secondary forest, dioecious species showed weak advantage in demographic rates compared with monomorphic species; dioecious species showed considerably both lower relative growth and mortality rates compared to the hermaphrodites in the primary forest over 10 years, consistent with a priori predictions. Hermaphrodites showed strong growth-mortality trade-offs across forest stages, even when possibly confounding factors had been accounted for. These results suggest that sexual system influences community succession and assembly by acting on the rates of growth and mortality, and the trade-off between them. As vegetation develops, the demographic differences between breeding systems are much larger. Our results demonstrate the association between breeding system, succession, and community assembly and that this relationship is succession-stage dependent. Our findings support the suggestion that the demographic advantage of dioecious species facilitates the coexistence of sexual systems in primary forest.

KEYWORDS
breeding system, demographic rate, forest succession, growth rate, mortality rate, temperate forest
Sexual systems are key determinants of the ecological and evolutionary dynamics of plant populations (Barrett & Harder 1996; Charlesworth, 2006) and their links to the succession and assembly of plant communities have gradually become the focus of researchers recently (Queenborough et al., 2009; Sinclair, Korte, & Freeman, 2013; Réjou-Méchain & Cheptou, 2015; Bruinjng et al., 2017). In an ultimate manner, the dynamics of plant communities are driven by plant demographic rates (growth and mortality; Pacala et al., 1996; Rees, Condit, Crawley, Pacala, & Tilman, 2001; Silvertown, 2004). Differences in these rates between species are major determinants of ecological succession (Schneider, Ashton, Montagnini, & Milan, 2014) and stand structure (Harper, 1977; Seifert, 2014; Semwal, Nautiyal, Maikhuri, Rao, & Saxena, 2013). In terms of sexual system, it has been found that the dioecious species tend to have a higher propensity (proportion of dioecious species or individuals) to colonize communities in early successional stages (temperate in Sinclair et al., 2013; tropical in Réjou-Méchain & Cheptou, 2015), however, the drivers generating this pattern remain unclear. Thus, there is a need to understand how breeding systems drive demographic rates across communities at different stages of succession.

An evolutionary-driven association between dioecy and colonization ability has been proposed to be a potential advantage of dioecy over cosexual breeding systems in young successional areas, which are typically characterized by stressful conditions (Réjou-Méchain & Cheptou, 2015; Sinclair et al., 2013). Young successional forest stands which have been subject to logging, fire or other disturbance, are usually drier, have higher insolation, and are hotter, because early plant communities have small stature, offer little cover, have small basal area and a small leaf area index (Alvarez-Añorve, Quesada, Sánchez-Azofeifa, Avila-Cabadilla, & Gamon, 2012; Lebrija-Trejos, Meave, Poorter, Pérez-García, & Bongers, 2010). That is, under stressful conditions, hermaphroditic seed production may be more impeded than the female seed production of dioecious populations, leading to a demographic advantage of females over hermaphrodites (Ashman, 2006; Costich, 1995; Litrico, Pailler, & Thompson, 2005). This hypothesis has been often tested in gynodioecious populations (Ashman, 2006), but community-level studies are lacking; If this hypothesis is correct then at the community level, we predict dioecious species should have an advantage in demographic performance (in terms of growth and survival) over monomorphic species in the earlier successional stages.

As succession proceeds, plants from late successional stages tend to be longer-lived and more competitive (Bazzaz 1979; Prach et al. 1997; Garnier et al., 2004; Vile et al. 2006). In stable primary forest, theoretical models suggest that dioecious seedlings tend to be more competitive than cosexual ones and that this benefits the persistence of dioecy (Heilbuth et al. 2001). This is because dioecious species face relatively more intense density-dependent recruitment of seedlings: only females produce seeds and hence seeds of dioecious species are more spatially clumped (Heilbuth, Ilves, & Otto 2001). Moreover, Charlesworth and Charlesworth (1978a, 1978b) have suggested that dioecious species are good competitors owing to the increased genetic variability that results from outcrossing. Dioecy is also found to be correlated with longevity (the proxy being woody growth; Renner & Ricklefs, 1995; James & Ramírez, 1999; Vamosi, Otto, & Barrett, 2003), which can increase the probability of multiple mating over time, and therefore increasing the opportunity of successful reproduction (James & Ramírez, 1999). At the metapopulation level, it has been found that population turnover was higher in hermaphroditic compared to dimorphic populations (Dorken, Freckleton, & Pannell, 2017).

Thus, based on these observations, we expect dioecious species would on average would have lower rates of growth and mortality than hermaphroditic and monoeony in late successional communities.

Demographic variation within communities have been linked to a number of functional traits (Poorter et al., 2008; Wright et al., 2010; Lida et al. 2014) and ecological processes (e.g., seed dispersal and density-dependence, Ma et al. 2016). In terms of understanding the multiple traits driving successional differences, seed mass, leaf mass per area, woody density, and maximum height of trees received a great deal of attention (Westoby et al. 2002, Westoby & Wright 2006; Poorter et al., 2008; Chave et al. 2009; Norden, Letcher, Boukili, Swenson, & Chazdon, 2012; Buzzard, Hulshof, Birt, Violle, & Enquist, 2016). However, comparative analyses of demographic performance of species with contrasting sexual systems in diverse forests at different successional stages are lacking. Further, compared with later successional stages, forest communities in early succession are usually dominated by faster-growing species and have higher mortality and recruitment, and strongly limited by N and water available (Milton, Laca, & Demment, 1994; Pretzsch, 2009). However, many successional effects cannot be detected if the studies are confined solely to stands of older or younger forest (Milton et al., 1994).

