

Abiotic Niche Divergence of Hybrid Species from Their Progenitors

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ABSTRACT: Although more frequently discussed recently than previously, the role of ecology in homoploid hybrid and allopolyploid speciation has not been subjected to comparative analysis. We examined abiotic niche divergence of 22 assumed homoploid hybrid species and 60 allopolyploid species from that of their progenitors. Ecological niche modeling was employed in an analysis of each species' fundamental niche, and ordination methods were used in an analysis of realized niches. Both analyses utilized 100,000 georeferenced records. From estimates of niche overlap and niche breadth, we identified for both types of hybrid species four niche divergence patterns: niche novelty, niche contraction, niche intermediacy, and niche expansion. Niche shifts involving niche novelty were common and considered likely to play an important role in the establishment of both types of hybrid species, although more so for homoploid hybrid species than for allopolyploid species. Approximately 70% of homoploid hybrid species versus 37% of allopolyploid species showed shifts in the fundamental niche from their parents, and ~86% versus ~52%, respectively, exhibited shifts in the realized niche. Climate was shown to contribute more than soil and landform to niche shifts in both types of hybrid species. Overall, our results highlight the significance of abiotic niche divergence for hybrid speciation, especially without genome duplication.

Keywords: digitized data, hybrid speciation, niche shift, climate, soil, landform.

Introduction

Interspecific hybridization occurs frequently in nature and contributes greatly to global biodiversity (Stebbins

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1959; Rieseberg 1997; Seehausen 2004; Mallet 2005, 2007; Rieseberg and Willis 2007; Abbott and Rieseberg 2021). In contrast to bifurcating divergence from an ancestral lineage, hybrid speciation involves the combination and recombination of divergent genomes through sexual hybridization between two or more distinct species (Rieseberg 1997; Abbott et al. 2009, 2013; Lamichhaney et al. 2018; Ru et al. 2018; Abbott and Rieseberg 2021). This generates novel genotypes that may exhibit novel traits allowing colonization of previously unoccupied ecological niches (Seehausen 2004; Gompert et al. 2006; Mallet 2007). Such ecological niche shifts often cause spatial isolation of hybrids from their parents and consequently a reduction in likelihood of competition and backcrossing with them, thus playing an important role in hybrid speciation (Rieseberg et al. 2003; Gompert et al. 2006; Yakimowski and Rieseberg 2014; Runemark et al. 2019).

Two distinct modes of hybrid speciation are recognized: allopolyploid speciation, in which the genome of the hybrid experienced at least one duplication, and homoploid hybrid speciation, in which no change in chromosome number occurs in the hybrid. A doubling of a hybrid's chromosome number in allopolyploid speciation creates a ploidy barrier between the hybrid and its parents (due to mishaps in chromosome pairing and segregation during meiosis in hybrid-parent offspring), causing immediate postzygotic reproductive isolation of the hybrid from its progenitors (Soltis and Soltis 1999; Mallet 2007; Abadie et al. 2012; Abbott et al. 2013; but see Sutherland and Galoway 2017). Such isolation can allow newly formed allopolyploids (neoallopolyploids) to coexist with their parents without niche shift. In contrast, newly formed homoploid hybrid species need to be reproductively isolated from their

parent species by other barriers (which might also contribute to reproductive isolation in neoallopolyploids). Homoploid hybrid species may originate via transgressive traits (Rieseberg 1997; Schwarz et al. 2005; Gompert et al. 2006), genomic and/or chromosomal restructuring (Templeton 1981; Hermansen et al. 2011), and/or the inheritance of postzygotic and prezygotic reproductive isolation from the parents (Yakimowski and Rieseberg 2014; Lamichhaney et al. 2018; Runemark et al. 2019; Wang et al. 2021). Each of these mechanisms may either trigger or accompany niche shifts.

Theoretical modeling predicts extensive ecological shifts in homoploid hybrid species to promote reproductive isolation (Buerkle et al. 2000; Karrenberg et al. 2007). Habitat divergence in such species is common (Rieseberg et al. 2003; Gompert et al. 2006; Mao and Wang 2011), although in only a few instances has divergence been quantitatively examined (Mao and Wang 2011; Yakimowski and Rieseberg 2014). The establishment of three sunflower (*Helianthus*) homoploid hybrid species in desert dunes and salt seeps markedly different from the relatively mesic habitats of their widespread parental species remains one of the best-studied examples of habitat divergence in homoploid hybrid species (Rieseberg et al. 2003).

Despite neoallopolyploid species exhibiting strong postzygotic ploidy barriers from their parents, they too will benefit from a niche shift, so as to avoid competition and overcome the minority cytotype disadvantage they might suffer when occurring in sympatry with one or both parents (Fowler and Levins 1984). However, the role of niche divergence in the establishment of an allopolyploid species is not yet fully understood. Whereas allopolyploids often show considerable niche conservatism (Glennon et al. 2014; Blaine Marchant et al. 2016; Baniaga et al. 2019) or occupy intermediate abiotic niches that overlap those of their parents (Blaine Marchant et al. 2016), a recent global analysis of polyploids suggests that niche differentiation plays an important role in polyploid speciation, with only a minority (46%) of allopolyploid species having niches overlapping those of their parents (Baniaga et al. 2019).

