


LETTER

Polyploid plants have faster rates of multivariate niche differentiation than their diploid relatives

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Abstract

Polyploid speciation entails substantial and rapid postzygotic reproductive isolation of nascent species that are initially sympatric with one or both parents. Despite strong postzygotic isolation, ecological niche differentiation has long been thought to be important for polyploid success. Using biogeographic data from across vascular plants, we tested whether the climatic niches of polyploid species are more differentiated than their diploid relatives and if the climatic niches of polyploid species differentiated faster than those of related diploids. We found that polyploids are often more climatically differentiated from their diploid parents than the diploids are from each other. Consistent with this pattern, we estimated that polyploid species generally have higher rates of multivariate niche differentiation than their diploid relatives. In contrast to recent analyses, our results confirm that ecological niche differentiation is an important component of polyploid speciation and that niche differentiation is often significantly faster in polyploids.

Keywords

Climatic niche, niche breadth, polyploid, speciation, sympatric speciation.

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INTRODUCTION

Among vascular plants, polyploidy or whole genome duplication (WGD) is associated with an estimated 15–30% of speciation events (Wood *et al.* 2009). These WGD events are also common throughout the evolutionary history of vascular plants (Landis *et al.* 2018), such as the ancestry of seed plants (Jiao *et al.* 2011; Li *et al.* 2015), angiosperms (Amborella Genome Project 2013), core eudicots (Tuskan *et al.* 2006; Jallion *et al.* 2007; Jiao *et al.* 2012; Vekemans *et al.* 2012), as well as taxonomically rich clades like the Asteraceae (Barker *et al.* 2008; Huang *et al.* 2016; Barker *et al.* 2016a; Badouin *et al.* 2017) and Poaceae (Paterson *et al.* 2004; Paterson *et al.* 2009; Estep *et al.* 2014; McKain *et al.* 2016). However, most nascent polyploid lineages have lower estimated net diversification rates than their diploid relatives (Mayrose *et al.* 2011). This may be due to the multiple ecological and evolutionary obstacles that newly formed polyploid species face such as small population sizes and competition with their diploid relatives (Otto & Whitton 2000; Comai 2005; Arrigo & Barker 2012; Barker *et al.* 2016b).

Competition significantly influences the ecological niches of species (Connell 1961; MacArthur 1972), and the niches of closely related species tend to be more similar to each other than to those of more distantly related ones (Harvey & Pagel 1991; Wiens 2004; Pyron *et al.* 2015). Considering the abrupt origins of polyploid species, interspecific competition likely plays an important role in whether polyploid species establish and persist. This is because newly formed polyploid species are initially imbued with substantial postzygotic

isolation from their progenitors, while also sympatric and competing with either one or both parental species (Ramsey & Schemske 1998, 2002). Mathematical models indicate that polyploid establishment is promoted by high selfing rates, high rates of polyploid formation, local propagule dispersal and ecological niche differentiation (Levin 1975; Fowler & Levin 1984; Felber 1991; Rodriguez 1996; Husband 2000; Baack 2005; Rausch & Morgan 2005; Fowler & Levin 2016). The importance of ecological niche differentiation is also supported by species coexistence theory (Tilman 1982, 1985; Chesson 2000, 2004) which suggests that coexistence of related species, such as polyploid and progenitor species, is possible if they have different resource needs or utilisation strategies.

Some polyploid species are long known to have different geographical distributions, novel ecological niches and wider niche breadths than their progenitors (Hagerup 1932; Tischler 1937; Wulff 1937; Love & Love 1943; Clausen *et al.* 1945; Stebbins 1950; Stebbins 1971; Levin 1975). However, previous analyses have found mixed support for the importance of ecological niche differentiation to polyploid establishment (Stebbins 1971; Felber-Girard *et al.* 1996; Petit & Thompson 1999; Martin & Husband 2009; Glennon *et al.* 2014; Marchant *et al.* 2016). This is surprising given that polyploids may adapt faster than diploids (Orr & Otto 1994; Otto & Whitton 2000; Otto 2007; Selmecki *et al.* 2015).

To better understand the role of ecological niche differentiation during polyploid speciation, we evaluated the rates of climatic niche differentiation of polyploids and their diploid

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relatives. We explored two aspects of climatic niche differentiation in polyploid species. First, we analysed the amount of climatic niche overlap between allopolyploid species and their diploid progenitors in 25 genera of plants. We then examined whether polyploid species, in which we did not know whether they were allo- or autopolyploid, evolved multivariate climatic niche traits (mean and breadth) at faster rates than their diploid relatives in 33 genera of plants. We hypothesised that if climatic niche differentiation is not important for polyploid establishment, then the rates of climatic niche differentiation of polyploid species would not be significantly different than those of diploid species. Conversely, if climatic niche differentiation is important for polyploid establishment, we expected polyploid species to have faster rates of climatic niche differentiation than related diploids. Our results provide insight into the importance of ecological divergence for polyploid species establishment, and highlight the role of ecological divergence in speciation processes generally.

