ECOLOGY LETTERS

Ecology Letters, (2014) doi: 10.1111/ele.12259

LETTER

Evidence for shared broad-scale climatic niches of diploid and polyploid plants

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Abstract

Whole-genome duplication (polyploidy) occurs frequently and repeatedly within species, often forming new lineages that contribute to biodiversity, particularly in plants. Establishment and persistence of new polyploids may be thwarted by competition with surrounding diploids; however, climatic niche shifts, where polyploids occupy different niches than diploid progenitors, may help polyploids overcome this challenge. We tested for climatic niche shifts between cytotypes using a new ordination approach and an unprecedentedly large data set containing young, conspecific diploids and polyploids. Despite expectations of frequent niche shifts, we show evidence for alternative patterns, such as niche conservatism and contraction, rather than a prevalent pattern of niche shifts. In addition, we explore how interpreting climatic niches plotted on environmental niche (principal component) axes can generate hypotheses about processes underlying niche dynamics. Dispersal capabilities or other life-history traits, rather than shifts to new climatic niches, could better explain polyploid persistence in the long term.

Keywords

Cytotype, environmental habitat, niche modelling, polyploidy, speciation.

Ecology Letters (2014)

INTRODUCTION

Whole-genome duplication (polyploidy) is a widespread event in angiosperm evolution (Wood *et al*. 2009), and is known to occur repeatedly within species and even within populations (Soltis & Soltis 1993, 1999). Polyploidy is a major mechanism of speciation in plants, yet the factors that contribute to polyploid establishment and persistence remain unresolved. Extinction risk may be high as polyploids generally form in sympatry with their diploid parents (Ramsey & Schemske 1998, 2002), which reduces establishment probability due to competition between cytotypes. Persistence of polyploid lineages may be enhanced when polyploids escape competition by moving into unoccupied habitats. Phenological, physiological and morphological changes (Segraves & Thompson 1999; Maherali *et al*. 2009) are common and may increase stress tolerance, enabling polyploids to occupy more extreme environments relative to diploids (Brochmann *et al*. 2004), thus facilitating polyploid establishment and persistence (Fowler & Levin 1984; Felber 1991; Rodriguez 1996). Observations that support this idea show that the frequency of polyploid individuals increases at the periphery of species' ranges (Levin 1975; Fowler & Levin 1984; Felber 1991) and that they can occur in ecologically extreme environments relative to their diploid counterparts (Hijmans *et al*. 2007), including some of the most extreme environments on Earth (Brochmann *et al*. 2004). Thus, a key to understanding speciation and biodiversity patterns in plants is to test if climate plays a general role in allowing polyploids to escape competition and persist with their diploid progenitors.

A long-standing hypothesis is that polyploids establish and persist by specialising on different ecological niche conditions than diploids (Levin 1975, 2003; Husband & Schemske 2000), here referred to as the 'niche shift hypothesis' [NSH]. Differentiation of niches between cytotypes has been considered a 'prerequisite' for polyploid success (Levin 2003) and marked spatial segregation that is frequently reported between cytotypes of the same species is often considered *prima facie* evidence for niche shifts (Lumaret *et al*. 1987). Although a number of possible ecological factors can reduce competition between cytotypes, climate is a primary determinant of plant distributions (Woodward 1987) and is thought to be a critical basis for spatial separation of polyploids and diploids. However, collective results from studies primarily comparing ecological and climatic niche components of diploid and polyploid plant lineages have been inconclusive (Felber-Girard *et al*. 1996; Baack & Stanton 2005; Raabová *et al*. 2008; Kao & Parker 2010). Consequently, the extent to which climate-based niche shifts, exclusive of alternative ecological dimensions, have occurred consistently between diploids and polyploids remains an open question.

One possible explanation of the paucity of studies that explore the generality of diploid–polyploid niche relationships is the difficulty associated with a large-scale comparative analysis. Recent advancement of ecoinformatic approaches, such as ecological niche modelling (Warren *et al*. 2008) and multivariate analyses of niche variables (Broennimann *et al*. 2012), enables large-scale comparative analyses to explore if climate plays an important role in aiding the establishment and persistence of polyploid individuals. Although these approaches open a new avenue for comparative work, these tests cannot replace the knowledge obtained by classic reciprocal transplant experiments. Findings from broad comparative work offer the opportunity to determine the generality of the NSH, which can then be tested using reciprocal transplant experiments in small-scale studies (e.g. transplanting cytotypes of one or two species).

Niche modelling methods have been used to explore niche evolution for some time (for review, see Peterson 2011), but statistically quantifying differences (or similarities) between two entities' niches has lagged in comparison (but see Warren *et al*. 2008; Broennimann *et al*. 2012). As studies continue to explore niche divergence between groups, the capacity to investigate how niches differ, not only if niches differ, is important (Wiens & Graham 2005). A general approach is to statistically quantify niche overlap between groups to test for niche evolution (or niche conservatism). Currently, the two most frequently used statistical tests that quantify niche overlap and test hypotheses of niche divergence or conservatism are the niche similarity test and the niche equivalency test (Warren *et al*. 2008). The niche similarity test determines if one group's climatic niche is better at predicting the second group's niche than randomly generated niches from a background region, whereas the niche equivalency test directly compares the niches of two groups to determine how identical the two niches are to each other (for details see Methods). Although informative, discrepancies can arise when quantifying niche overlap between niche models using these tests (Fig. 1). For instance, results from the highly conservative niche equivalency test may differ from that of the niche similarity test (Fig. 1, Panel b) due to the range of climatic variables that exist across certain niche types that are included in the analysis. If group A individuals occupied a wider range (increased variance) of climatic niches than group B individuals, but the means of the climatic niches are the same, the niche equivalency test would indicate that these two groups have distinct niches. However, group B may instead occupy a subset of group A's climatic niche and that other factors, like interspecific competition, may prevent group B from flourishing in group A's climatic niche. This discrepancy may be due to the extent of the regions modelled or artefacts introduced via model fitting (Broennimann *et al*. 2012).