Considerable variation in the response of mating system traits to the environment and habitat variation has been observed (Holtsford & Elstrand 1992; Litrico et al., 2005; Levin, 2010; Cheptou 2012). Comparative analyses, based on correlations between breeding systems and ecological conditions, are valuable complements to studies on adaptive behavior (Leisler, Winkler, & Wink, 2002), because similar breeding system changes have evolved repeatedly (Charlesworth, 2006). Moreover, breeding systems are highly labile in angiosperm trees and often showed strong phylogenetic conservatism (Queenborough et al., 2009) as most species evolved from outcrossing to predominant self-fertilization (Barrett & Crowson, 2016). Monoeity in the plant lineage correlates with the evolution of dioecy (occurring in the same tree families and/or in closely related families; Renner & Ricklefs, 1995). However, phylogenetic relationships between species may influence comparisons among species in terms of responses to both biotic and abiotic conditions in natural habitats (Norden et al., 2012; Russo et al., 2010). Quantifying the relationships between demographic dynamics and breeding systems considering the effects of phylogeny at different successional stages could provide new insights into the complex interacting processes that shape community dynamics across large temporal scales (Chang & HilleRisLambers, 2016).
In this study, we use data from two long-term temperate forest dynamics plots in Northeast China to explore the growth-mortality dynamics in species with contrasting breeding systems at different stages of succession. We predict that (a) hermaphrodite and monoecy, on average, are disadvantageous compared to dioecy in younger successional stages with stressful conditions; in contrast; (b) in stable primary forest, dioecy should show demographic advantage over monomorphic species; (c) we predict that breeding system is linked with the trade-off between growth and mortality; (d) dioecy should have demographic advantage in secondary forest than the primary stage. Here we present, to our knowledge, the first study should have demographic advantage in secondary forest than the both ecological and evolutionary perspectives in natural forests.

2 | METHODS AND MATERIALS

2.1 | Study site

The study was conducted at the Changbai Mountain Natural Reserve (42°23′N, 128°05′E) in the northeastern PR China. Two forest tree communities in different successional stages were chosen for this study. The first is a 5-ha (250 × 200 m) secondary poplar-birch forest naturally regenerating after clear-cutting or fire (Bai et al. 2014). The poplar-birch forest (~80 years) is an important stage in the secondary succession of the broad-leaved Korean pine forest (Xu, 2001; hereafter secondary forest). The other is a 25-ha (500 × 500 m) broad-leaved Korean pine (Pinus koraiensis) mixed forest (abbreviated here as primary forest), which is the most common vegetation type in northeastern China and well known for high species richness (Stone, 2006; Yang & Xu, 2003). The climate of the study region is characterized by low temperature and high precipitation (Yang, Li, Wang, & Han, 1985). Mean annual precipitation is approximately 700 mm and most of this occurs from June to September (480–500 mm). Mean annual temperature is 2.88°C, with a January mean of 13.78°C, and a July mean of 19.63°C (Yang & Li, 1985).

2.2 | Regular plot surveys

Both large forest dynamics plots were fully censused using the methods described by Condit (1998): all free-standing trees ≥1 cm diameter at breast height (dbh = 1.3 m above the ground) were mapped, tagged and identified to species when the plot was established in 2005 (secondary plot) and 2004 (primary plot). The re-censuses were carried out for secondary forest between July and August 2010 and 2015, and in 2009 and 2014 for primary forest, respectively. The status of trees (live or dead) was recorded in the re-censuses for both plots (Zhang, 2016). More detailed information including mean stand density and mean basal area of living stems in first survey is summarized in Table 1.

2.3 | Environmental factors

To measure water content, we first divided both study sites into a grid of number of 20 × 20 m quadrats (20 for secondary forest and 100 for primary forest, respectively). The volumetric soil water content (%) was obtained by taking three samples from each of the four corners in each quadrat across both forest plots, using a Time Domain Reflectometers (TDR) probe at a depth 20 cm. Then we took the average of six values within each 50 × 50 m. For total nitrogen, we sampled soils according to the methods of John et al. (2007): using a regular grid of points every 30 m and also selected another two sample points (2, 5 or 15 m) in a several directions (N, NE, E, SE, etc.) from each base point (Supporting Information Figure S1; John et al., 2007; Yavitt et al., 2009). At each sample location, we obtained three subsamples of 0.2 m around the point using a 5-cm diameter cylinder at a depth of 10 cm (Yuan et al., 2013). Then we calculated the mean total nitrogen within each 50 × 50 m subplot.

