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RESEARCH ARTICLE

Autopolyploid lineage shows climatic niche expansion but not divergence in *Arabidopsis arenosa*

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PREMISE OF THE STUDY: Successful establishment of neopolyploids, and therefore polyploid speciation, is thought to be contingent on environmental niche shifts from their progenitors. We explore this niche shift hypothesis in the obligate outcrosser *Arabidopsis arenosa* complex, which includes diploid and recently formed autotetraploid populations.

METHODS: To characterize the climatic niches for both cytotypes in *Arabidopsis arenosa,* we first gathered climatic data from localities with known ploidy types. We then estimated the climatic niches for diploids and autotetraploids and calculated niche overlap. Using this niche overlap statistic, we tested for niche equivalency and similarity. We explored differences in niches by estimating and comparing niche optimum and breadth and then calculated indices of niche expansion and unfilling.

KEY RESULTS: Climatic niche overlap between diploids and autotetraploids is substantial. Although the two niche models are not significantly divergent, they are not identical as they differ in both optimum and breadth along two environmental gradients. Autotetraploids fill nearly the entire niche space of diploids and have expanded into novel environments.

CONCLUSIONS: We find climatic niche expansion but not divergence, together with a moderate change in the niche optimum, in the autotetraploid lineage of *Arabidopsis arenosa*. These results indicate that the climatic niche shift hypothesis alone cannot explain the coexistence of tetraploid and diploid cytotypes.

KEY WORDS *Arabidopsis arenosa*; autopolyploidy; Carpathian Mountains; environmental niche models; minority cytotype disadvantage; niche expansion; niche shift hypothesis; polyploid speciation; whole-genome duplication.

Speciation initiated by whole-genome duplication, or polyploidy, is widespread throughout plant evolution (Grant, 1981; Soltis et al., 2007; Wood et al., 2009). Despite the high incidence of polyploidization, the success of a new polyploid lineage is thought to be largely dependent on its ability to ecologically diverge from the progenitor lineage(s). It has been hypothesized that neopolyploid lineages will be successful only if they establish a new ecological niche or spread to a new geographic location and therefore avoid competing with and mating with parental lineages (Levin, 1975, 1983, 2002; Fowler and Levin, 1984). Although this has been a long-standing hypothesis (Hagberg and Ellerström, 1959; Cavanah and Alexander, 1963; H. Lewis, 1967; W. Lewis, 1967; Anderson, 1971; Borrill and Lindner, 1971), recent advances in niche analyses can provide novel insights into if and how successful establishment of polyploid lineages involves shifts in their niches (Parisod and Broennimann, 2016).

In general, new species face two challenges: (1) they must evolve reproductive isolation to prevent gene flow with closely related species; and (2) they must establish a unique niche, either through ecological divergence or successfully outcompeting other species (Coyne and Orr, 2004; Via, 2009; Barton, 2010). Because crosses between plants of different ploidy levels frequently result in reduced hybrid fertility (Husband and Schemske, 2000; Husband and Sabara, 2004; Sweigart et al., 2008; Borges et al., 2012; Greiner and Oberprieler, 2012; Gross and Schiestl, 2015; Roccaforte et al., 2015; Pegoraro et al., 2016; however, see Lafon-Placette et al., 2017), it has been suggested that polyploidization causes instantaneous speciation (Schluter, 2000, 2001; Rundle and Nosil, 2005). However, for a new polyploid lineage to become a new species, it must also overcome the challenge of establishing a self-sustaining population. In this way, ecological adaptation can play a significant role in the process of polyploid speciation.

A central challenge faced by neopolyploids is avoiding costly hybridization with parental lineages. Levin (1975) described this selection against newly formed polyploids as the "minority cytotype disadvantage" (MCD). When initially formed neopolyploids are rare relative to their progenitor lineages, they will often mate with the more frequent diploid lineages. These cross-cytotype matings often fail or result in sterile hybrids and therefore significantly impede successful propagation and establishment of a stable polyploid population (Husband, 2000). Hence, the MCD represents a significant challenge for polyploid establishment and speciation.

One primary mechanism by which the MCD can be overcome is through habitat segregation by niche divergence or what is known as the "niche shift hypothesis" (NSH) (Husband, 2000; Levin, 2004). The study of niche divergence has experienced recent advances due to the availability of global climate data and the development of novel analytical approaches (Wiens and Graham, 2005; Warren et al., 2008; Broennimann et al., 2012). These advanced methods and data availability combined with taxon distribution data have allowed for the development of refined environmental niche models (ENMs) that characterize species niches and allow assessment of how niches vary between species (Guisan et al., 2014). Niche divergence is characterized by the extent of niche overlap, which is evaluated using tests for niche equivalency and niche similarity (Warren et al., 2008).

Niche equivalency is a conservative test that determines if two observed niches are identical. Rejecting this null hypothesis indicates that the two niches are not statistically equivalent (Fig. 1). The niche similarity test determines if niches are more similar than expected by chance, testing if the ENM of one taxon predicts the ENM of another taxon better than a null model (Fig. 1). The null model in the niche similarity test controls for the geographic distribution of the species to determine if the two niches are more similar than would be expected given the niches available across the geographic range of the species (Warren et al., 2008). The niche similarity test is less stringent than the niche equivalency test but is often underpowered to detect significant similarity or differences between niches. If ENMs are not conserved, as indicated by the niche equivalency and the niche similarity test, they can differ in niche optimum, niche breadth, or both. Differences in niche optimum are caused by differences in the occupied environmental conditions (i.e., differences in the "mean" niche), while differences in niche breadth are caused by the expansion of a niche or the "unfilling" of taxa's ecological tolerances (Petitpierre et al., 2012; Guisan et al., 2014; Di Cola et al., 2017).