Given that niche shifts are likely beneficial to the establishment of both newly originated homoploid and allopolyploid hybrid species, it is of interest to know whether they are equally frequent (and therefore possibly equally beneficial) in both types of these species or more frequent in homoploid hybrid species than in allopolyploids. To date, no broad-scale comparative analysis has been undertaken to examine this. Two approaches are typically used to quantify a species' ecological niche and niche shift: a model prediction approach and a direct observation (or ordination) approach (Broennimann et al. 2012; Guisan et al. 2014). The former relies on constructing ecological niche models (ENMs; also termed species distribution models;

Guisan and Thuiller 2005; Peterson et al. 2011) and quantifying niche on the basis of the predicted geographical distribution of a species. The niche estimated in this way assumes that a species is at equilibrium with its environment and predicts the fundamental niche of the species (Guisan and Theurillat 2000; Guisan and Thuiller 2005). In contrast, the ordination approach uses direct observations to quantify the niche, either through univariate (Lauzeral et al. 2011) or multivariate (e.g., principal component analysis [PCA]; Broennimann et al. 2010) tests. This predicts the realized niche of a species, which unlike the fundamental niche is also affected by interspecific relationships and competition (Hutchinson 1957; Colwell and Futuyma 1971; Soberón and Nakamura 2009; Soberón and Arroyo-Peña 2017). Whereas the fundamental niche indicates where a species is able to live, the realized niche is where the species actually lives. For hybrid species systems especially, divergence based on realized niches may be more important than that based on fundamental niches because of the expected strong competition likely to occur between hybrid species and their parents.

Here, we compare niche shifts of homoploid hybrid and allopolyploid species to determine their relative importance in the establishment of both types of hybrid species. In an examination of 22 homoploid hybrid and 60 allopolyploid systems (each consisting of a hybrid species and its progenitors), we employed ENM and ordination approaches to quantify the fundamental and realized niche shifts, respectively, of each hybrid species and its parents. In particular, we aimed at addressing the following questions. First, are niche shifts more frequent in homoploid hybrid species? Second, is there consistency in the major environmental factors leading to niche divergence in each type of hybrid species? In attempting to answer these questions, we have focused on abiotic niches constructed from climate, soil type, and land form variables, extracted from existing databases and relevant literature.

Material and Methods

Selection of Homoploid Hybrid and Allopolyploid Systems for Analysis

We searched the literature and selected homoploid hybrid species according to the following criteria. First, they should show genetic admixture and reproductive isolation from their progenitors (Schumer et al. 2014; Nieto Feliner et al. 2017). Second, their niches and those of their parental species could be quantified. We removed some assumed homoploid hybrid species, whose niches could not be estimated by ENM (e.g., aquatic organisms, microorganisms, parasites, and those for which there were no natural distributional records). For allopolyploid systems,

selection was based on possession of two sets of genomes in the allopolyploid donated from two identified parents. Our search yielded 22 homoploid hybrid and 60 allopolyploid systems for analysis (tables S1, S2).

Species Occurrences

We retrieved more than 8,000,000 georeferenced occurrence records for all selected homoploid hybrid, allopolyploid, and parental species from the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>, accessed August 2019 and December 2020) as well as from peer-reviewed literature (tables S1, S2). When duplicate records were present within 1 km² according to spatially correlated coordinates, latitudes, and longitudes, we removed all but one record using the function duplicated in the R package dismo (Hijmans et al. 2017; R Core Team 2019). We also excluded occasional records of species far away from their main distribution, stemming possibly from recording errors or artificial introductions. For species with fewer than five occurrences in GBIF, we selected occurrences from recorded localities following two rules: first, the elevation was within the species' elevational range; second, the habitat type was suitable for the species. For species with a worldwide distribution, we randomly selected 15,000 occurrences from all distribution records. The distribution range of each species was further checked through a search of relevant literature (tables S1, S2).

Environmental Data

We considered three aspects of abiotic niches: climate, soil, and land form. To describe each climatic niche, we downloaded all 19 bioclimatic layers from the CHELSA V2.x-V1.xx database (<https://chelsa-climate.org/downloads/>, accessed April 2019). These bioclimatic layers were derived from recent (1979–2013) records of temperature and precipitation (Karger et al. 2017). Physical and chemical soil properties—including sand, silt, clay, coarse fragment, and organic carbon content; pH; and cation exchange capacity at depths of 0–5, 5.1–15, and 15.1–30 cm—were downloaded from the SoilGrids database (<https://soilgrids.org/>, accessed April 2019; Hengl et al. 2014). The average value of all four layers for each soil property was calculated and used in analysis. The monthly soil-water stress layers were downloaded from the CGIAR-CSI database (<https://cgiarcsi.community/data/global-high-resolution-soil-water-balance/>, accessed April 2019). The average value of all 12 layers (annual soil-water stress) was calculated and used in analysis. Terrain layers, including altitude above sea level, sine of aspect, roughness, and slope, were downloaded from the EarthEnv database (<https://www.earthenv.org/topog>

raphy, accessed April 2020; Amatulli et al. 2018). All environmental layers had the length of grids with 30 arcsec (~1 km). Environment variables' abbreviations, full names, and download fields are listed in table S3.

Niche Quantification by the ENM Method

We divided the 22 homoploid hybrid and 60 allopolyploid systems into six groups for subsequent analysis according to their geographical distribution: East Asia, Europe, Latin America, North America, South America, and worldwide (tables S1, S2). For each region, we clipped environment layers and calculated Pearson's correlation coefficients for each pair of environment layers using the function `corr.test` in the R package `psych` (Revelle and Revelle 2015). Only those environment layers having correlation coefficients with other variables less than $|0.75|$ were retained, to reduce the effects of multicollinearity. Variables analyzed for each region and the whole world are listed in table S4.