2.4 | Breeding system

The breeding system of each species was identified using the following sources in a descending order of use: Flora of China (www.eflora.cn), Seeds of Woody Plants in China, Flora of Liaoning, and a series of recent publications including Gleiser & Verdú (2005), Sun (2005), Li, Liu, and Su (2008), Zhang et al. (2010), Zhang and Shang (2010), Wang (2014), Zhu et al. (2015). For many species, it was possible to verify breeding system using multiple sources. Conflicting reports were resolved with reference to the most recent treatment.

| TABLE 1 | Summary of forest plots included in this study |
|----------------|-----------------------------------------------|
| **Stand type (age/year)** | **Tree density (per hectare) and proportion (%)** | **Basal area (m²/ha)** | **Dominant species** |
| | Dioecy | Hermaphrodite | Monoecy | Density (stems/ha) | | |
| Secondary forest (~80) | 318 (33.11) | 1,128 (37.54) | 1,159 (51.88) | 4,021 | 28.79 | *Betula platyphylla, Populus davidiana, Pinus koraiensis, Tilia amurensis, Quercus mongolica* |
| Primary forest (~300) | 199 (14.25) | 305 (21.87) | 892 (63.87) | 2,366 | 43.75 | *Pinus koraiensis, Tilia amurensis, Quercus mongolica, Fraxinus mandshurica* |

Note. The proportions of the species, density and basal area representing different breeding systems were the value in first census (2005 for secondary forest and 2004 for primary forest). Primary forest is the Broad-leaved Korean pine mixed forest and secondary forest is the Poplar-birch forest. Density = Mean stand density of living stems, basal area = Mean basal area of living stems.
2.5 | Statistical analysis

We calculated growth rates (both growth and mortality rates) from the 5- and 10-year period census intervals (Sheil et al. 1995):

\[ \text{RGR} (%) = \frac{D_t - D_0}{D_0 \times \Delta t} \times 100. \]

where RGR represents the relative growth rate, \(D_0\) and \(D_t\) are the stem diameter at breast height (dbh) from first and last measurements, respectively, \(t\) is the time interval:

\[ m = 1 - \left( \frac{N_t}{N_0} \right)^{\frac{1}{t}}. \]

where \(m\) is the mean mortality per year, \(N_0\) is the stem abundance in the first census, \(N_t\) is the number of living stems in the \(t\)-year re-census.

Both secondary and primary forests were divided into subplots of 50 × 50 m. Thus, there were 20 and 100 subplots for secondary and primary forests, respectively. We performed species-level analyses of tree growth and mortality by separately analyzing each of the species in all three censuses for both plots and all subplots.

2.6 | Model construction

Breeding system has previously been shown to demonstrate significant phylogenetic conservation (Wang et al. unpublished data). The Phylomatic software was employed to generate the phylogeny with branch lengths provided by one of the available mega trees (http://phylodiversity.net/phylomatic/, Zanne et al. 2014). Phylogenetic analyses were conducted in the R package "ape" (Paradis 2004, R Development Core Team 2015).

First, to examine how the relationship between breeding system and demographic rate (growth and mortality) changes with forest successional stages [SS], we treated relative growth and mortality rates as the dependent variables separately and included breeding system as the explaining variable in the phylogenetically corrected linear mixed-effects kinship model fit by maximum likelihood (lmekin) within the "coxme" package. To consider the environmental effects of different successional stages on demographic rate of plant individuals, we included environmental factors (water content and total Nitrogen). We also included the interaction between forest type and breeding systems of plant species, because proportions of species with different breeding systems vary across the successional stages. RGR was included as a covariate in the models of mortality rate ~ breeding system and species name was taken as a random factor.

In addition, to evaluate the role of breeding system in the trade-off between RGR and mortality rate, and because of the well-known effects of seed mass [SM], woody density, maximum height of trees, and leaf mass per area on growth-mortality trade-off (McMahon, Metcalf, & Woodall, 2011; Poorter et al., 2008; Wright et al., 2010, 2010), these covariates were also included in the models. The values of the continuous explanatory variables were standardized by subtracting the mean value of the variable and dividing by 1 standard deviation (Schielzeth 2010). Pairwise correlations showed that there was no multicollinearity following the threshold of 0.7 (Dormann et al. 2013, Supporting Information Table S1).

To test for differences in tree growth and mortality among the species with different breeding systems in each forest stage, we conducted phylogenetically generalized least squares regression ("pgls") using the "caperp" package in R (Orme, 2012). The influence of phylogenetic nonindependence of breeding systems on growth and mortality rates was modeled by incorporating the phylogenetic covariance matrix in the pgls. All statistics were calculated in R 3.2.2 (R Core Team 2015).

3 | RESULTS

Overall, there was significant difference in both the frequencies of abundance and species with each breeding system between two forest stages (Figure 1 and Supporting Information Figures S2 and S3). Secondary forest showed higher RGR (1.76%) and mortality rate (2.34%) than the primary forest (0.86% and 2.12%, respectively) during the 10-year period. In secondary forest stage, RGR was negatively associated with mortality (coefficient correlation \(r = -0.30\), \(p < 0.01\)) when combining the two monitoring periods, while this relationship was significantly positive in the primary forest \(r = 0.33\), \(p < 0.001\); Figure 2 and Supporting Information Figure S4).

Having controlled for water content, total nitrogen, seed mass, wood density, maximum height of trees, and leaf mass per area, the fitted models revealed that, on the whole, dioecious species had significantly lower RGR and mortality rates than monoecy and hermaphrodites across two forest successional stages (Table 2). The effects of being monoecious or hermaphrodite on RGR and mortality rate were much stronger than the leaf mass per area, woody density and maximum height. The interaction between hermaphrodite and secondary stage of forest had a stronger effect on both RGR and mortality rate (Table 2).