Previous empirical analyses of niche divergence between diploids and polyploids have produced inconsistent results across species leading to ambiguous patterns. Most of the reported examples about ecological consequences of polyploidization, which use niche-modeling approaches, come from studies focused on allopolyploids. Although several studies show niche divergence between allopolyploids and at least one of their progenitors (Glennon et al., 2012, 2014; Theodoridis et al., 2013; Harbert et al., 2014; Han et al., 2015; López-Alvarez et al., 2015; Marchant et al., 2016), other studies show allopolyploid lineages have intermediate or non-divergent ecological niches (Oberprieler et al., 2012; Glennon et al., 2014; Harbert et al., 2014; Boucher et al., 2016; Marchant et al., 2016; Casazza et al., 2017). For autopolyploids, some studies have found significant ecological segregation between polyploids and their ancestors (Schönswetter et al., 2007; Stahlberg, 2009; Thompson et al., 2014; Hülber et al., 2015; Zozomová-Lihová et al., 2015; Lazaroff et al., 2016; Mandák et al., 2016; Mered'a et al., 2016; Sonnleitner et al., 2016; Visger et al., 2016), and yet other studies find no ecological divergence between cytotypes (Godsoe et al., 2013; Hanzl et al., 2014). Most of the reported studies are limited to evaluating if niches are conserved but do not investigate how the niches of the two cytotypes differ in aspects such as optima and breadths (but see Kirchheimer et al., 2016). Understanding if and how polyploids undergo ecological niche shifts remains a persistent challenge.

We performed a thorough characterization of whether and how polyploid niches diverge from progenitor niches using the *Arabidopsis arenosa* (L.) Lawalrée (Sand rock-cress) complex (Brassicaceae). *A.*

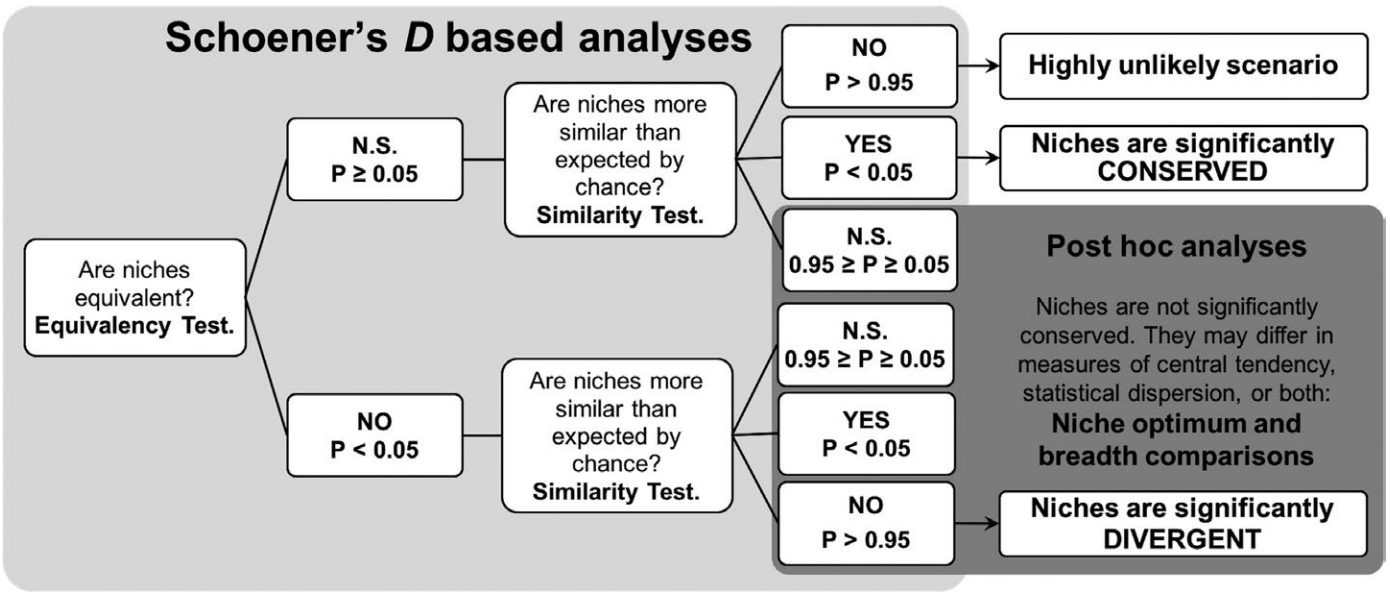

FIGURE 1. Workflow diagram describing the niche evolution analyses performed in this study, and the conclusions derived from the possible test results. N.S. represents a non-significant result.

arenosa is an obligate outcrosser closely related to *A. lyrata* (L.) O'Kane & Al-Shehbaz and the genetic model plant *A. thaliana* (L.) Heynh. (Al-Shehbaz and O'Kane, 2002). Diploid (2n = 2x = 16) *A. arenosa* populations are found in Eastern Europe and the Balkans, and along the southern Baltic Coast in Poland, whereas polyploid (2n = 4x = 32) populations are broadly distributed through Central and Northern Europe. Recent genome-wide sequence analyses have resolved the phylogenetic relationships and demographic histories within the *A. arenosa* complex (Kolář et al., 2016a; Novikova et al., 2016; Yant and Bomblies, 2017; Monnahan et al., 2018 [preprint]). Although these phylogenetic results differ from the previously described taxonomy of the group based on morphology (e.g., Měsíček and Goliašová, 2002; Schmickl et al., 2012; Hohmann et al., 2014), we will use the demographic history inferred from the genome-wide analyses as the evolutionary framework for our study.