We performed ENM for each species in the relevant geographical regions using occurrence data and ecological layers in Maxent (ver .3.3; Phillips et al. 2006; Phillips and Dudik 2008). All ecological layers were converted to ASCII format using the toolset conversion in ArcGIS (ver. 10.2) to satisfy the requirements of Maxent (ver .3.3; Phillips et al. 2006). We ran 10 runs of Maxent for each species by randomly choosing 75% of occurrence records for model calibration and the remainder for testing and calculating the average of 10 models. For each average model, we calculated the area under the receiver operating characteristic curve (AUC; Hanley and McNeil 1982), which in ordinary cases represents a measure of the model's ability to discriminate between suitable and unsuitable areas (Marmion et al. 2009). We also checked the results of each average ENM manually by comparing it with the distribution range obtained from the literature. Finally, we deleted hybrid species systems in which the AUC value of ENM was lower than 0.70 or the simulated range of ENM differed from the known distribution according to the literature. The remaining hybrid species systems and their ENM results were used to calculate the fundamental abiotic niche breadth and niche overlap with the R package ENMTools (Warren et al. 2010).

Fundamental niche breadth for each species was calculated according to the formula for Levins's inverse concentration measure (Levins 1968). Here, the suitability score per grid predicted by ENM was interpreted as a measure of the smoothness of the probability in the geographic distribution for a species and used to calculate Levins's B .

Pairwise niche overlap was calculated in terms of Schoener's D similarity index (Schoener 1968; Warren et al. 2008) using the equation

$$D_{ij} = 1 - \frac{1}{2} \sum_a |P_{ia} - P_{ja}|,$$

where D_{ij} represents the niche overlap between species i and species j ; P_{ia} (or P_{ja}) denotes the probability assigned by the ENM for species i (or j) to grid square a . Schoener's D has been widely used to compare habitat suitability within the geographical ranges of two species, with the index ranging from 0 (indicating no niche overlap) to 1 (indicating identical niches). Then, we tested whether the niche breadth of a hybrid species was significantly lower than that between its parents using a single-tailed Wilcoxon rank sum test (R Core Team 2019). We also used this test to determine whether the parent-hybrid overlap was significantly smaller than the parent-parent overlap and whether the parent-hybrid overlap in homoploid hybrid systems was significantly smaller than that in allopolyploid systems.

Niche Quantification by Ordination Method

For ordination, we extracted the values of each ecological layer for each occurrence of a species using the toolset extraction in ArcGIS (ver. 10.2). The package *ecospat* in R was then used to produce abiotic niche envelopes and to quantify abiotic realized niche overlap and breadth (Broennimann et al. 2012). This approach mitigates potential deviation in geographic representation caused by insufficient sampling (Broennimann et al. 2012; R Core Team 2019). The package *ecospat* initially conducts PCA of the values of abiotic factors extracted according to the occurrence of each species and maps the species occurrences to a two-dimensional multivariate environment space (i.e., PC1 vs. PC2). It then structures a niche envelope for each species by smoothing the density of occurrences in each cell in this environment space through a kernel density function. Finally, based on the niche envelopes of the two species in the environment space, niche overlap is calculated in terms of Schoener's D (using the equation above but with each P replaced by the respective species distribution density of each grid). To estimate realized niche breadth (area) of each studied species based on niche envelopes, we multiplied the variances from PC1 and PC2 (Gómez et al. 2016). Finally, the single-tailed Wilcoxon rank sum test was employed, as in the ENM method.

Niche Divergence Patterns

Based on niche breadth and overlap, we assigned each hybrid species to one of four types of niche divergence patterns: niche novelty, niche contraction, niche expansion, and niche intermediacy (following Blaine Marchant et al.

2016). Niche novelty is defined as an ecological preference by the hybrid species that deviates greatly from that of its parents. This is characterized by low niche overlap between the hybrid species and its parents; that is, any D value for a hybrid-parent pair is lower than the average D values of all parent-parent pairs. High niche overlap, in contrast, is defined as the opposite. When a hybrid species showed a high level of niche overlap with its parents, the niche divergence pattern was classified as niche contraction, niche expansion, or niche intermediacy, corresponding to a smaller, broader, or intermediate niche, respectively, compared with both of its parents.

Environmental Factors Associated with Niche Divergence of a Hybrid Species

We divided environmental variables into three types (factors)—climate, soil, and landform—to build niche models for each of these factors for each species. We then calculated the overlap of the different ecological niches constructed in this way between each hybrid species and its parents as well as between each pair of parental species. For each hybrid species system, the environmental factor showing the least niche overlap between parents and between the hybrid species and its parents was considered the most important with regard to niche differentiation.

Results

Our study included 14 angiosperm, four gymnosperm, and four animal homoploid hybrid species and their parents and 41 angiosperm and 19 fern allopolyploid species and their parents. The final data set contained more than 100,000 occurrences for 198 species (tables S1, S2). The number of occurrences for each species ranged from five for *Pinus funebris* to 15,000 for *Passer domesticus*.