In secondary forest, RGR differed little among dioecious species, monoecious species, and hermaphrodite during 10 years when controlling phylogeny, while hermaphrodite species had (marginally not) significantly higher mortality rate (Tables 3 and 4). By contrast, phylogenetic independence analysis showed that dioecy had higher relative growth rate and lower mortality rate compared to hermaphrodite (Supporting Information Figure S4). In primary forest, hermaphrodite species had both significantly higher RGR and mortality rates than both dioecious and monoecious ones \((p < 0.05\), Figure 2e,f; Tables 3 and 4). Phylogenetic independence analysis revealed similar results (Supporting Information Figure S4). Further comparison showed that the difference between RGR and mortality rate for dioecious species between two successional stages was insignificantly (Figure 2c,d).

4 | DISCUSSION

In this study, we evaluated growth and mortality rates in two permanent temperate forest dynamics plots at different successional stages...
in Northeast China and found that demographic rates were linked with variation in breeding system. Interspecific variation in RGR was negatively correlated with mortality rate in the early successional forest. In contrast, this demographic trade-off between growth and mortality was positive in the primary forest community. We have provided weak evidence that in the younger successional stages, dioecious species have weak demographic advantage over monomorphic species. And dioecious species showed on average lower rates of growth and mortality than hermaphrodite (thus higher demographic advantage for dioecy) in the primary community. Comparison between two stages showed that dioecy also had no demographic advantage in secondary forest than the primary stage. Nevertheless, our results also revealed that breeding system, together with environmental factors, and other well-known functional traits (e.g., seed mass and leaf mass per area), contributed to the growth-mortality trade-off in plant communities and played a greater role compared with those functional traits.

4.1 | Trade-off between growth and mortality as succession proceeds

In the secondary forest community, we found that RGR and mortality rate were negatively correlated. This is consistent with previous findings in other secondary forest with a comparable mean basal area (28 m²/ha) as our 5-ha plot: as tree growth rate declines, the probability of mortality increases (Monserud, 1976; Wyckoff & Clark, 2002). In stark contrast, in primary forest, the interspecific variation in RGR was positively correlated with mortality rate, in accordance with previous studies (Poorter et al., 2008; Wright et al., 2010; Iida et al. 2014). In general, forests at early stages are in the process of accumulating biomass rapidly (Van Breugel, Martínez-Ramos, & Bongers, 2006). As the vegetation develops, taller longer-lived plant species in late successional stages progressively replace the species which are faster-growing, having higher mortality, recruitment, stem density, and lower basal area (Garnier et al., 2004). Thus, both RGR and mortality rate decline with increasing tree size (Wyckoff & Clark, 2002; Iida et al. 2014) and stand age (Xu et al., 2012).

4.2 | Demographic comparison between breeding systems in earlier forest

Inconsistent with this prediction, there was only weak demographic advantage in terms of both RGR and mortality rates for dioecious compared with hermaphrodite species in the secondary forest community where dioecious species (richness here) are more common than in the old-growth. That is, in relatively newly colonized areas which are relatively stressful environments, monomorphic species showed no demographic advantage over dioecious species, although a single self-compatible immigrant can initiate a sexually reproducing colony without the aid of an external agent for pollination (Baker, 1955, 1967). Harsh or stressful conditions have been considered to favor the evolution and maintenance of separate sexes from combined sexes (Barrett, Dorken & Case 2001; Ashman, 2006). Therefore owing to the limited resources availability for plant growth, there is a trade-off between reproduction and growth (Harper, 1977; Obeso, 2002), especially in stressful environments (Vilà-Cabrera, Martínez-Vilalta, & Retana, 2014). This may be consistent with our findings that dioecy had a higher proportion of richness but lower proportion of abundance in secondary forest. This suggests that the demographic advantage of monomorphic species over dioecious species is reduced in disturbed areas, most likely by a lower investment in the female function of hermaphroditic species (Costich, 1995; Litrico et al., 2005). This is because female function is much more costly than male function (Freeman, Doust, El-Keblawi,
The adaptive strategies of dioecy in disturbed areas contributed to a demographic advantage for dioecy and a comparable species richness for both breeding systems in early successional stages.

4.3 | Demographic comparison between breeding systems in primary forest

Dioecious species showed lower rates of growth and mortality than hermaphrodite and monoecious ones in the primary forest community, supporting prior predictions. These results suggest that dioecious species had a demographic advantage over the cosexual ones, which may reflect that the dioecious species were better competitors in terms of survival than the hermaphrodite to some degree (Kunstler et al., 2016). It might be expected that being unisexual would reduce inbreeding depression and prevent competition for resources between male and female flowers (Charlesworth & Charlesworth, 1978a, 1978b), thus obligate outcrossing of dioecious species has been viewed as the trade-off for the loss of effective reproductive population (Charlesworth