Diploid populations of *Arabidopsis arenosa* are split into three highly divergent lineages (Kolář et al., 2016a; Monnahan et al., 2018 [preprint]): (1) The Carpathian lineage, found in the mid-altitudes to high altitudes of the western Carpathians in Slovakia, and mid-altitudes of southern and eastern Carpathians in Romania and the southern Dinarides in Serbia. The Carpathian lineage also includes diploid populations found along the Baltic sea coast; (2) the Dinaric lineage, found in the foothills of the Dinaric Alps and their surroundings in Slovenia, Croatia, and Bosnia and Herzegovina; and (3) the Pannonian lineage, found in the Pannonian lowlands of Hungary and southern Slovakia. The Carpathian and Dinaric lineages diverged approximately 650,000 generations ago, whereas the Pannonian lineage diverged approximately 760,000 generations ago from the Carpathian-Dinaric ancestor (Kolář et al., 2016a). The widespread *A. arenosa* tetraploid cytotype represents an autopolyploid lineage with chromosome segregation during meiosis showing no evidence of pairing preference (Hollister et al., 2012; Arnold et al., 2015, 2016). The autotetraploids likely originated from a single ancestral population that arose approximately 11,000-30,000 generations ago in the Carpathian Mountains, where its closest living diploid relatives are still found (Arnold et al., 2015; Monnahan et al., 2018 [preprint]), and the two cytotypes broadly overlap (Schmickl et al., 2012; Kolář et al., 2016b). Although gene flow from both tetraploid *A. lyrata* and diploid *A. arenosa* into tetraploid *A. arenosa* has been reported (Jørgensen et al., 2011; Arnold et al., 2016; Novikova et al., 2016; Baduel et al., 2018; Monnahan et al., 2018 [preprint]), even the hybrid lineages show fully random chromosome pairing and trace back to a single origin with subsequent gene flow between geographically proximal taxa.

Here, we applied ENM to estimate the climatic niche spaces of autotetraploid lineage and the diploid progenitor lineage (the Carpathian lineage). We restrict our analyses of diploids to just the Carpathian lineage because the tetraploid lineage arose from the Carpathian lineage far more recently than the Carpathian lineage divergence from the other diploid lineages. We used an ordination-based analysis of climate variables to assess shifts in environmental space between cytotypes. Then, we applied a resampling method to evaluate differences in ENM optimum and breadth between cytotypes. If climatic niche differentiation was important for autotetraploid *Arabidopsis arenosa* establishment, we hypothesize that the niches of the two cytotypes are divergent. However, we find climatic niche expansion but not divergence, together with a moderate change in the niche optimum, in the autotetraploid lineage.

MATERIALS AND METHODS

Locality and climate data collection

To characterize the climatic niches for both cytotypes (diploid and autotetraploid) in *Arabidopsis arenosa,* we retrieve climate data from specific locations where the species is known to grow. We only used locality information from occurrences for which ploidy was determined using flow cytometry (Schmickl and Koch, 2011; Schmickl et al., 2012; Yant et al., 2013; Wright et al., 2015; Kolář et al., 2016a, b; Novikova et al., 2016). We sampled every known population that fit our criteria at the time of our analysis. We collected a total of 311 presence data points corresponding to 103 Carpathian diploid populations (the ancestral lineage for the tetraploids, including 10 presence data points from the Baltic Sea coast) and 208 autotetraploid populations (Fig. 2, Appendix S1) (see the Supporting Information tab online with this article). These populations are from both the allopatric portion of the lineages' ranges as well as the sympatric region where there is some history of inter-ploidy hybridization (Monnahan et al., 2018 [preprint]). As reported in Appendix S2, we also performed our analyses on diploid populations from across the *A. arenosa* range by