MATERIALS AND METHODS

Climatic niche overlap between allopolyploid species and their diploid progenitors

Data on allopolyploids and their known diploid parents were collected from the literature. We used the Taxonomic Name Resolution Service v4.0 (Boyle *et al.* 2013) to verify taxonomy and filter non-valid species. This filtering left 52 trios comprised of two diploid parents and an allopolyploid, which included 131 unique taxa from 16 families and 25 genera. In this dataset, 18 diploid species were parents of at least two or more allopolyploid species.

For each species we downloaded all available georeferenced locations from the union of the Global Biodiversity Information Facility (GBIF.org 2016), the Consortium of California Herbaria 2016, and SEINet Portal Network 2016. Georeferenced data were cleaned by removing duplicate records using the R *dismo* package duplicated function, and any record in which latitude or longitude was not precise to two decimal points was excluded. Occurrences were then manually examined for erroneous records. Refinements were based on literature data in cases of unclear species ranges.

We used Ecospat to quantify the multivariate climatic niche overlap among the taxa of a trio (Broennimann *et al.* 2012). We chose to employ Ecospat for two key reasons. First, it applies a kernel density function to occurrence points to mitigate potential biases in geographic representation related to sampling effort. Second, it reduces the dimensionality of climate data into two dimensional space, and projects this onto a gridded landscape for direct calculation of niche metrics. Background areas which represent the potential geographic distribution of a taxon were defined by adding one decimal degree to a taxon's maximum and minimum known geographic coordinates (Barve *et al.* 2011). All 19 current bioclimatic variables 1960–1990 (Hijmans *et al.* 2005) at 2.5 min resolution were used to estimate Schoener's D as implemented by Ecospat (Schoener 1968; Warren *et al.* 2008). In this implementation, Schoener's D represents an unbiased measure of the occurrence density of two species ranging from no overlap

($D = 0$) to complete overlap ($D = 1$). Schoener's D was calculated for the species in each trio (allopolyploid + parent 1; allopolyploid + parent 2; parent 1 + parent 2) with 100 pixel resolution for the grid of environmental space.

After pairwise calculations of Schoener's D for each trio, trios were grouped into three classes of climatic niche overlap, defined by the amount of climatic niche overlap of an allopolyploid species with its parents relative to the amount of climatic niche overlap shared between parents. These include 'P DD' where the allopolyploid species has less overlap with both parents than parents to parents; 'PD D' where the allopolyploid species has less overlap with one parent than parents to parents; and 'DPD' where the allopolyploid species has more overlap with both parents than parents to parents (Figure 1). A two-tailed binomial exact test was used to assess if the observed distribution of these relationships was different than our null expectation of equal frequencies ($p = 0.333$).

Rates of climatic niche differentiation in polyploid and diploid species

We developed a database of vascular plant polyploid and diploid species including their chromosome numbers in which the state of allo- or autopolyploid was not completely known for all members of a genus (Barker *et al.* 2016c). We filtered the database for genera with > 20 taxa with known chromosome counts. This filtering left a total of 33 genera from 20 families comprising 1706 taxa of which 537 were listed as polyploid species. Members of eight of the allopolyploid trios from the section above were also represented in this dataset.

For each taxon, all georeferenced locations were downloaded from GBIF. Data were then cleaned by removing duplicate records, imprecise records < 2 decimal points, and erroneous misspecification of decimal degree format. Six current bioclimatic variables 1960–1990 (Hijmans *et al.* 2005) important to defining a species climatic niche (BIO1 Annual Mean Temperature, BIO5 Max Temperature of Warmest Month, BIO6 Min Temperature of Coldest Month, BIO12 Annual Precipitation, BIO16 Precipitation of Wettest Quarter, BIO17 Precipitation of Driest Quarter) at 30 arcsecond resolution were extracted for each locality using the R package 'dismo' (Hijmans *et al.* 2016). These bioclimatic variables were chosen because they highlight climatic averages as well as extremes important to defining a species climatic niche (Kozak & Wiens 2006).

Using these six bioclimatic variables, we constructed four multivariate niche traits for each species of a genus; 'PC1 and PC2 Niche Mean' and 'PC1 and PC2 Niche Breadth'. The PC1 and PC2 Niche Mean was constructed in several steps. First, by constructing a matrix of the arithmetic mean of each bioclimatic variable for each species. In this matrix, each column represents a bioclim variable, each row represents a species, and each cell represents the mean of a species for that bioclim variable across its geographic range. Second, we standardised each column by dividing the standard deviation of each genus bioclim value by each species value. This was done for all six bioclim variables so that variables with larger possible ranges did not bias the ordination. Third, all six bioclim columns for each species of the