### TABLE 2
Summary of phylogenetically corrected linear models designed to detect effects of breeding systems on relative growth rate and mortality rate for both forest types during 10 years. Values in bold are significant at $P < 0.05$

| Parameter | Relative growth rate | Mortality rate |
|-----------|----------------------|---------------|
|           | Value    | SE   | p-value | Value    | SE   | p-value |
| Hermaphrodite | 1.887 | 0.350 | <0.0001 | 0.005 | 0.001 | <0.0001 |
| Monoecy | 2.258 | 0.520 | <0.0001 | 0.003 | 0.002 | 0.022 |
| Water content | 0.033 | 0.072 | 0.640 | 0.001 | <0.001 | 0.034 |
| Total nitrogen | 0.165 | 0.065 | 0.011 | <0.001 | <0.001 | 0.330 |
| Leaf mass per area | −0.605 | 0.202 | 0.003 | 0.001 | 0.001 | 0.240 |
| Woody density | −0.919 | 0.164 | <0.0001 | −0.002 | 0.001 | <0.0001 |
| Maximum height | −0.363 | 0.279 | 0.190 | −0.003 | 0.001 | <0.001 |
| Seed mass | −0.087 | 0.322 | 0.790 | 0.002 | 0.001 | 0.053 |
| Secondary | 1.227 | 0.238 | <0.0001 | −0.001 | 0.001 | 0.370 |
| Hermaphrodite: secondary | −0.869 | 0.294 | 0.003 | −0.003 | 0.001 | 0.019 |
| Monoecy: secondary | −0.148 | 0.322 | 0.650 | −0.003 | 0.002 | 0.042 |
| Relative growth rate | −0.0004 | <0.001 | 0.190 |

Note. The models controlled for water content, total nitrogen, seed mass, wood density, maximum height of trees, leaf mass per area, successional stage, and the interactions between breeding system and successional stages.

### TABLE 3
Summary of Phylogenetic Generalized Least Square models designed to detect effects of breeding systems on relative growth rates for both forests during 10 years. Values in bold are significant at $P < 0.05$

| Study period | Parameter | Secondary forest | Primary forest |
|--------------|-----------|------------------|---------------|
|              | Estimate  | SE   | $p_e$   | $p_m$ | Estimate  | SE   | $p_e$ | $p_m$ |
| Period 1     | Hermaphrodite | −0.447 | 0.827 | 0.590 | 0.762 | 1.944 | 0.493 | <0.0001 | 0.007 |
|              | Monoecy   | 1.205 | 1.078 | 0.260 | 0.026 | 0.490 | 0.747 | 0.510 |
| Period 2     | Hermaphrodite | −0.365 | 0.505 | 0.470 | 0.127 | 1.193 | 0.318 | <0.001 | <0.001 |
|              | Monoecy   | −0.419 | 0.885 | 0.640 | 0.534 | 0.727 | 0.471 | 0.120 |
| 10 years     | Hermaphrodite | 1.472 | 0.655 | 0.025 | 0.545 | 2.339 | 0.788 | 0.003 | <0.001 |
|              | Monoecy   | 0.958 | 0.900 | 0.290 | 0.519 | 1.956 | 1.501 | 0.190 |

Note. $p$ showed the significance of the difference in relative growth rate between breeding systems. And Estimates showed the difference between dioecious and nondioecious species. Period 1 indicates 2005–2010 for secondary forest and 2004–2009 for primary forest; period 2 indicates 2010–2015 for secondary forest and 2009–2014 for primary forest. In accordance with, the 10 years are 2005–2015 for secondary forest and 2004–2014 for primary forest.
& Charlesworth, 1978a, 1978b; Lloyd, 1979). In contrast, most
cosexual individuals, experiencing inbreeding depression, are
less competitive at every stage of their life history (Charlesworth &
Charlesworth, 1978a, 1978b; Sakai, Karoly, & Weller, 1989).
This competitive advantage may possibly contribute to the co-
existence of dioecious plants and other breeding systems in
the absence of fecundity and population density advantages in
primary forest communities (Vamosi, Mazer, & Cornejo, 2008;
Queenborough et al., 2009; Yunyun Wang et al. unpublished).

4.4 | The role of breeding system in the trade-off
between growth and mortality

The trade-off between growth and mortality has been found to
be associated with a number of functional traits that relate to the
ability to disperse (seed mass), acquire resources (leaf mass per
area), and grow rapidly (woody density; Liu et al., 2016; McMahon
et al., 2011; Poorter et al., 2008; Wright et al., 2010). The analy-
ysis presented here revealed that sexual system (e.g., dioecy and
hermaphrodite) was one of the key traits correlated with RGR
and mortality rate across successional stages of forest (Table 2,
Figures 2, Supporting Information Figure S5), which suggests that
breeding system played a significant role in driving demographic
rates and community dynamics. The growth-mortality relation-
ship represents a trade-off between a species’ ability to grow
quickly to exploit abundant resources versus avoiding mortality
when resources are scarce (Russo, Brown, Tan, & Davies, 2008).
In early successional areas with stressful conditions, hermaphro-
dites would decrease the emphasis on seed production to avoid
more waste of resources (Ashman, 2006). In the primary forest
in which various species begin to compete for space, light, and
nutrients (Clements 1916), while adaptations for fast growth can
provide a competitive advantage by way of rapid exploitation of
resources for hermaphrodite, an inability to acclimate to reduced
resource availability could increase mortality risk (Russo et al.,
2008).