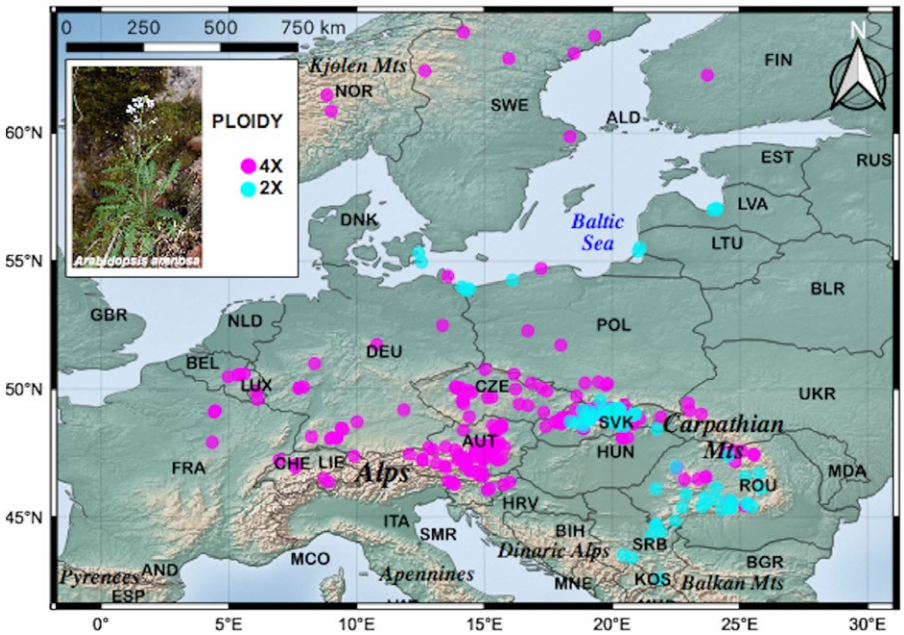

FIGURE 2. Map of *Arabidopsis arenosa* populations used for niche modeling analyses (n = 311) in Central and Northern Europe with ploidy verified by flow cytometry. Magenta circles represent autotetraploid (4x, n = 208), and cyan circles represent Carpathian diploid (2x, n = 103) populations. Photo of *A. arenosa* courtesy of K. Bomblies.

adding 47 populations from the Pannonian and Dinaric lineages to our data set (Appendix S1). We extracted climate data for each georeferenced location from the WorldClim version 1.4 database: http://www.worldclim.org/current (Hijmans et al., 2005) at a ~1 km^2 resolution, using '*raster*' package (Hijmans and Van Etten, 2012) in R version 3.5.0 (R Core Team 2012). The WorldClim database is based on spatially interpolated data between weather stations and average values of climate variables from 1950 to 2000. We included all available climate variables in our analyses (Appendix S3).

We estimated the 'background region' to extract climate data for the niche similarity analyses (see below). The background region is a set of data points in the vicinity of the presence data of both cytotypes that establishes the environmental domain available to the taxa given the geographic range. This area is much broader than the presence data, which include just the conditions under which a species is known to occur. To create the background region, we projected the geographic coordinates for each population in ArcGIS version 9.3 (Environmental Systems Research Institute, Redlands, California, USA) and drew a convex polygon around all projected data points to delineate the observed geographic range. We then randomly select points within this polygon to create a climate 'background region'.

Niche-modeling analyses

Our ENM analyses were divided into four parts. First, we estimated the niches for diploids and tetraploids and calculated niche overlap. Second, we tested for ENM equivalency and similarity. Third, we estimated and compared ENM optima and breadths. Finally, we calculated ENM expansion-unfilling indices.

Niche overlap estimates—We estimated the ENMs using the package '*ecospat*' (Broennimann et al., 2012; Di Cola et al., 2017) in R version 3.5.0 (R Core Team 2012). Specifically, we used an ordination approach (Principal Component Analysis, PCA) to estimate the occurrence and climatic factor densities along environmental axes (PCA-env) and used these densities to calculate ENM overlap. ENM overlap was evaluated using the Schoener's *D* metric (Schoener, 1968) that varies from 0 (no overlap) to 1 (complete overlap).

Niche equivalency and similarity tests—Equivalency and similarity tests are complementary measures of ENM divergence, but they test slightly different hypotheses. The niche equivalency test evaluates if ENMs are statistically identical when compared directly with each other using a bootstrap resampling approach (Warren et al., 2008; Broennimann et al., 2012). For each ENM comparison, we generated a null distribution of divergence based on all the observed presence data points. Specifically, we pooled all the presence data points for both cytotypes in the comparison and resampled by randomly reassigning presence points to two sets. We then calculated *D* on these resampled sets. We resampled 1000 times to create a null distribution of *D*. If the observed *D* is less than the null distribution of *D*, then the hypothesis of niche equivalency is rejected, and ENMs are not equivalent. If niches were not equivalent, we evaluated differences in niche optimum and breadth to determine why (Fig. 1).

The ENM similarity test uses bootstrap resampling to evaluate if one ENM predicts the other better than a randomly generated ENM from the geographic range (Warren et al., 2008; Broennimann et al., 2012). We estimated a null distribution of ENM similarity by extracting climate variables from a randomly generated set of geographic localities within the 'background region' containing both cytotypes. The ENM based on these background points is our 'random' ENM. We compared this random ENM to the actual ENM of each lineage calculated by the presence data using the D statistic. For each comparison, we resampled the background points 1000 times comparing actual diploid and tetraploid ENM to random background ENM. Observed *D*'s greater than the null distribution indicate that ENMs are more similar than expected given their geographic ranges, while values significantly less than the null distribution indicate ENMs divergence. A non-significant result from the similarity test indicates that there is low power to detect similarities or differences or the expected similarity between niches given the null hypothesis pulled from the geographic ranges is very high, and thus the actual niche differentiation merely is what is expected by chance. If niches were not similar, we proceeded to test differences in niche optimum and breadth (Fig. 1).

Niche optimum and breadth estimates—Schoener's *D* offers an estimate of niche conservatism versus divergence; however, it carries limited information regarding how the niches of the two cytotypes vary. Specifically, Schoener's *D,* and therefore our tests of equivalency and similarity, do not discriminate between differences in niche optima and breadths (Glennon et al., 2014).