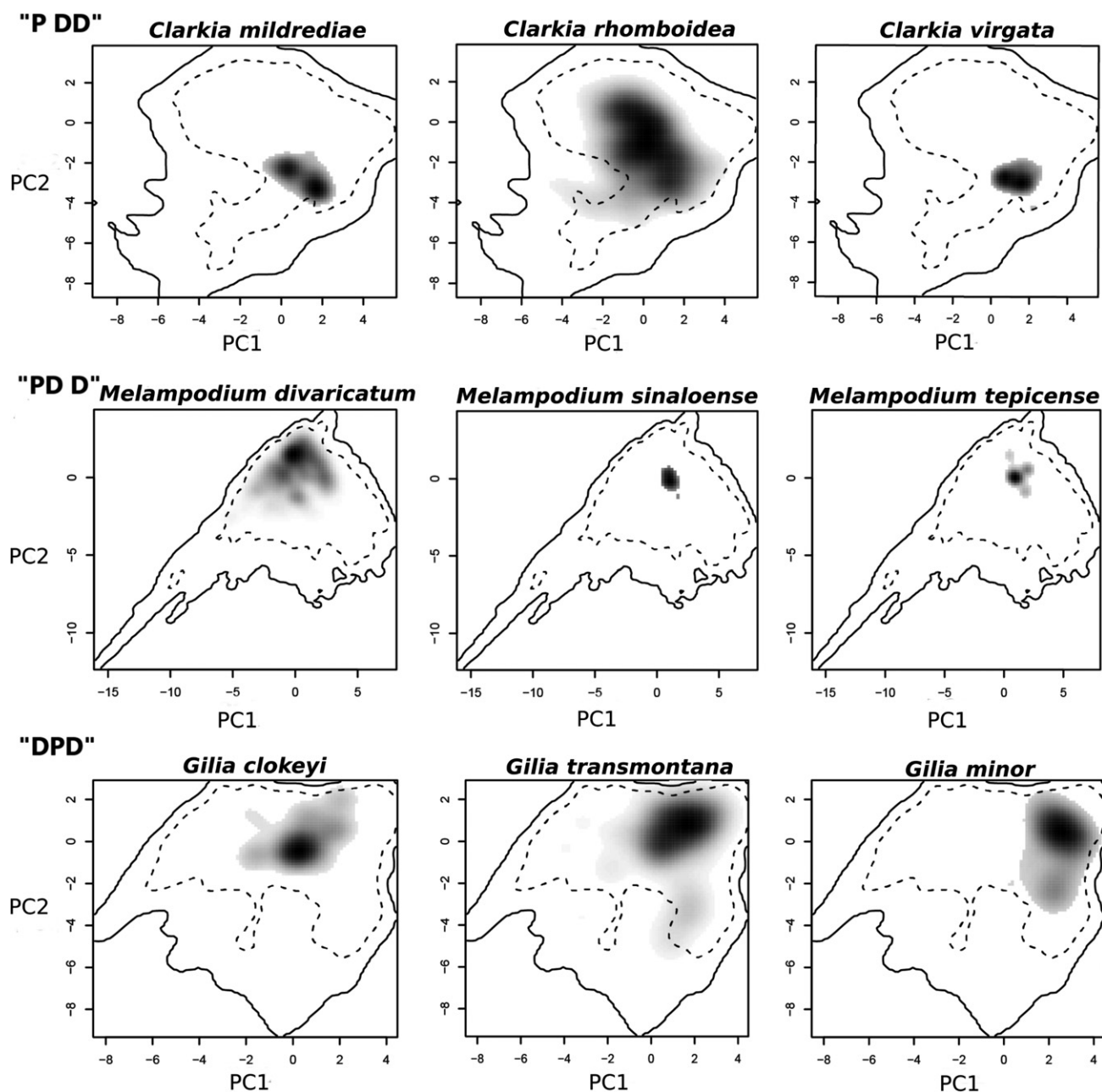


Figure 1 Climatic niche overlap in allopolyploid species and their diploid progenitors. Examples of three classes of climatic niche overlap, defined by the amount of climatic niche overlap an allopolyploid species shares with its parents relative to that found between parents. Climatic niche overlap diagrams produced by R ecospat (Broennimann et al. 2012). The grey shading represents the density of occurrences of each species. The solid and dashed contour lines show 100 and 50% of the available (background) environmental space. Parental diploid species are represented on the left and right, and allopolyploid species are represented in the middle. Representative examples include: Example 1 ('P DD') the allopolyploid species has less overlap with both parents than parents to parents; Example 2 ('PD D') the allopolyploid species has more overlap with both parents than parents to parents; Example 3 ('DPD') the allopolyploid species has more overlap with both parents than parents to parents.

matrix were analysed with a principal component analysis (PCA) using the R 'prcomp' function (see Table S1 and S2). From this PCA we extracted the principal component scores for each species on axes one (PC1) and two (PC2) to represent our multivariate Niche Mean PC1–PC2. We also used the R 'FactoMineR' package to examine the average contribution of each bioclimatic variable to each of the four multivariate climatic niche traits. Niche breadth was calculated

in the same manner with another matrix, and instead of calculating arithmetic mean we calculated the variance a species experiences across its range for a given bioclimatic variable. We used these four multivariate climatic niche traits (PC1–PC2 Niche Mean; PC1–PC2 Niche Breadth) for each species of a given genus to explore whether polyploids had similar, slower, or faster rates of climatic niche differentiation than diploids of the same genus.