4.5 | Stage-dependence of breeding systems in
demographic dynamics

It is interesting that our results indicated that there is a switching of
difference in demographic rates between dioecious and hermaph-
roditic species as succession proceeds. This phenomenon is likely to
reflect the response of the sexual system to the contrasts in stem
density, canopy structure characteristics, and biomass level as the
succession proceeds and becomes well established. Forests at sec-
ondary stage are likely at higher tree density (greater frequency of
colonists/pioneers) of small diameter and face intense competition
for abundant resources (e.g., light; Milton et al., 1994), while the
importance of competition increases with succession because re-
sources become limited as stand biomass increases (Grubb, 1977).
Such increased competitive pressure will lead to differentiat-
ed strategies to obtain the increasingly scarce resources, with concomitant
different functional traits, a progress leading to increasingly limited
trait similarity (Lohbeck et al., 2014). Such trait differentiation over
habitat gradients may also apply to sexual systems: changing sex
ratio (equal sex ratios or male-biased) could benefit dioecious species
(Queenborough, Burslem, Garwood, and Valencia (2007). In some
species, females show different or stronger habitat associations than
males. This differences in physiology and function between female and
male in certain setting may partly contribute to the transforma-
tion from a similar demographic rate between dioecy and hermaph-
rodite in secondary forest to a significant difference in primary forest.

Ecological variables that are associated with resources available
for pollinators (e.g., quantity of inflorescence) have a great impact
on population structure through their effect on the pollinator be-
havior and plant mating (Case & Ashman, 2009; Gervasi & Schiestl,
2017; Iwata, Nagasaki, Ishii, & Ushimaru, 2012). In addition, the
sex ratio of species can vary considerably in response to tree size,
density and stand age if the plants are growing in a stressful envi-
ronment (Charlesworth, 2006; Lloyd & Bawa, 1984; Ortiz, Arista,
& Talavera, 2002), which likely explains the frequency and role
changing of hermaphrodite over succession. A study analyzing the

| TABLE 4 | Summary of Phylogenetic Generalized Least Square models designed to detect the difference in terms of the effects of breeding systems on mortality rates for both forests during 10 years. Values in bold are significant at P < 0.05 |

| Study period | Parameter   | Secondary forest | Primary forest |
|--------------|-------------|------------------|---------------|
|              | Estimate    | SE   | p_e | p_m |             | SE   | p_e | p_m |
| Period 1     | Hermaphrodite | -0.033 | 0.043 | 0.450 | <0.0001 | 0.051 | 0.018 | 0.005 | <0.001 |
|              | Monoecy     | 0.027 | 0.042 | 0.520 |           | -0.004 | 0.025 | 0.880 |           |
| Period 2     | Hermaphrodite | 0.068 | 0.042 | 0.100 | <0.001  | 0.062 | 0.027 | 0.024 | <0.01  |
|              | Monoecy     | -0.005 | 0.052 | 0.920 |           | 0.014 | 0.040 | 0.720 |           |
| 10 years     | Hermaphrodite | 0.006 | 0.005 | 0.190 | <0.001  | 0.070 | 0.028 | 0.011 | <0.01  |
|              | Monoecy     | <0.001 | 0.006 | 0.940 |           | -0.050 | 0.042 | 0.240 |           |

Note. p Showsed the significance of the difference in mortality rate between breeding systems. And Estimates showed the difference between dioec-
ious and nondioecious species. Period 1 indicates 2005–2010 for secondary forest and 2004–2009 for primary forest; period 2 indicates 2010–2015
for secondary forest and 2009–2014 for primary forest. In accordance with, the 10 years are 2005–2015 for secondary forest and 2004–2014 for
primary forest.
sex ratios of 126 dioecious species has showed nearly continuous variation from strong male to strong female bias, and exhibit male-biased sex ratios in some younger populations, but close to even sex ratios in older populations in which all individuals were reproductively primary (Barrett, Yakimowski, Field, & Pickup, 2010). In an ultimate manner, the changing sex ratio was attributed to the longer time required for females to reach reproductive maturity because of costs associated with serotinous cone production (Harris & Pannell, 2010), in which significant resource is also invested.

4.6 | Caveats

Forest succession is a long process that includes a series of stages as its disturbance. Within or between different successional stages, one or several particular forest successional stage(s) could reflect some growth and mortality dynamics in breeding systems. In general, community-assembly studies have gradually considered sexual systems, together with the development of long-term forest dynamics plots across the world (http://www.ctfs.si.edu/), ongoing efforts will constitute a very strong test of patterns arising during succession.

5 | CONCLUSION

Breeding system has been considered to play an important role in community dynamics and assembly, but how it contributes and changes community dynamics during succession has not been tested. Here, we have shown that plant breeding system is strongly linked with demographic rates in two temperate forest communities at different successional stages. Demographic rates are clearly stand-dependent (Harper, 1977). It is interesting that there is then a switch in ecological advantage of dioecious species in different forests: a marginally similar demographic rate between dioecy and hermaphrodite in secondary forest to a significant difference in primary forest.

We propose that breeding systems that relate to colonization propensity and competitive ability are closely associated with the growth-mortality trade-off in both early and late successional forests, which may be a key mechanism driving the community succession and assembly (Réjou-Méchain & Cheptou, 2015). These results improve our understanding of how breeding system links to demographic performance, and community successional, dynamics, and assembly.

ACKNOWLEDGMENTS

We acknowledge the hundreds of field workers who collected data in the plots used here. We thank financial supports from The national Key Research and Development Program and China (2016YFC0500300), the National Natural Science Foundation of China (31730015, 41671050 and 31770666) and Youth Innovation Promotion Association of the Chinese Academy of Sciences (2017241).