If compared niches were not significantly equivalent, we calculated the ENM optimum and the ENM breadth, respectively, as the median and the length of the 95% inter-percentile interval along the first two PCA-env axes (Broennimann et al., 2012). We evaluated if diploid and autotetraploid differed in ENM optimum and breadth using a bootstrap resampling approach. For each comparison, we generated a null distribution of differences in the ENM optima and the ENM breadths based on all the observed presence data points. Specifically, we pooled all the presence data points for both cytotypes and resampled by randomly reassigning presence points to two sets. Then, we calculated the median and the length of the 95% inter-percentile interval on these two resampled sets and estimated their differences. We resampled 1000 times to create a null distribution of differences in the ENM optima and the ENM breadths. If the observed difference in the median is higher than the null distribution of median differences, then the hypothesis of similar ENM optima is rejected. If the observed difference in 95% inter-percentile interval is higher than the null distribution, then the autotetraploid ENM has expanded with respect to the diploid ENM. To calculate the observed differences in breadth, we subtracted diploid from autotetraploid estimates.

Niche dynamic indices of expansion and unfilling—Niche overlap between cytotypes can be characterized by niche unfilling and niche expansion. To calculate the degree of unfilling and expansion of autotetraploids we used the package '*ecospat*' (Di Cola et al., 2017) in R version 3.5.0 (R Core Team 2012). Unfilling is the proportion of the diploid ENM density located outside the tetraploid ENM. Expansion is the proportion of the autotetraploid ENM density located outside the diploid ENM density. This classification provides additional information about the drivers of the niche dynamic between diploid and autotetraploid lineages (Petitpierre et al., 2012; Guisan et al., 2014; Di Cola et al., 2017).

RESULTS

We estimated a climatic niche overlap of 54.1% between the progenitor diploid and the tetraploid *Arabidopsis arenosa* (Schoener's D = 0.541). Schoener's D based tests of equivalency and similarity show that diploid and autotetraploid niches are not equivalent (P = 0.002) but are more similar than expected by chance in both comparisons (2x → background: P = 0.042 and 4x → background: P = 0.045) (Fig. 3). We found qualitatively similar results when we compared the tetraploid linages to the all diploid lineages (Appendix S2).

The first two components of our principal components' analysis (PCA-env) explain 74.38% of the total variance observed in the climatic dataset. PC1 corresponds to a precipitation axis and describes 44.11% of the variance with BIO12 (annual precipitation), BIO17 (precipitation of driest quarter), and BIO19 (precipitation of coldest quarter) having the greatest contributions. PC2 corresponds to a temperature axis and describes 30.27% of the variance with BIO11 (mean temperature of coldest quarter), BIO6 (minimum temperature of coldest month), and BIO1 (annual mean temperature) having the greatest contributions (Fig. 4, Appendix S3).

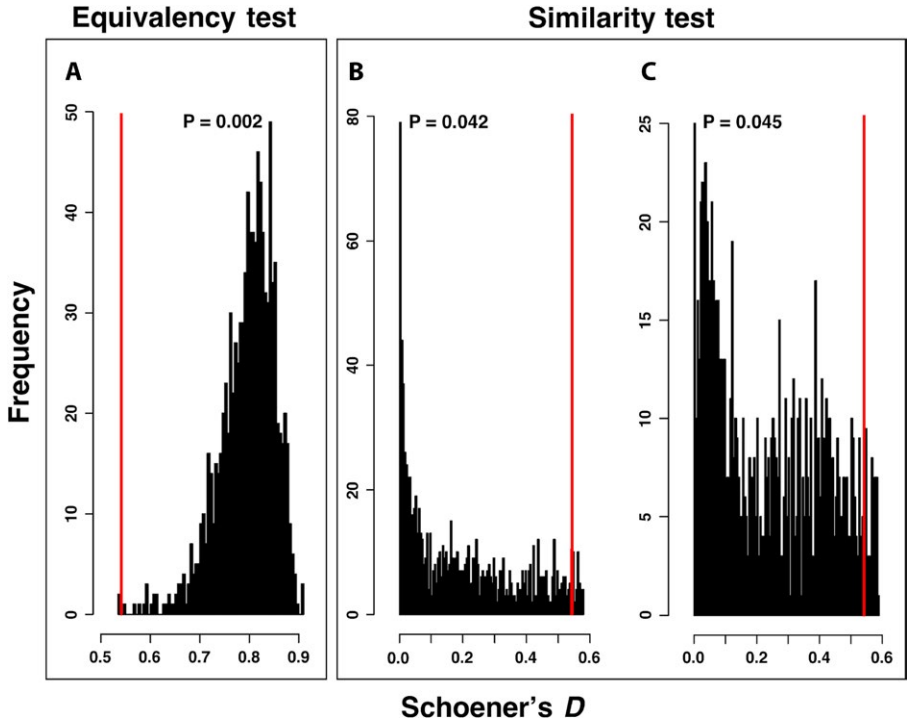

FIGURE 3. Histograms of Schoener's D based bootstrap tests with 1000 resamples. Black bars indicate resamples of estimated and red line represents observed D = 0.541. (A) Equivalency test, which predicts no statistically significant differences between alternative niche models. (B) Similarity test (2x → background), and (C) Similarity test (4x → background).

Analyses of niche optimum and breadth show that tetraploid and diploid niches differ in both optimum and breadth along the two PCA-env axes. Optimum along PC1 differs 0.116 PC units (P < 0.01) and optimum along PC2 differs 1.023 PC units (P < 0.001). Breadth along PC1 differs 0.849 PC units (P < 0.001) and breadth along PC2 differs 2.489 PC units (P < 0.001) (Fig. 5, Table 1, Appendix S4). Finally, niche dynamic indices reveal that the tetraploid niche has expanded 24% from of the diploid niche and has left <1% of the diploid niche unfilled.