In order to infer the rate of change of our multivariate niche traits throughout the evolutionary history of a given genus we built a phylogeny. First, we collected either a plastid or nuclear molecular marker for all species of a genus with sequence data on GenBank (Table S3). We then used BLASTN to identify an outgroup species for each genus with the highest sequence similarity to members of the genus. Then, genus level phylogenies were inferred with MrBayes v3.1.2 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). We accounted for topological uncertainty by sampling 50 trees from the posterior distribution of the MrBayes output (Table S4). Branch lengths were rescaled to have the same distance from tip to root in each of the 50 trees with the 'chronos' function in the R ape package (Paradis *et al.* 2004) under a correlated clock model and a smoothing parameter (λ) = 1.

We then inferred ploidal changes in the evolutionary history of the species in a genus using chromEvol v1 (Mayrose *et al.* 2010), which provides likelihood estimates of different chromosomal changes at each node in a phylogeny. For our chromEvol analyses, we used the highest posterior probability tree for each genus as our species tree, and all available chromosome counts from the literature (Table S2). The maximum likelihood estimates of ploidal changes occurring at each node were examined and used to identify species and clades that shared a WGD event. In this framework, any species that had one or more WGDs in its history was classified as a polyploid. We did not identify polyploid species as auto- or allopolyploids. After pruning the outgroup and species that did not have a chromosome count (Table S2), we mapped ploidal changes on each of the 50 trees using SIMMAP in R (Revell 2012).

With our four multivariate climatic niche traits (PC1–2 Niche Mean and PC1–2 Niche Breadth), and 50 trees with mapped character states (diploid vs. polyploid), we performed our rate analyses using OUwie (Beaulieu *et al.* 2012) for each genus. For each of the four multivariate climatic niche traits (PC1–PC2 Niche Mean; PC1–PC2 Niche Breadth), we tested whether polyploid and diploid species had the same (BM1) or different rate (BMS) of multivariate climatic niche differentiation. In the OUwie framework this corresponds to the same brownian motion rate parameter (σ^2 polyploids = σ^2 diploids) inferred for the two states, or a different brownian motion rate parameter inferred for the two states (σ^2 polyploids, σ^2 diploids). We selected the best fitting model using two approaches: (1) a likelihood ratio test (LRT) with an alpha of 0.05 and (2) the corrected Akaike Information Criterion (AICc) where the more sophisticated model (BMS) was preferred when $\Delta\text{AICc} > 4$.

When the two rate model was better supported (BMS), we divided the inferred rate parameter for polyploid species (σ^2 polyploids) by the inferred rate parameter for diploids (σ^2 diploids). In instances when the BM1 model was preferred, polyploid and diploid species had the same inferred rate parameter (σ^2 polyploids = σ^2 diploids) and we set the rate = 1. These rate calculations were summarised for each multivariate niche trait (PC1, PC2) by calculating the geometric mean of all 50 rate tests and binning each into three classes: higher (σ^2 polyploids > σ^2 diploids), lower (σ^2

polyploids < σ^2 diploids), or no difference (σ^2 polyploids = σ^2 diploids) in rate of niche differentiation between polyploids and diploids. We used a two-tailed binomial exact test ($P < 0.05$) to assess whether the number of genera observed having a higher, lower, or no difference in the rate of niche differentiation between polyploid and diploid species was significantly different from chance.

To assess the power of our analyses, we compared the observed frequencies of each rate class per genus to the distributions of rate classes found in a permutation test. Permutation tests were conducted for each genus and each multivariate niche trait by randomly assigning the status diploid/polyploid to each taxon, weighted by the number of taxa that were polyploid in that genus, and performing the OUwie model test 100 times per tree for a total of 5000 permutations per trait per genus. Model selection was performed as above with selection by a LRT and AICc. Each rate test was binned into a rate class where polyploids had higher, lower, or no difference in the rate of climatic niche differentiation compared to diploids. These frequencies were used to calculate expected frequencies. A chi-square test ($P < 0.05$, d.f. = 2) was performed on whether the observed values of the number of trees per genus in each rate class deviated from the expected number in each of the three rate classes.

RESULTS

Climatic niche overlap between allopolyploid species and their diploid progenitors

Our analyses supported the prediction that most polyploid species had different climatic niches than their diploid progenitors. Of the 52 comparisons involving one allopolyploid species and its two diploid progenitors, 28 (54%) had a 'P DD', 10 (19%) had a 'PD D' pattern, but only 14 (27%) had a 'DPD' pattern. Assuming an equal probability of each of these three patterns, we found a statistically significant excess of 'P DD' ($P < 0.01$) relative to the other two patterns (see Table S5 for all comparisons).