AUTHOR CONTRIBUTIONS

Wang, Y.Y. and Freckleton, R.P. conceived the ideas and designed methodology. Wang, Y.Y., Wang, B.J., Kuang, X., Yuan, Z.Q., Lin, F., Ye, J., Wang, X.G. and Hao, Z.Q. performed the experiments. Wang, Y.Y. and Kuang, X. analyzed the data, Freckleton, R.P. consulted on data analyses. Wang, Y.Y. led the writing of the manuscript, Freckleton, R.P. contributed critically to the drafts. All authors gave final approval for publication.

ORCID

Yunyun Wang
http://orcid.org/0000-0002-2019-8996
Xu Kuang
http://orcid.org/0000-0003-0329-537X
Zhanqing Hao
http://orcid.org/0000-0003-2875-6419

REFERENCES

Alvarez-Assignment, M. Y., Quesada, M., Sánchez-Azeoféira, G. A., Avila-Cabadilla, L. D., & Gamon, J. A. (2012). Functional regeneration and spectral reflectance of trees during succession in a highly diverse tropical dry forest ecosystem. American Journal of Botany, 99, 816–826. https://doi.org/10.3732/ajb.1100200
Ashman, T. L. (2006). The evolution of separate sexes: A focus on the ecological context. In L. D. Harder, & S. C. H. Barrett (Eds.), Ecology and evolution of flower (pp. 204–222). New York, NY: Oxford University Press.
Bai, X. J., Breces-Arregués, T., Ye, J., Wang, X. G., Lin, F., Yuan, Z. Q., ..., Hao, Z. Q. (2014). Dynamics of two understory shrub species in old growth and young secondary forests. PLoS ONE, 9, e98200. https://doi.org/10.1371/journal.pone.0098200
Barrett, H. G. (1955). Self-compatibility and establishment after “long-distance” dispersal. Evolution, 9, 347–348.
Barrett, H. G. (1967). Support for Bakers law as a rule. Evolution, 21, 853–856. https://doi.org/10.1111/j.1558-5646.1967.tb03440.x
Barrett, S. C. H., & Crowson, D. (2016). Mating systems in flowering plants. In R. M. Klimam (Ed.), Encyclopedia of evolutionary biology, Vol. 2 (pp. 473–479). Oxford, UK: Academic Press. https://doi.org/10.1016/B978-0-12-800049-6.00161-X
Barrett, S. C. H., & Harder, L. D. (1996). Ecology and evolution of plant mating. Trends in Ecology & Evolution, 11, 73–79. https://doi.org/10.1010/1659-3479(96)81046-9
Barrett, S. C. H., Dorken, M. E., & Case, A. L. (2001). A geographical context for the evolution of plant reproductive systems. In J. Silvertown, & J. Antonovics (Eds.), Integrating ecological and evolutionary processes in a spatial context (pp. 341–364). Oxford, UK: Blackwell.
Barrett, S. C., Yakimowski, S. B., Field, D. L., & Pickup, M. (2010). Ecological genetics of sex ratios in plant populations. Philosophical Transactions of the Royal Society of London B: Biological Sciences, 365, 2549–2557.
Bazzaz, F. (1979). The physiological ecology of plant succession. Annual Review of Ecology and Systematics, 10(10), 351–371. https://doi.org/10.1146/annurev.es.10.110179.002031
Bruijning, M., Visser, M. D., Muller-Landau, H. C., Wright, S. J., Comita, L. S., Hubbell, S. P., ..., Jongejans, E. (2017). Surviving in a cosplay world: A cost-benefit analysis of dioecy in tropical trees. American Naturalist, 189, 297–314. https://doi.org/10.1086/690137
Buzzard, V., Hulshof, C. M., Birt, T., Violle, C., & Enquist, B. J. (2016). Re-growing a tropical dry forest: Functional plant trait diversity and community assembly during succession. Functional Ecology, 30, 1006–1013. https://doi.org/10.1111/1365-2435.12579
Harris, M. S., & Pannell, J. R. (2010). Canopy seed storage is associated with sexual dimorphism in the woody dioecious genus Leucadendron. *Journal of Ecology*, 98, 509–515. https://doi.org/10.1111/j.1365-2745.2009.01623.x

Heilbuth, J. C., Ilves, K. L., & Otto, S. P. (2001). The consequences of dioecy for seed dispersal: modelling the seed-shadow handicap. *Evolution*, 55, 880–888. https://doi.org/10.1554/0014-3820(2001055)080:TCODFS2.0.CO;2

Holtsford, T. P., & Ellstrand, K. (1992). Genetic and environmental variation in floral traits affecting outcrossing rate in Clarkia tembloriensis (Onagraceae). *Evolution*, 46, 216–225. https://doi.org/10.1558/0014-3820.46.1.216

Iwata, T., Nagasaki, O., Ishii, H. S., & Ushimaru, A. (2012). Inflorescence architecture affects pollinator behaviour and mating success in *Spiranthes sinensis* (Orchidaceae). *New Phytologist*, 193, 196–203. https://doi.org/10.1111/j.1469-8137.2011.03892.x

Jaines, I., & Ramirez, N. (1999). Breeding systems in a secondary deciduous forest in Venezuela: The importance of life form, habitat, and pollination specificity. *Plant Systematics and Evolution*, 215, 23–36. https://doi.org/10.1007/BF00984645

John, R., Dalling, J. W., Harms, K. E., Yavitt, J. B., Stallard, R. F., Mirabello, M., … Foster, R. B. (2007). Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 864–869. https://doi.org/10.1073/pnas.0604661010

