Distinct Niche Divergence Characterizes the Homoploid Hybrid Speciation of *Pinus densata* on the Tibetan Plateau

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**Abstract:** Ecological divergence and selection for novel adaptations to new habitats have been theoretically proposed to play important roles in promoting homoploid hybrid speciation (HHS). The successful establishment of *Pinus densata* on the Tibetan Plateau is one of the few known examples of HHS. In this study, we carried out extensive field expeditions to obtain representative coverage of occurrence sites of *P. densata* and its two putative parents. We then applied a series of geographic information system–based analyses to define the patterns of environmental variation within and among the three pine species, to remove potentially confounding effects of spatial autocorrelation in the environmental data due to allopatric ranges, and to build species distribution models. All results consistently indicated that the ecological preferences of *P. densata* and its parental species have diverged, and they identified candidate ecological factors associated with habitat-specific adaptation. Projections from niche modeling indicated that *P. densata* could extend across a vast range along the parallel valley systems of the southeastern Tibetan Plateau. Our findings provide evidence of a distinct niche shift in *P. densata* and support the hypothesis that local adaptation and geographic isolation help maintain and reinforce between-species differences and reproductive isolation in the species complex.

**Keywords:** ecological differentiation, hybrid speciation, local adaptation, reproductive isolation.

**Introduction**

Homoploid hybrid speciation (HHS) is a process of hybridization that results in a derivative hybrid species without alteration in chromosome number (Grant 1981; Arnold 1997). Previous authors have suggested that, theoretically, reproductive isolation in speciation may arise through several processes, including rapid chromosomal restructuring, ecological divergence, and/or spatial separation (Grant 1981; Rieseberg et al. 2003; Coyne and Orr 2004). Changes in ecological attributes of hybrid populations and ecological selection promoting adaptation to novel habitats may be particularly important in HHS since there are no ploidy changes, which isolate incipient hybrids reproductively from their progenitors almost instantaneously (Lewontin and Birch 1966; Buerkle et al. 2000; Gross and Rieseberg 2005). Instead, in HHS divergent selection leading to local adaptation to new hybrid habitats may provide critical ecological isolating barriers between hybrids and their progenitors (Rieseberg et al. 2003). The colonization of novel habitats may allow hybrid species to avoid introgression and competition with their parental species, and the colonization of extreme or “transgressive” habitats may contribute particularly strongly to the ecological divergence defining the biology of hybrid lineages (Rieseberg et al. 1999; Schwarzbach et al. 2001). Hence, the identification and characterization of ecological niches unique to hybrids may facilitate elucidation of the genetic basis of novel adaptations and species divergence. An example of HHS that appears to fit theoretical models is the speciation and successful establishment of *Pinus densata* on the Tibetan Plateau.

*Pinus densata* forms extensive, pure forests on the southeastern Tibetan Plateau at elevations ranging from 2700 to 4200 m above sea level (asl; Guan 1990). Genetic analyses suggest that *P. densata* originated from hybridization between *Pinus tabuliformis* and *Pinus yunnanensis* with no alteration of ploidy level (Wang and Szmidt 1994; Wang et al. 2001; Liu et al. 2003; Song et al. 2003). Previous studies have also hypothesized that the evolution of *P. densata* into a stabilized taxonomic unit after the initial hybridization events was promoted by the availability of new, empty habitats on the Tibetan Plateau and that successful hybrid lineages colonized a territory that is inaccessible to both of the parental species (Wáng and Szmidt...