Fundamental Niche

The ENMs of all species were, in general, well supported with a mean AUC score of 0.941. The lowest AUC score was 0.708 for *Passer domesticus* (tables S5, S6), which is consistent with its widespread distribution (Lobo et al. 2008). Examples of ENMs for four hybrid systems (one homoploid hybrid and three allopolyploid systems) are shown in figure 1. The mean niche breadth of hybrid species was significantly smaller than that of parental species, and this was particularly evident for homoploid hybrids (table S8). On average, the fundamental niche breadth of homoploid hybrids (0.014; range, 0.0001–0.103) was approximately five times smaller ($P < .001$) than that of their parents (0.072; range, 0.001–0.382), and on an individual

species basis this was evident for 19 (86%) of 22 homoploid hybrid species (e.g., the three *Helianthus* species), with only two having an intermediate-sized niche (*Ostryopsis intermedia*, *Yucca gloriosa*) and one a broader niche (*Senecio squalidus*; table S5). In contrast, the mean niche breadth of allopolyploids (0.143; range, 0.0005–0.928) was only ~1.25 times smaller ($P < .005$) than that of their parents

(0.181; range, 0.002–0.936), with 57% of allopolyploid species (34 of 60) having a narrower niche than their parents, 14 (~23%) having intermediate sized niches, and 12 (20%) having broader niches (table S6).

Estimates of Schoener's D indicated that in both homoploid and allopolyploid hybrid systems, hybrid species exhibited less niche overlap with their parents than

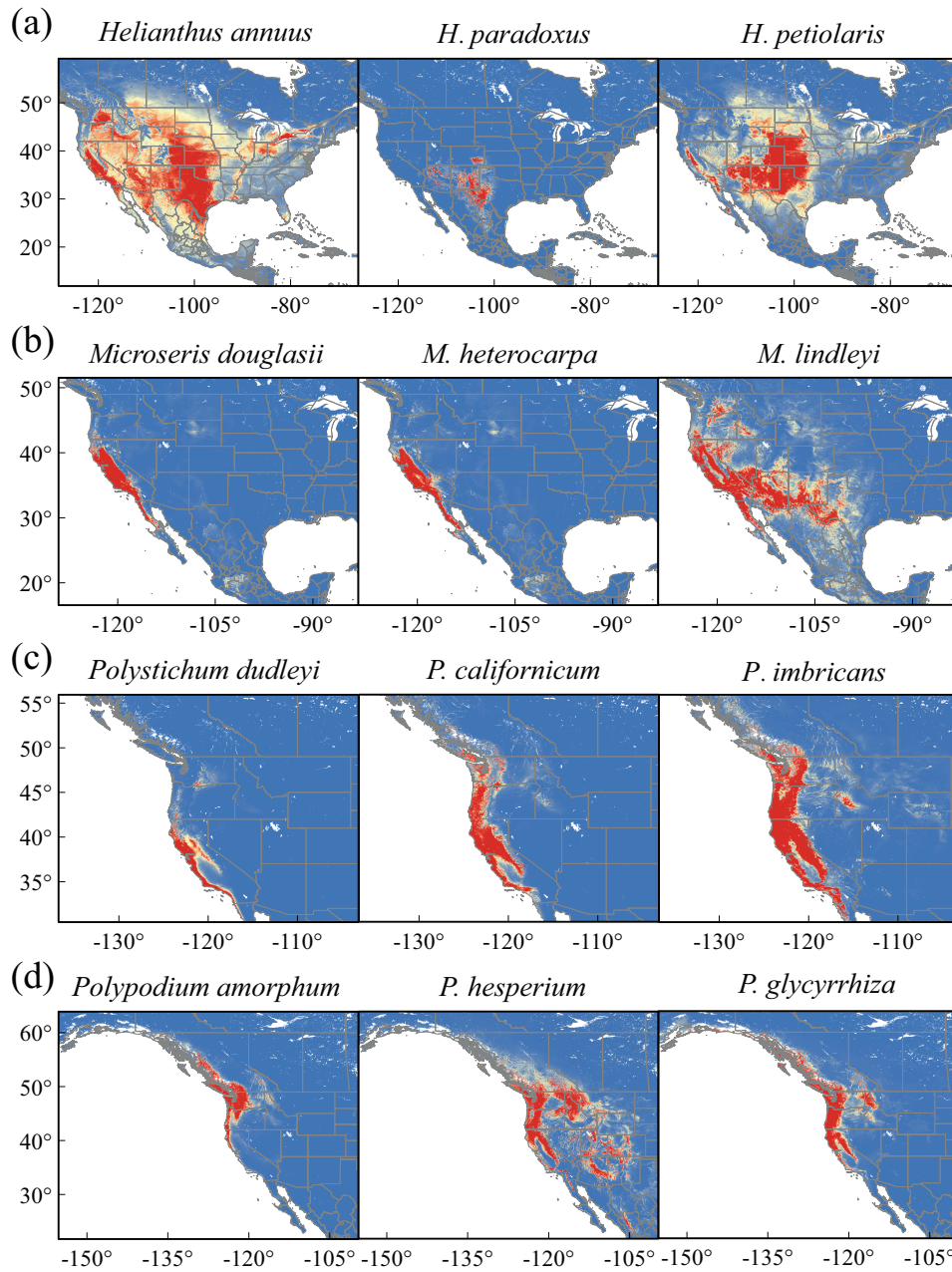


Figure 1: Fundamental abiotic niches of hybrid species (*middle*) and their progenitors (*left, right*) for a homoploid hybrid species system in which the hybrid species shows niche novelty (*a*) and three allopolyploid systems in which the allopolyploid shows niche contraction (*b*), niche intermediacy (*c*), and niche expansion (*d*).