DISCUSSION

Polyploid lineages must persist in the face of competition and costly hybridization with its diploid progenitors. The niche shift hypothesis (NSH) proposes that the ecological niche of polyploid lineages must diverge for these lineages to successfully establish (Levin, 1975; Fowler and Levin, 1984). Some studies support the NSH. For instance, it has been reported that polyploids are generally found in drier (Hagerup, 1932; Watanabe, 1986; Maherali et al., 2009; Treier et al., 2009) and more exposed habitats than diploids (Rothera and Davy, 1986; Watanabe, 1986; Lumaret et al., 1987; Brammall and Semple, 1990). However, the extent to which polyploids are adapted to more extreme environments and therefore differentiated from diploids remains controversial (te Beest et al., 2012). Our work uses refined analyses of environmental niches to test the NSH in the autotetraploid lineage of *Arabidopsis arenosa*. We found that the tetraploid niche has a significant degree of overlap with the diploid niche, and yet is not conserved. Niche differences result from an increase in tetraploid niche breadth and a small but significant change in optimum.

Recent advances in ecological niche modeling analyses provide new opportunities to understand whether and how neopolyploid lineages have altered their niches to allow successful establishment. We used Schoener's D, as a summary statistic for niche overlap, to test the hypothesis of niche conservatism versus niche divergence (Warren et al., 2008). Niches are conserved when two specific criteria are satisfied (Fig. 1): (1) niche equivalency hypothesis is not rejected (i.e., $0.025 \leq P \leq 0.975$); and (2) niche similarity test is significant (i.e., $P < 0.05$). If niches are divergent, or not conserved, they can vary in their breadth, optimum, or both.

We determined if and how the *Arabidopsis arenosa* tetraploid niche diverged from the diploid progenitor. In general, we found that the niche overlap between cytotypes was equal or higher for *A. arenosa* than has been observed in other diploid-autopolyploid species complexes (Glennon et al., 2012; Thompson et al., 2014; Kirchheimer et al., 2016; Visger et al., 2016). Despite a high degree of overlap, the autotetraploid niche is not identical to the diploid niche, as evaluated by the equivalency test, but when controlling for geographic range, the two niches are statistically "similar." Although both equivalency and similarity tests assess niche conservatism, their approaches are slightly different, and therefore this type of inconsistency is common when comparing niches (e.g., Glennon et al., 2014).

The test for niche equivalency is conservative as it directly compares two niches and asks if they are identical. The test for niche similarity controls for the geographic range of the taxa by asking if, given the possible niches available in their ranges, two species maintain similar niches or shift and expand into new niches. The ability to detect significant similarity is therefore

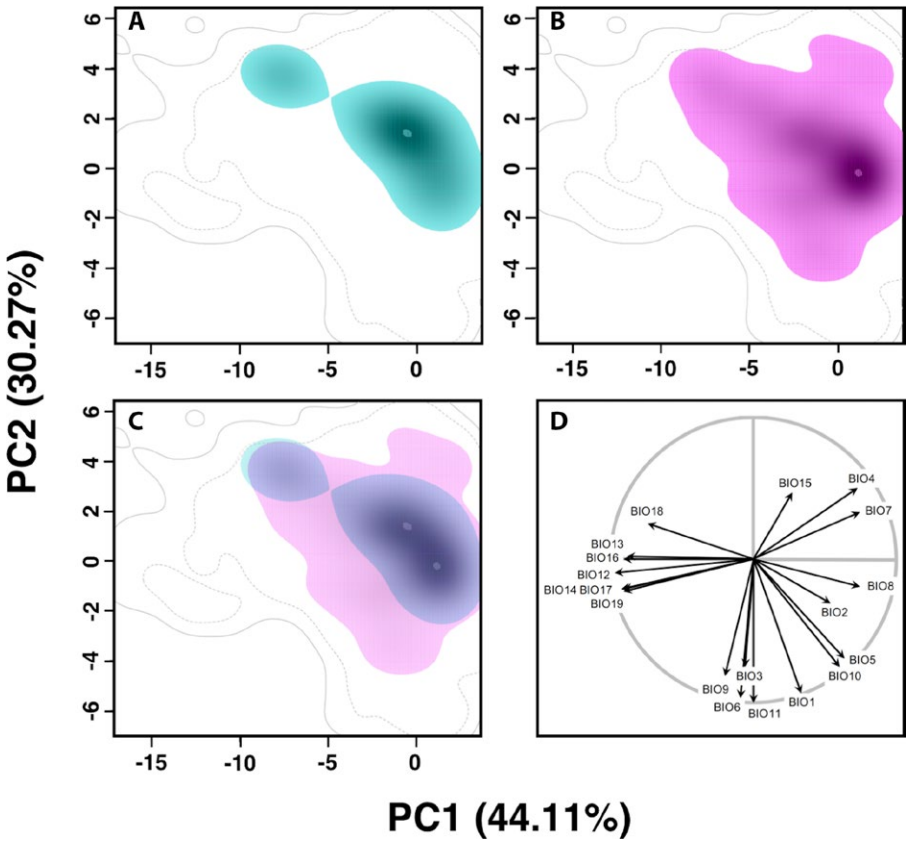

FIGURE 4. Niche dynamics observed comparing diploid (n = 103) and tetraploid (n = 208) *Arabidopsis arenosa* cytotypes in Central and Northern Europe. (A) Diploid niche model. (B) Tetraploid niche model. (C) Overlap between diploid and tetraploid models. Continuous gray line delimits the full environmental space available within the background area; dashed gray line delimits the 75th percentile of the environmental space available within the background area. Darker shading indicates a higher density of presence data. Clearer dots represent niche centroids. (D) Correlation circle of WorldClim variables used in the PCA-env (complete list of climatic variables and respective contributions at Appendix S3).