Rates of multivariate climatic niche differentiation in polyploid and diploid species

Across all genera, PC1 and PC2 on average cumulatively explained 54.1 and 84.8% of the variation in the data for Niche Mean. Similarly, PC1 and PC2 on average cumulatively explained 55.9 and 82.6% of the variation in the data for niche breadth across all genera (see Table S1; S2). On average Mean Annual Temperature (BIO1) and Annual Precipitation (BIO12) contributed the most to PC1 and PC2 for both Niche Mean and Breadth (Table 1).

Polyploid species had stronger multivariate climatic niche differentiation relative to congeneric diploids than that expected by chance ($P < 0.01$). Polyploid species consistently had significantly higher rates under different model selection approaches (AICc and LRT), and across all four multivariate climatic niche traits of Niche Mean (PC1–2) and Niche Breadth (PC1–2). In general, the AICc and LRT found qualitatively similar results (Fig. 2), but quantitative estimates of

Table 1 Bioclimatic variable importance. The average contribution (%) of each bioclimatic variable calculated across all genera to each multivariate niche trait (full results in S2). The rows ‘SUM Niche Mean’ and ‘SUM Niche Breadth’ correspond to the sums of each bioclimatic variable (PC1 + PC2)

	BIO1	BIO5	BIO6	BIO12	BIO16	BIO17
PC1 Niche mean	19.99	16.66	12.82	19.2	14.18	17.14
PC2 Niche mean	17.3	16.17	14.12	18.29	19.25	14.86
SUM Niche mean	37.29	32.83	26.94	37.49	33.43	32
PC1 Niche breadth	20.95	18.84	13.82	17.45	13.91	15.02
PC2 Niche breadth	18.1	17.28	16.34	19.4	13.11	15.77
SUM Niche breadth	39.05	36.12	30.16	36.85	27.02	30.79

rates of niche differentiation (Table S6) and maxima as well as minima differed (Table 2).

The following brief descriptions of genus variability in multivariate niche differentiation consider results from the more conservative AICc models. Within a genus, similar trends were found for multivariate Niche Mean (PC1–2) and Breadth (PC1–2) with few exceptions. These include genera where there was no inferred difference between polyploid and diploid

species on one PC axis but a difference was found on the other PC axis. Except for the genera *Orobanche* (Orobanchaceae), *Plantago* (Plantaginaceae) and *Silene* (Caryophyllaceae), that had either lower or no difference in inferred rates for polyploid species across all niche traits, all other genera had at least one multivariate niche trait with a greater inferred rate of niche differentiation in polyploid species.

We used a permutation test to assess if the correlated trends in the rates of multivariate niche differentiation could have been inferred by chance. Most genera had zero or one multivariate niche trait with a distribution that was indistinguishable from our observed frequencies (Table S7). However, the genera *Draba* (Brassicaceae), *Ranunculus* (Ranunculaceae) and *Veronica* (Plantaginaceae) – which had high proportions of polyploid species – also had the only instances where two or more niche traits were inferred to have a pattern similar to chance.

DISCUSSION

Polyploid speciation is one of the most common forms of sympatric speciation in plants. These species begin with