parents did with each other. Thus, for homoploid systems average D equaled 0.267 (range, 0.021–0.638) for comparisons between hybrid species and their parents and 0.358 (range, 0.025–0.776) for comparisons between parents (table S7), while for allopolyploid systems average D equaled 0.390 (range, 0.020–0.998) and 0.433 (range, 0.040–0.928), respectively. However, in neither hybrid system was the difference significant, although it was close to significant in homoploid hybrid systems (homoploid hybrid systems: $P = .053$; allopolyploid systems: $P = .232$). Importantly, parent-hybrid overlaps in homoploid hybrid systems were significantly smaller than in allopolyploid systems ($P < .001$), although parent-parent overlaps did not differ significantly between these two systems ($P = .139$).

Realized Niche

Examples of realized niche envelopes constructed using the ordination method for four hybrid systems (one homoploid hybrid and three allopolyploid systems) are shown in figure 2. Estimates of realized niche breadth also indicated that homoploid and allopolyploid hybrid species have narrower niches compared with those of their parents. Again, this was more evident for homoploid hybrid than allopolyploid systems, with the average realized niche breadth of progenitors of homoploid hybrids (0.828; range, 0.006–9.268) almost seven times ($P < .001$) that of their descendant homoploid hybrid species (0.121; range, 0.00005–1.436; table S5), whereas that of the parents of allopolyploids (0.414; range, 0.004–4.270) was approximately 1.5 times ($P < .001$) that of allopolyploids (0.271; range, 0.002–3.137; table S6).

Regarding niche overlap, average D was similar between progenitors of both homoploid (0.378; range, 0.002–0.676) and allopolyploid (0.387; range, 0.019–0.725) species ($P = .440$; table S7). Also, for each hybrid system, parent-hybrid overlaps in realized niche were significantly smaller than parent-parent overlaps (homoploid hybrid systems: $P < .001$; allopolyploid systems: $P < .05$). However, homoploid hybrids, on average, had a realized niche overlap with their parents (0.179; range, 0.0003–0.566) significantly lower ($P < .001$) than that of allopolyploids with their parents (0.329; range, 0–0.847; table S8).

Niche Shifts of Hybrid Species

Detection of abiotic niche shifts in hybrid species (i.e., contraction, intermediacy, expansion, or occupation of a novel niche) was based on estimates of niche breadth and overlap. Hybrid species showing niche novelty occupy niches that differ and show little overlap with those of their parents (figs. 1a, 2a), while those exhibiting niche contraction, intermediacy, and expansion patterns have

niches that largely overlap those of their progenitors but are smaller, intermediate, or larger in breadth, respectively (figs. 1b–1d, 2b–2d). Hybrid species exhibiting a novel niche show greater niche divergence from their parents relative to the average degree of divergence among their parents.

In our results, 16 of the 22 homoploid hybrid species (i.e., ~73%; fig. 3a) showed fundamental niche novelty with low niche overlap ($D < 0.358$), five (~23%) exhibited niche contraction, and one (~4%) showed niche intermediacy with high niche overlap ($D > 0.358$) with both parents (fig. 2a; table S9). In comparison, a much lower proportion (~37%) of the 60 allopolyploid species exhibited fundamental niche novelty with low niche overlap ($D < 0.433$) with their parents, while one-third exhibited niche contraction, 11 (~18%) exhibited niche intermediacy, and 7 (~12%) exhibited niche expansion with high niche overlap ($D > 0.433$) with both parents (table S10).

Similar findings were obtained for estimates of realized niches. Thus, 19 (~86%) of the 22 homoploid hybrid species showed realized niche novelty with low niche overlap ($D < 0.378$), one exhibited niche intermediacy, and two showed niche expansion with high niche overlap ($D > 0.378$) of both parents (fig. 3b; table S9). In contrast, 53% of allopolyploid species showed niche novelty with low niche overlap ($D < 0.378$), while 10 exhibited niche contraction, nine showed niche intermediacy, and nine showed niche expansion with high niche overlap ($D > 0.378$) with both parents (table S10).

Taken overall, our analyses of both fundamental and realized niches indicate that niche divergence is more frequent in homoploid hybrid species compared with allopolyploid species.

Environmental Factors Associated with Niche Divergence of Hybrid Species

The environmental factors contributing to niche differentiation between hybrid species and progenitors, as well as between progenitors, varied across both homoploid and allopolyploid hybrid systems, with climate being the most common factor of importance, followed by soil and land form (tables 1, S7, S8, S11). In addition, we found that in most homoploid hybrid and allopolyploid systems the major factors contributing to niche divergence between hybrid species and progenitors differed from those causing niche differences between parents. This was the case for 64% of homoploid hybrid systems and 65% of allopolyploid systems based on the analysis of fundamental niches and 68% of homoploid hybrid systems and 70% of allopolyploid hybrid systems based on the analysis of realized niches (tables S7, S8).