highly dependent on the geographic ranges of the two species. This difference between the tests likely explains the seemingly contradictory results in the *Arabidopsis arenosa* species complex. The autotetraploid lineage experienced a geographic range expansion since formation from the diploid ancestors (Arnold et al., 2015). Relative to the diploid niche, the possible niche divergence across this range expansion is considerable. Thus, there is a high null expectation of how much the autotetraploid and diploid niches could diverge. Compared to this null expectation, the two niches remained more similar than expected even though they are not identical.

This climatic niche stability between diploid and autotetraploid cytotypes in *Arabidopsis arenosa* is consistent with the notion that autopolyploid lineages exhibit lower rates of niche evolution than allopolyploids. For instance, a previous study conducted in the *Alyssum montanum* L. (Brassicaceae) species complex showed that allopolyploids expand into different climatic conditions than those of their diploid congeners, but autopolyploids occupy ecological niches similar to their ancestors and are limited to peripheral and less competitive geographic areas (Arrigo et al., 2016).

Our exploration of the divergence between the autotetraploid and diploid niches revealed significant differences in both breadth and optimum. The autotetraploid niche expanded to encompass broader temperature tolerances and underwent a slight change in the niche optimum such that more populations inhabit climates with a greater variability throughout the year. Therefore, our finding of expansion in the autotetraploid niche shows weak support for the hypothesis that polyploid lineages are more tolerant than their diploid progenitors of extreme environmental conditions.

It is possible that our ENMs did not incorporate an important axis of ecological variation and thus we missed key aspects of divergence. For example, we could not evaluate microclimate, soil, phenology, or biotic interactions. Tetraploid lineages may have diverged in other ways besides climatic niche to better compete or coexist with the diploid ancestors. For example, the tetraploids may have shifted their life-history timing to not reproduce simultaneously with the diploids.

Furthermore, tetraploid *Arabidopsis arenosa* exhibits a tetrasomic inheritance (Hollister et al., 2012; Arnold et al., 2015, 2016) which is a crucial autopolyploid feature that consists in the random pairing of the two sets of homologous chromosomes such that the four alleles at a given locus pair and segregate at random. All tetraploid *A. arenosa* populations that have been tested are in Hardy-Weinberg equilibrium assuming a random pairing tetraploid model, even those from hybrid regions (Hollister et al., 2012; Arnold et al., 2015, 2016). Autotetraploids may be able to compete with diploids as a result of having twice as much genetic material per individual. Consequently, autotetraploid populations are distinguished by high heterozygosity and by nearly doubled effective population size as compared to diploids (Ronfort et al., 1998; Ronfort, 1999; Arnold et al., 2012). These features may result in selection being more efficient within tetraploid populations than diploid populations allowing for more rapid adaptation. However, the efficiency of selection and the long-term adaptive potential of autopolyploids remain mostly unexplored (Parisod et al., 2010). The potential advantages of tetrasomic inheritance may have allowed for autotetraploid lineages of *A. arenosa* to more rapidly establish in disturbed landscapes following the last deglaciation period.

In fact, Monnahan et al. (2018 [preprint]) found a higher proportion of nonsynonymous polymorphisms fixed by positive selection in tetraploid compared to diploid *Arabidopsis arenosa*, which implies that autotetraploid populations may respond faster to directional selection (Selmecki et al., 2015). Indeed, tetraploid *A. arenosa* has extended its range beyond their diploid ancestor range, including new human-made habitats and postglacial environments (Kolář et al., 2016a), suggesting an improved capability to establish in novel environments. In general, it has been suggested that in extreme or