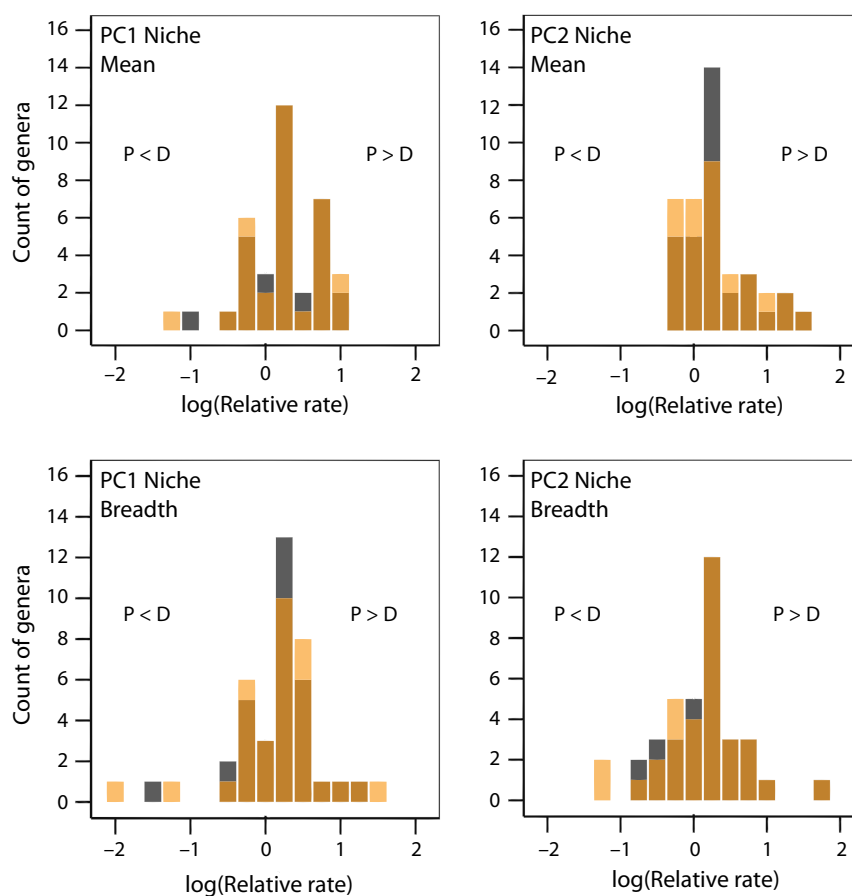


Figure 2 Relative rate estimates for multivariate climatic niche mean and breadth. The x-axis represents the log transformed relative rate (σ^2 polyploids/ σ^2 diploids) between the polyploid species (P) of a genus and their diploid congeners (D) for each multivariate niche trait. The y-axis represents the number of genera in each bin (binwidth = 0.25). A relative rate value of 0 represents scenarios where polyploid species had no difference in the rate of climatic niche differentiation between polyploid and diploid species ($P = D$). Labels further denote counts of genera where polyploid species had lower inferred rates than their diploid congeners ($P < D$), and faster inferred rates for polyploid species ($P > D$). The results from both the AICc (black) and LRT (orange) models are displayed.

Table 2 Summary of multivariate niche mean and breadth analyses

Multivariate climatic niche trait	Higher rate in polyploids	No rate difference	Lower rate in polyploids	Maximum relative rate	Minimum relative rate
AICc					
PC1 Mean	23**	3	7	9.44 (<i>Muhlenbergia</i>)	0.15 (<i>Eragrostis</i>)
PC2 Mean	19**	9	5	18.21 (<i>Aconitum</i>)	0.68 (<i>Cuphea</i>)
PC1 Breadth	22**	3	8	21.66 (<i>Muhlenbergia</i>)	0.033 (<i>Centaurea</i>)
PC2 Breadth	20**	5	8	36.59 (<i>Asplenium</i>)	0.24 (<i>Centaurea</i>)
LRT					
PC1 Mean	23**	2	8	9.76 (<i>Muhlenbergia</i>)	0.071 (<i>Eragrostis</i>)
PC2 Mean	19**	7	7	18.75 (<i>Aconitum</i>)	0.68 (<i>Cuphea</i>)
PC1 Breadth	21**	3	9	21.66 (<i>Muhlenbergia</i>)	0.0082 (<i>Centaurea</i>)
PC2 Breadth	20**	3	10	36.59 (<i>Asplenium</i>)	0.074 (<i>Anemone</i>)

The number of genera in each of the three rate classes: a higher rate inferred for polyploids than diploids, no rate difference, and a lower inferred rate for polyploids than diploids of the same genus. Maximum and minimum relative rate estimates (σ^2 polyploids/ σ^2 diploids) are displayed and the corresponding genus. Results are presented for both the Akaike Information Criterion (AICc) and likelihood ratio test (LRT) model selection criteria. The level of significance displayed ($P < 0.01$)** is based on a two-tailed binomial exact test assuming an equal probability of each rate scenario ($P = 0.333$).

substantial post-zygotic reproductive isolation, but there has been mixed support for the importance of ecological differentiation during polyploid speciation (Felber-Girard *et al.* 1996; Petit & Thompson 1999; Martin & Husband 2009; Glennon *et al.* 2014; Marchant *et al.* 2016). We found that the ecological niches of polyploid species often differentiated faster than their diploid relatives across vascular plants. This was the case in both assessments of ecological niche divergence – comparisons of niche overlap with diploid relatives and phylogenetic estimates of the rates of multivariate niche differentiation. We found a majority of 52 allopolyploid species to have less climatic niche overlap with their parents than the parents had with each other. Consistent with this observation, we also found that a majority of polyploid species from 33 genera had significantly faster rates of multivariate Niche Mean and Niche Breadth differentiation compared to their diploid relatives. Thus, our analysis indicates ecological differentiation is a common and likely important component of polyploid speciation.

Our finding that polyploid species have different climatic niches, and a faster rate in which they assemble these niches than their diploid relatives is consistent with theoretical expectations. A significant ecological obstacle to polyploid establishment is minority cytotype disadvantage (Levin 1975). Nascent polyploid species are initially present at low numbers in populations of their diploid progenitors and must overcome frequency dependent gametic competition with their parents. Although regional coexistence may be possible without niche differentiation through stochastic processes and local dispersal (Baack 2005), simulations consistently find that polyploid establishment is promoted by ecological niche differentiation (Levin 1975; Fowler & Levin 1984; Felber 1991; Rodriguez 1996; Husband 2000; Rausch & Morgan 2005; Fowler & Levin 2016). Analyses of paleopolyploidy also indicate that polyploid species survived mass extinction events better than their diploid relatives (Vanneste *et al.* 2014; Lohaus & Van de Peer 2016). The relatively fast rates of ecological differentiation we observed may explain this phylogenetic pattern. Our results confirm that ecological divergence from progenitor species is a common and likely critical step in polyploid speciation. Polyploid species may also be differentiated from their

progenitors in other dimensions, such as phenology or pollinators. Our current estimates should be considered a lower bound on the degree of ecological differentiation of polyploid and diploid species. Future work that leverages the growing body of trait data (Maitner *et al.* 2017) could extend our analyses of climatic niches to better capture the ecological divergence of polyploids.