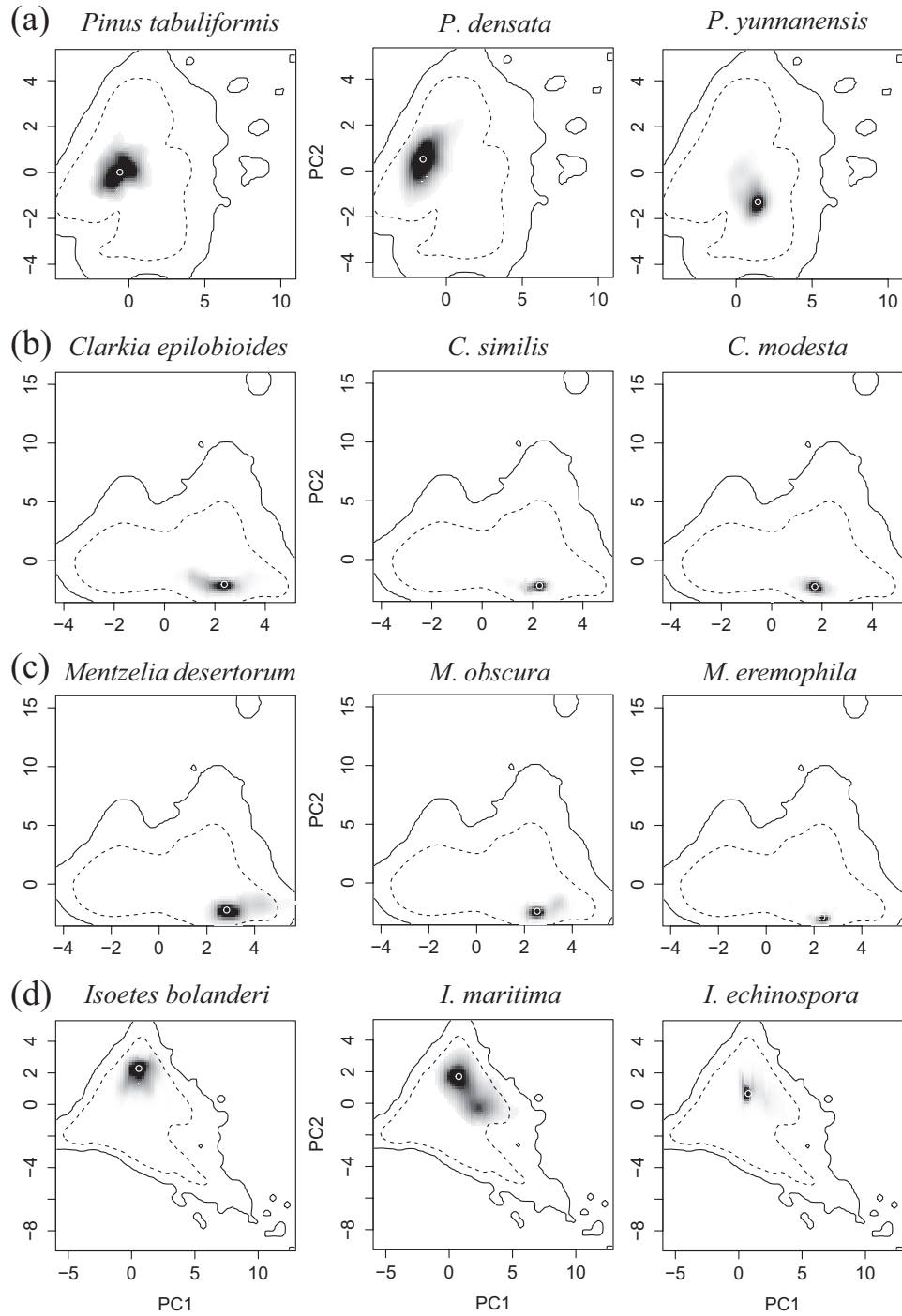


Figure 2: Realized abiotic niche of hybrid species (*middle*) and their progenitors (*left, right*) with different niche divergence patterns for a homoploid hybrid species system in which the hybrid species shows niche novelty (*a*) and three allopolyploid systems in which the allopolyploid shows niche contraction (*b*), niche intermediacy (*c*), and niche expansion (*d*).