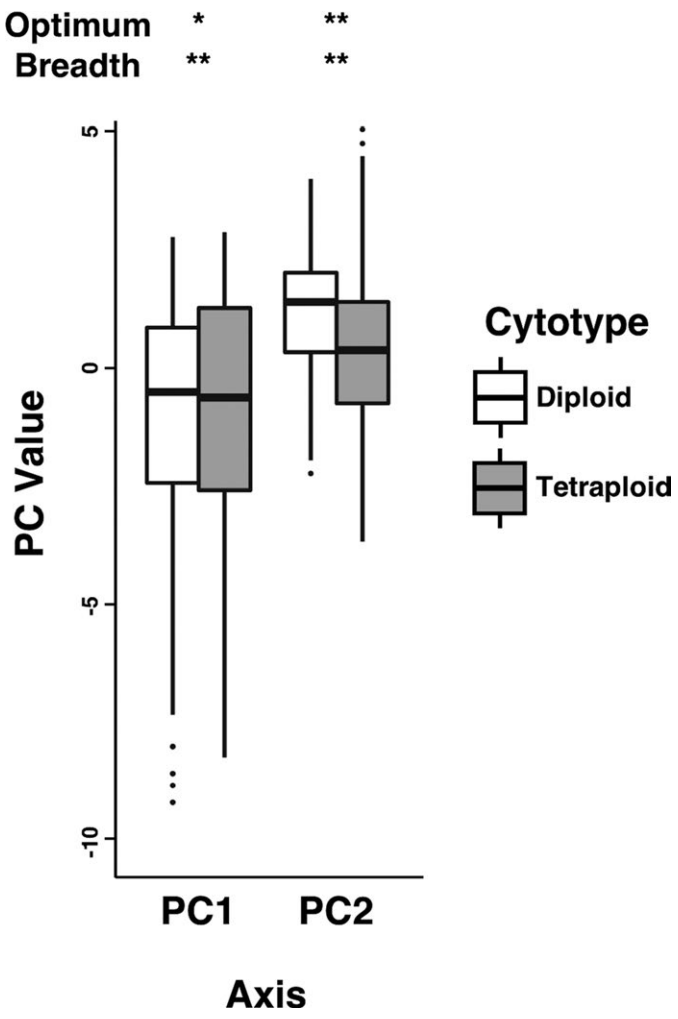

FIGURE 5. Values of principal components along the two environmental gradients (PCA-env axes). Comparisons are made between diploid (n = 103) and tetraploid (n = 208) cytotypes of *Arabidopsis arenosa* in Central and Northern Europe. Niche optimum and breadth correspond to the median and the length of the 95% inter-percentile interval along the two PCA-env axes respectively. * $P < 0.01$, ** $P < 0.001$.

TABLE 1. Comparisons of the niche optimum and breadth along the two environmental gradients (PCA-env axes).

Axis	Cytotype	Optimum	Breadth
PC1	2x	–0.510	11.948
	4x	–0.626	11.099
	Difference	**0.116**	**0.849**
PC2	2x	1.393	6.222
	4x	0.370	8.711
	Difference	**1.023**	**2.489**

Notes: comparisons are made between Carpathian diploid (n = 103) and tetraploid (n = 208) cytotypes of *Arabidopsis arenosa* in Central and Northern Europe. Niche optimum and breadth values correspond to the median and the length of the 95% inter-percentile interval along the two PCA-env axes respectively. Both optimum and breadth show significant differences along the two environmental axes ($P < 0.01$; Fig. 5).

regularly glaciated environments, the increased available genetic diversity in polyploid individuals relative to diploids can allow for more rapid colonization (Brochmann et al., 2004; Comai, 2005; Novikova et al., 2018).

Additionally, polyploidy might decrease the negative consequences of interspecific hybridization and introgression (Alix et al., 2017). Indeed, hybridization is broadly recognized as a source of variation for adaptation to new environments (e.g., Lewontin and Birch, 1966; Rieseberg et al., 1999; Seehausen, 2004). Interploidal gene flow from diploid into tetraploid *Arabidopsis arenosa* and gene flow from tetraploid *A. lyrata* into tetraploid *A. arenosa* have been previously reported (Jørgensen et al., 2011; Arnold et al., 2015, 2016; Baduel et al., 2018; Monnahan et al., 2018 [preprint]). Multiple events of introgression into tetraploid *A. arenosa* may offer an additional substrate for local adaptation. Specifically, population genomics analyses have suggested that migrant alleles from tetraploid *A. lyrata* may have facilitated adaptation of tetraploid *A. arenosa* to the challenging serpentine habitat in the Austrian Alps (Arnold et al., 2016); in the same sense, adaptive introgression from Baltic diploid populations may have facilitated the evolution of early flowering in tetraploid *A. arenosa* adapted to a railway environment in Berchtesgaden in the Bavarian Alps (Baduel et al., 2018). These findings suggest that hybridization and introgression could have played a role in the observed niche expansion in the diploid to autotetraploid transition in *A. arenosa*.

From our data, we concluded that expansion of niche breadth, together with a slight change in the niche optimum, but not a significant ecological niche shift, occurred during (or after) the *Arabidopsis arenosa* autotetraploids moved out of the Carpathian Mountains. Whether climatic niche differences between the diploid and autotetraploid were an immediate consequence of polyploidy (i.e., tetrasomic inheritance), a result of subsequent evolution (i.e., gene flow) or a combination of both is beyond the scope of this study. Therefore, it is important to consider our findings as representing a combination of both autopolyploidy and subsequent evolution.

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AUTHOR CONTRIBUTIONS

Y.F.M.H. conceived the ideas, collected the data, and analyzed the data; Y.F.M.H. and R.H. wrote and discussed the ideas in the manuscript.

DATA ACCESSIBILITY

All climatic data used during this research are openly available from the WorldClim – Global Climate Data site: http://www.worldclim.org/current (Hijmans et al., 2005).

SUPPORTING INFORMATION

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

APPENDIX S1. List of georeferenced localities for 358 (103 Carpathian diploid, 208 autotetraploid, 27 Pannonian diploid, and 20 Dinaric diploid) populations of *Arabidopsis arenosa* and their respective bibliographic sources.

APPENDIX S2. Niche dynamics observed comparing all diploid lineages (n = 150) and tetraploid (n = 208) *Arabidopsis arenosa* cytotypes in Central and Northern Europe.

APPENDIX S3. List of WorldClim variables used in the PCA-env analysis and their respective contributions on PC1 and PC2.

APPENDIX S4. Histograms of bootstrap tests with 1000 resamples.

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