The divergence in climatic niches we observed in polyploid species may stem from the immediate phenotypic effects of WGD. Recently formed polyploid species manifest allometric phenotypic changes from an increase in nuclear DNA content due to positive relationships with cell size and volume (Speckman *et al.* 1965; Bennett 1972; Cavalier-Smith 1978; Melargno *et al.* 1993; Beaulieu *et al.* 2008; Chao *et al.* 2013). These effects on the phenotype are numerous, at times idiosyncratic, but important to how nascent polyploids interact with the abiotic and biotic environment. For example, Chao *et al.* (2013) found that the increase in cell size that accompanied WGD caused increased potassium uptake and salinity tolerance. This type of abrupt, genotype independent change of ecological niche may explain some of the divergence in ecological niche observed in our analyses. Other physiological differences associated with WGD include changes in propagule volume (Barrington *et al.* 1986), size and density of stomata (Sax & Sax 1937; Maherli *et al.* 2009), resistance to drought and cold (Levin 1983), and secondary metabolites and phenology (Levin 1983; Segraves & Anneberg 2016). The many cases examined in our analyses provide a starting point for exploring the contribution of these potential avenues for WGD – independent of genotype – to alter plant physiology and ecological niche.

Polyploid species may also diverge in their climatic niches faster than their diploid relatives because of differences in genetic variation and selection associated with ploidal level increase. Evolutionary genetic theory predicts that polyploid species may adapt faster than diploid species depending upon how beneficial mutant alleles are masked (Orr & Otto 1994; Otto & Whitton 2000; Otto 2007). Recent experiments support these predictions in yeast (Selmecki *et al.* 2015). The capacity for a greater response to selection may stem from increased genetic diversity from WGD paralogs, although the

proximate mechanisms are diverse. Immediately following WGD an increase in alleles may mask deleterious mutations and increase the probability of acquiring new beneficial mutations (Otto 2007). Paralogs can also diverge in function through sub- or neofunctionalisation (Force *et al.* 1999; Lynch & Force 2000), which may lead to the evolution of novel adaptive traits (Levin 1983; Flagel & Wendel 2009; Edger *et al.* 2015). In addition, the increased genetic variation of polyploid species may come from rapid and diverse structural genomic changes (Song *et al.* 1995; Chester *et al.* 2012) and the multiple origins of such populations (Ownbey 1950; Werth *et al.* 1985; Brochmann *et al.* 1992; Soltis & Soltis 1999; Doyle *et al.* 2003). Recent analyses of how polyploids respond to abiotic stress (Bardil *et al.* 2011; Akama *et al.* 2014; Paape *et al.* 2016; Takahagi *et al.* 2018) suggest this variation is important for polyploid establishment and that it may play a role in the climatic niche differences we observed.

Previous analyses of niche differentiation in polyploid species found less consistent patterns (Felber-Girard *et al.* 1996; Petit & Thompson 1999; Martin & Husband 2009; Glennon *et al.* 2014; Marchant *et al.* 2016). Our observation of on average faster rates of climatic niche differentiation in polyploid species relative to diploids may be because of three main factors. First, we did not restrict our dataset of diploid and polyploid species to either a single clade or a single regional or continental area. This allowed us to expand our sample size to the largest dataset to date of polyploid and related diploid species. Second, our analyses took into account phylogeny and sequence divergence in relation to the change in climatic niche. Although previous analyses have investigated smaller datasets of auto- or allopolyploid species and their diploid progenitors (Glennon *et al.* 2014; Marchant *et al.* 2016; Visger *et al.* 2016), none examined a genus with the phylogeny taken into account. Finally, our dataset may be biased towards allopolyploids. Our first analysis focussed solely on these taxa. Auto- and allopolyploids are present, on average, in nearly equal proportions in nature (Barker *et al.* 2016c). However, autopolyploids are much less likely to be named than allopolyploids and probably under-represented in our analyses. Given that this bias is inherent in the taxonomy of polyploid species, most analyses of polyploid biogeography are likely impacted by it.

The hybrid origins of allopolyploid species may provide a significant source of increased genetic diversity compared to autopolyploid species. Hybridisation can increase the amount of additive genetic variance which can be adaptive depending upon the environmental context (Anderson 1949; Stebbins 1959; Lewontin & Birch 1966; Stebbins 1985; Seehausen 2012; Bailey *et al.* 2013; Eroukhanoff *et al.* 2013; Grant & Grant 2016). This genetic variance can also lead to a range of different phenotypes including intermediate, mosaic or transgressive phenotypes (Rieseberg *et al.* 1999; Dittrich-Reed & Fitzpatrick 2013). Allopolyploid species inherit these novel evolutionary combinations, which may allow them to explore divergent ecological niches from their diploid progenitors. Indeed, recent evidence from natural populations of the *Alyssum montanum* species complex (Brassicaceae) highlights the importance of hybridisation in the evolution of climatic niches. Allopolyploid cytotypes of *A. montanum* have more

divergent and higher rates of climatic niche differentiation than their related autopolyploid cytotypes and diploid progenitors (Arrigo *et al.* 2016). Whether such biology is the norm for polyploid species remains to be tested, but our results indicate that it could be common across vascular plants.