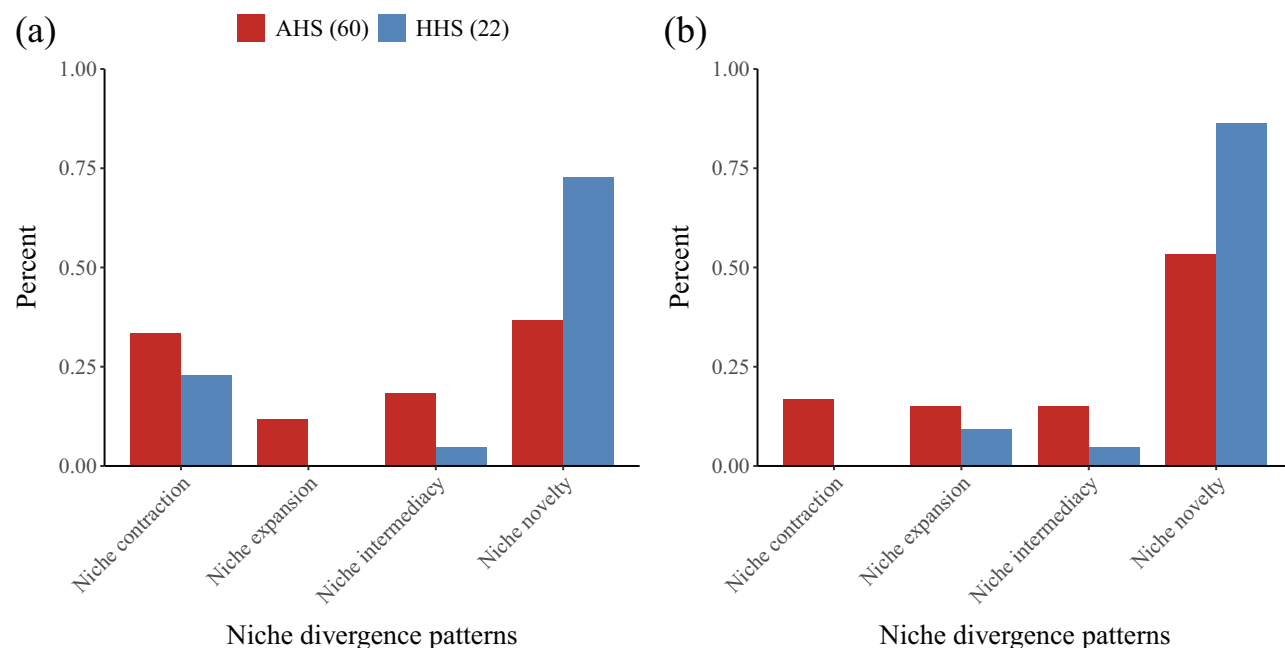


Figure 3: Proportion of niche divergence patterns in 22 homoploid hybrid species (HHS) and 60 allopolyploid systems (AHS) based on ecological niche modeling (a) and ordination analysis (b).

Discussion

Although the importance of ecological selection and habitat shift in homoploid hybrid species is widely acknowledged (Gross and Rieseberg 2005), the ecological divergence of homoploid hybrids from their parents has not been compared with that of allopolyploids species from their parents within a unified framework and across multiple systems. The comparison reported here involved analyses of 22 homoploid hybrid and 60 allopolyploid systems and showed that though abiotic niche novelty is frequent in both types of hybrid species, it is more prevalent in homoploid hybrid species. Also, niche novelty was greater for realized than for fundamental niches, with 73% and 86% of homoploid hybrid species occupying novel fundamental and realized abiotic niches, respectively, compared with 37% and 53% of allopolyploid spe-

cies, respectively. These results quantitatively support the hypothesis that homoploid hybrid speciation is more dependent than allopolyploid speciation on abiotic niche differentiation.

Niche Shift in Hybrid Species

There are two possible reasons for why abiotic niche novelty is more common in homoploid hybrid species than in allopolyploid species. First, homoploid hybrid species may often exhibit weak postzygotic reproductive isolation from their parents when first formed despite genomic/karyotypic restructuring and/or the inheritance of genetic incompatibilities between the parents (Templeton 1981; Schumer et al. 2014; Brennan et al. 2019). Consequently,

Table 1: Environmental factors (land form, climate, and soil) that contribute to niche divergence among all hybrid species and their progenitors (species number/ratio)

Factor	Fundamental niche (ENM)				Realized niche (ordination method)			
	AHS-P	P-P (AHS)	HHS-P	P-P (HHS)	AHS-P	P-P (AHS)	HHS-P	P-P (HHS)
Land form	20/.167	17/.283	3/.068	5/.227	1/.008	4/.067	0/0	1/.045
Climate	66/.550	25/.417	26/.591	14/.636	79/.658	27/.450	26/.591	17/.773
Soil	34/.283	18/.300	15/.341	3/.136	40/.333	29/.483	18/.409	4/.182

Note: Boldface type indicates statistical significance. AHS-P = allopolyploid and progenitor; ENM = ecological niche model; HHS-P = homoploid hybrid species and progenitor; P-P = two progenitors.

if these newly formed hybrids occur in sympatry with parents, they will likely be subject to considerable parental gene flow and quickly disappear following segregation in the offspring produced. In contrast, because of differences in ploidy, allopolyploids exhibit very strong post-zygotic reproductive isolation from their parents immediately following their formation and consequently may occur and be maintained sympatrically with them. Second, allopolyploids, which have larger genomes and higher heterozygosity than their corresponding progenitors, may be more successful than homoploid hybrid species in competing with their progenitors for sympatric niches, leading to persistent coexistence (Ehrendorfer 1980; Brochmann et al. 2004; Mallet 2007; Abbott et al. 2013; Rosser et al. 2015). In contrast, homoploid hybrid species may have to escape competition with their parents by colonizing new niches to ensure persistence (Stelkens and Seehausen 2009; Stelkens et al. 2009; Yakimowski and Rieseberg 2014).

The greater novelty estimated for realized relative to fundamental niches in both types of hybrid species may stem from realized niches being narrower in each case. Fundamental niches are estimated from modeled environments based on ecological variables (Hutchinson 1957; Colwell and Futuyma 1971; Soberón and Nakamura 2009; Soberón and Arroyo-Peña 2017). In addition to these variables, realized niches are likely affected by biological and other factors, for example, interspecific competition, species dispersal, and time of origin (Soberón and Arroyo-Peña 2017). With these additional factors taken into account, we might expect that niche novelty is more readily identified by an analysis of realized than fundamental niches. Interestingly, this might explain (at least in part) why the frequency of niche shifts for allopolyploid species was estimated to be lower by Blaine Marchant et al. (2016) from a comparison of fundamental niches than by Baniaga et al. (2019), who investigated realized niches.