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., … Aiba, M. (2016). Plant functional traits have globally consistent effects on competition. *Nature*, 529, 204–207. https://doi.org/10.1038/nature16476

Lebrija-Trejos, E., Meave, J. A., Poorter, L., Pérez-García, E. A., & Bongers, F. (2010). Pathways, mechanisms and predictability of vegetation change during tropical dry forest succession. *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 267–275. https://doi.org/10.1016/j.ppees.2010.09.002

Leisler, B., Winkler, H., & Wink, M. (2002). Evolution of breeding systems in acrocarpous bryophytes. The Auk, 119, 379–390. https://doi.org/10.1642/0004-8038(2002)119[0379:EOBSIA]2.0.CO;2

Levin, D. A. (2010). Environment-enhanced self-fertilization: Implications for niche shifts in adjacent populations. *Journal of Ecology*, 98, 1276–1283. https://doi.org/10.1111/j.1365-2745.2010.01715.x

Lida, Y., Kohyama, S. T., Swenson, G. N., Su, S.-H., Chen, C.-T., Chiang, J.-M., & Sun, I.-F. (2014). Linking functional traits and demographic rates in a subtropical tree community: the importance of size dependency. *Journal of Ecology*, 102, 641–650.

Li, Q., Liu, X., & Su, J. (2008). Study progress of Aceraceae plants in China. *Journal of Jiangsu Agricultural Sciences*, 6, 184–186 (In Chinese with English Abstract).

Litrico, I., Pailler, T., & Thompson, J. D. (2005). Gender variation and primary succession in a tropical woody plant, *Antirhea borbonica* (Rubiacae). *Journal of Ecology*, 93, 705–715. https://doi.org/10.1111/j.1365-2745.2005.01009.x

Liu, X., Swenson, N. G., Lin, D., Mi, X., Umaña, M. N., Schmidt, B., & Ma, K. (2016). Linking individual-level functional traits to tree growth in a subtropical forest. *Ecology*, 97, 2396–2405. https://doi.org/10.1002/ecy.1445

Lloyd, D. G. (1979). Evolution towards dioecy in heterostylous populations. *Plant Systematics and Evolution*, 131, 71–80. https://doi.org/10.1007/BF00984123

Lloyd, D. G., & Bawa, K. S. (1984). Modification of the gender of seed plants in varying conditions. *Evolutionary Biology*, 17, 255–338. https://doi.org/10.1007/BF00981697-9

Lohbeck, M., Poorter, L., Martínez-Ramos, M., Rodríguez-Velázquez, J., Breugel, M., & Bongers, F. (2014). Changing drivers of species...
Wang, J. (2014). Research on reproductive strategies for dioecious plants in coniferous and broadleaved mixed forest of northeast China. PhD thesis, Beijing Forestry University, Beijing.

Westoby, M., Falster, S. D., Moles, T. M., Vesk, A. P., & Wright, J. I. (2002). Plant Ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Wang, J. (2014). Research on reproductive strategies for dioecious plants in coniferous and broadleaved mixed forest of northeast China. PhD thesis, Beijing Forestry University, Beijing.

Westoby, M., Falster, S. D., Moles, T. M., Vesk, A. P., & Wright, J. I. (2002). Plant Ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452

Wright, S. J., Kitajima, K., Kraft, N. J., Reich, P. B., Wright, I. J., Bunker, D. E., ... Engelbrecht, B. M. (2010). Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, 91, 3664–3674. https://doi.org/10.1890/09-2335.1

Wyckoff, P. H., & Clark, J. S. (2002). The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *Journal of Ecology*, 90, 604–615. https://doi.org/10.1046/j.1365-2745.2006.02.004

Wyckoff, P. H., & Clark, J. S. (2002). The relationship between growth and mortality for seven co-occurring tree species in the southern Appalachian Mountains. *Journal of Ecology*, 90, 604–615. https://doi.org/10.1046/j.1365-2745.2006.02.004

Yuan, Z. Q., Gazol, A., Lin, F., Ye, J., Shi, S., Wang, X. G., ... Hao, Z. Q. (2013). Soil organic carbon in an old-growth temperate forest: Spatial pattern, determinants and bias in its quantification. *Geoderma*, 195–196, 48–55. https://doi.org/10.1016/j.geoderma.2012.11.008

Zhang, Z. C. (2016). Dynamics of Tree Mortality and Growth in Coniferous and Broad-leaved Mixed Forests in Changbai Mountain, 16–19. PhD thesis, University of Chinese Academy of Sciences, Beijing.

Zhang, L. Z., & Shang, H. (2010). Morphology and cytology of three flower phenotypes in a duodichogamous tree species, Acer mono. *Biodiversity Science*, 19, 551–557. (In Chinese with English Abstract).

Zhang, C. Y., Wang, D. S., Wei, Y. B., Zhao, X. H., Jia, Y. Z., & Zhou, H. C. (2010). Density-dependent sex ratios for Dioecious tree Species *Populus davidiana* and *Fraxinus mandshurica*. *Scientia Silvae Sinicae*, 46, 16–21. (In Chinese with English Abstract).

Zhu, Y. Y., Wang, J., Zhao, X. H., Pi, T. H., Zhang, Z. H., & Zhao, S. S. (2015). Correlation of functional traits and carbon contents in androdioecy plant *Acer mandshuricum*. *Acta Botanica Boreali-Occidentalia Sinica*, 35, 2089–2095.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of the article.