A majority but not all allopolyploid species were faster in their rate of climatic niche differentiation relative to their diploid progenitors or congeners. Such exceptions may be due to methodological limitations or a true lack of climatic niche differentiation of these allopolyploid species. In the analyses of climatic niche overlap, we included all nineteen bioclimatic variables at 2.5 min resolution which corresponds to roughly 21.62 km² at the equator or 12.58 km² at 40° latitude. Although this resolution increases with increasing latitude it may be too coarse to capture fine scale climatic niche differences (Baack & Stanton 2005; Glennon *et al.* 2014; Kirchner *et al.* 2016). Additionally, the abiotic conditions of climate comprise a subset of the many axes that may be important in defining a taxon's realised niche, and one set of abiotic axes that we did not consider are those related to edaphic conditions. Differences in edaphic tolerances have been shown to strongly differentiate closely related plant taxa (van der Niet & Johnson 2009; Anacker & Strauss 2014; Shimizu-Inatsugi *et al.* 2017), but will not leave a signature of climatic niche divergence because they will appear to have the same climatic niche. This is especially true of edaphic endemics when the progenitor(s) are geographically more widespread, such as the composite *Layia discoidea* (Gottlieb *et al.* 1985; Gottlieb 2004; Baldwin 2005), or populations on mine tailings as in the grass *Anthoxanthum odoratum* (Antonovics *et al.* 1971, 2006). Differences in edaphic tolerances may explain some of the cases in our analysis where similar climatic niches were observed between allopolyploid species and their diploid progenitors.

We also found that polyploid species consistently differentiate niche breadths at faster rates than their diploid congeners, but we did not explicitly examine whether polyploid species had broader or narrower niche breadths. Understanding the role of niche breadth on nascent polyploid establishment is ripe for future study because niche breadth has a strong relationship to both speciation and extinction processes and ultimately diversification (Janzen 1967). Depending on the conceptual framework, both broad and narrow niche breadths may promote diversification (Sexton *et al.* 2017). Broad niche breadths may promote diversification because generalists are more likely to have larger ranges (Slayter *et al.* 2013) and thus lower extinction rates due to a possible 'dead-end' effect of specialisation (Schluter 2000). However, species with narrow niche breadths have been found to have faster rates of niche evolution (Huey & Kingsolver 1993; Whitlock 1996; Fisher-Reid *et al.* 2012) as well as higher diversification rates (Hardy & Otto 2014; Rolland & Salamin 2016; Qiao *et al.* 2016). Future analyses that link changes in niche breadth to the genetic variation of polyploid species may contribute to our understanding of the macroevolutionary patterns of polyploid diversification.

Future analyses should also investigate when the changes, if any, in the ecological tolerances of polyploid species occur. Our analysis was not developed to understand when these

changes occurred, such as immediately upon polyploid formation or later on in their evolutionary trajectory, but rather to investigate a general pattern across vascular plants. We demonstrated that polyploid species more often than expected by chance have more rapid rates of climatic niche differentiation than their diploid relatives.

A central question of speciation research is how intrinsic postzygotic reproductive isolation arises within populations of reproductively compatible individuals. Many models of speciation, such as the classic Bateson-Dobzhansky-Muller model (Bateson 1909; Dobzhansky 1934; Muller 1939), solve this problem by proposing that postzygotic reproductive isolation evolves after geographic or ecological isolation. Although speciation with gene flow is possible (Barluenga *et al.* 2006; Niemiller *et al.* 2008; Nosil *et al.* 2009; Yeaman & Otto 2011; Yeaman & Whitlock 2011; Feder *et al.* 2012; Nosil & Feder 2012; Martin *et al.* 2013; Wolf & Ellegren 2016; Samuk *et al.* 2017), most models require some degree of physical separation for intrinsic postzygotic isolation to arise (Coyne & Orr 2004; Gavrillets 2004). In contrast, polyploid species begin with substantial postzygotic isolation from their progenitors while also sympatric with one or both parental species (Ramsey & Schemske 1998, 2002). By inverting the usual order of events during speciation, polyploid species provide a unique test of the importance of ecological differentiation to speciation in general. Our result that the climatic niches of polyploid species often differentiated faster than their diploid relatives across vascular plants highlights the importance of ecological differentiation for polyploid species.

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AUTHORSHIP

AB and MSB conceived of project. AB and NA generated the dataset. AB and HM performed analyses. AB and MSB co-wrote the manuscript.

DATA AVAILABILITY STATEMENT

All necessary R scripts, data, and files supporting the results are available from the Figshare Repository: <https://doi.org/10.6084/m9.figshare.9862781>.

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SUPPORTING INFORMATION

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

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