It is to be noted that the realized niche shifts of both types of hybrid species may have been underestimated by our analysis because only abiotic divergence was investigated. In fact, for some hybrid species it is known that biotic niche divergence is more important than abiotic divergence. For example, in the homoploid hybrid species *Penstemon clevelandii*, niche divergence is due largely to a change of pollinators to bees and hummingbirds from wasps and hummingbirds that pollinate its parents, *P. spectabilis* and *P. centranthifolius*, respectively (Rentsch and Leebens-Mack 2012). Also, in *Yucca gloriosa*, a homoploid hybrid species that co-occurs with both of its parents, niche divergence is due to a difference in flowering time (Trelease 1893; Rentsch and Leebens-Mack 2012). In neither of these two hybrid species did our analysis reveal an abiotic niche shift.

Abiotic Factors Causing Niche Shifts

Climate dominates the natural distribution of numerous plant species (Woodward 1987; Pearson and Dawson 2003), and not surprisingly, therefore, climatic factors often play a critical role in determining a species niche (Colwell and Rangel 2009; Atwater et al. 2018). Furthermore, niche divergence will often stem from an adaptive response to spatial and temporal changes of climate (Colwell and Rangel 2009). Our results confirmed the importance of climatic factors, more so than soil and land form factors, in niche shifts of both homoploid hybrid and allopolyploid species from their parents as well as between parents (tables 1, S11). However, niche shifts involving both land form and soil factors were evident for homoploid hybrid species (tables 1, S11).

An interesting finding from our analysis was that niche shifts between hybrid species and their parents often appeared to be driven by different environmental factors from those effecting divergence between their parents, and this was more apparent in homoploid hybrid than in allopolyploid systems. For example, the homoploid hybrid species *Picea purpurea* occurs at high elevations on the Qinghai-Tibet Plateau in Asia, where it is tolerant to strong solar radiation, whereas its two parents are distributed in different climates and soils at lower elevations (Sun et al. 2014; Ru et al. 2018; Wang et al. 2018). In addition, the three sunflower homoploid hybrid species—*Helianthus anomalus*, *H. deserticola*, and *H. paradoxus*—occur in habitats that differ from those of their progenitors in soil composition and salinity, while ecological divergence of their parents largely involves climatic factors (Rieseberg et al. 2003). Transgressive segregation during homoploid hybrid speciation, which generates genotypes exhibiting novel transgressive traits, is likely to be a major driver of such niche divergence (Schwarzbach et al. 2001; Rieseberg et al. 2003; Vereecken et al. 2010; Yakimowski and Rieseberg 2014).

On average, niche breadth of homoploid hybrid species was much smaller than that of their parents relative to that of allopolyploid species compared with their parents. This might be due, in part, to the greater heterozygosity of allopolyploids and their potential to occupy a broader range of environments as a result. Consequently, homoploid hybrids could be considered as specialists with allopolyploids considered more as generalists with regard to adaptation, resulting in homoploids having a relatively smaller niche breadth. However, in most cases both types of hybrids may be regarded as specialists compared with their parents, which in general have broader niches. Specialization in adaptation is favored in small populations as well as in the presence of interspecific competition (Whitlock 1996; Sargent and Otto 2006; Sexton et al. 2017). It is therefore perhaps not unexpected that hybrid species often have

narrower niches relative to their parents, given that their population sizes will be very small at their time of origin, when they will likely also be subjected to intense interspecific competition with their parents. However, exceptions to the rule of hybrid species having narrower niches than their parents were evident, particularly in allopolyploid systems where the greater heterozygosity of allopolyploids could be a potential cause. This needs investigating in greater detail in the future. Only one homoploid hybrid species was found to have a broader niche than its parents. This was the case for *Senecio squalidus*, which is widespread in the United Kingdom and geographically isolated from its parents, which are mainly restricted to high and low elevations, respectively, on Mount Etna, Sicily (Abbott et al. 2000). The spread of *S. squalidus* in the United Kingdom was aided by humans, both in terms of the introduction of hybrid material and the creation of railways and highly disturbed urban sites that it readily colonized free of competition from its parents (James and Abbott 2005).

Taken overall, our results highlight the significance of niche divergence in the establishment and persistence of hybrid species, particularly homoploid hybrid species, enabling them to escape competition and gene flow from their parents. In addition to niche divergence, selfing, assortative mating, and the inheritance of parental incompatibility alleles may also promote hybrid speciation, and the significance of these factors and their interactions with niche changes should be explored in the future. Because of human activities, species that were previously isolated from each other by geographical and ecological barriers are being brought together, increasing the frequency of interspecific hybridization (Vallejo-Marín and Hiscock 2016). Such activities often create new and open habitats and, therefore, opportunities for niche divergence to occur, which hybrid species can exploit (Brennan et al. 2014). It is therefore feasible that the frequency of hybrid speciation might be increasing at the present time and will continue to do so during the Anthropocene (Abbott 1992; Thomas 2015).

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Statement of Authorship

J.L., X.X., and Z.X. designed the research; D.W., H.Z., and J.F. collected data; D.W. analyzed data and visualized results; D.W. and X.X. wrote the original manuscript; and J.L. and R.J.A. revised the manuscript.

Data and Code Availability

Data and code supporting the findings of this work are available through the Dryad Digital Repository (<https://doi.org/10.5061/dryad.t4b8gtj39>; Wang et al. 2022). The file “GBIF” contains all used species occurrences downloaded from the Global Biodiversity Information Facility (GBIF). The files “occurrences_cleaned_allopolyploid” and “occurrences_cleaned_homoploid” contain the occurrence data from both GBIF and the literature.

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