These quantitative measures of niche overlap have increased the number of studies of niche evolution, but linking the patterns observed via niche modelling to processes that may influence niche patterns has been difficult. A recent ordination method (Broennimann *et al*. 2012) can improve the link between niche pattern and process because it not only statistically compares the climate niches of two groups but also enables a qualitative assessment of whether niche means and variances differ between groups. As a result, exploring alternative mechanisms of achieving spatial segregation without a change in the mean climatic niche conditions is now possible. For instance, examining the output from this ordination approach can inform how groups differ in environmental niche space, not only geographical niche space, which can then help to generate hypotheses about the biological processes underlying niche patterns. This leads to a need for a two-dimensional framework to describe not only if diploid and polyploid niches differ but also how the niches differ (changes in mean and variance in environmental space).

Here, we explored the evidence for climatic niche shifts between diploid–polyploid lineages to assess whether patterns of niche divergence are consistent with the NSH using the above ordination approach. We compiled an unprecedented data set that comprised 20 plant species that harbour relatively young polyploid (≤ 20 000 years old) and diploid lineages. Although cytotypes can be recognised as independent species, in our data set, both cytotypes bear the same species name. We used the ordination approach outlined by Broennimann *et al*. (2012) that incorporates statistical tests of niche overlap to compare climate conditions of diploids and polyploids within each species. This analysis represents a large increase in inferential power and statistical robustness (Warren *et al*. 2008; Godsoe 2010; Broennimann *et al*. 2012) over previous studies that have generally focused on a single species or species complex. Furthermore, we propose a two-dimensional framework of polyploid niche evolution to describe how changes in climatic niche mean and/or climatic niche variance may be responsible for the observed niche patterns. We show that a variety of niche patterns occur among a large number of species and that other processes (i.e. dis-

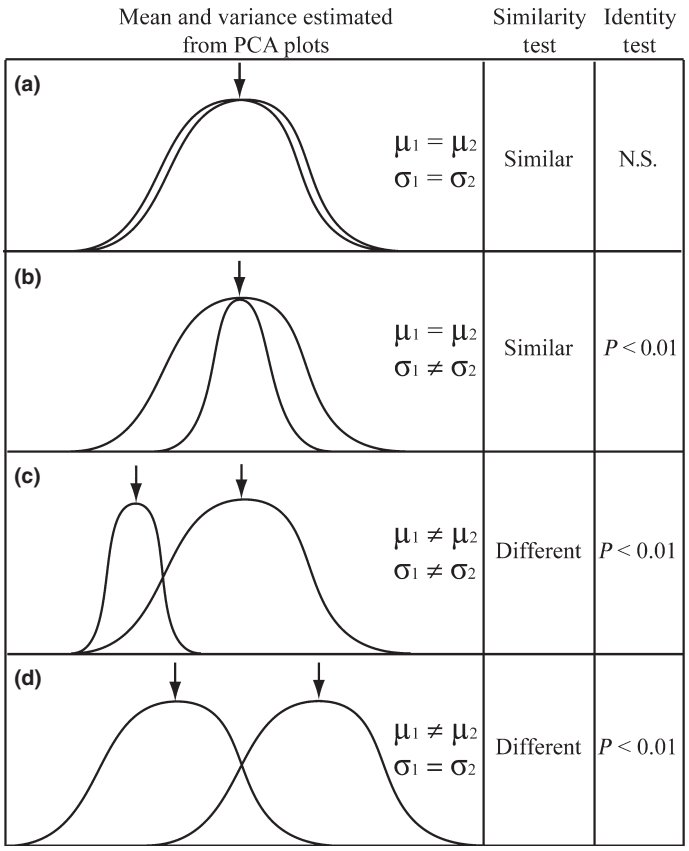

Figure 1 Scenarios when niche similarity (NS) and equivalency (NE) tests provide misleading results. Column 1 shows hypothetical distributions of climatic means (μ, arrows) and variance (σ, width) for a diploid–polyploid pair as observed from a PCA. Hypothetical outcomes from each test are shown in columns 2 and 3. (a) As expected, both tests detect conservatism due to similar μ and σ. (b) NS test shows conservatism (similar μ's), but NE shows differentiation due to different σ. As NE tests for strict conservatism, any difference indicates that niches are not equivalent. (c) Both tests find differentiation (μ, σ differ), but one niche is a subset of the second niche, therefore, potentially similar. (d) NS and NE tests find differentiation due to μ's, despite equal σ. Heterogeneous climates present a challenge for NS test, which cannot distinguish between background heterogeneity and niche σ. Thus, PCA is a useful complement to explore niche evolution.

persal mechanisms) may be more influential in polyploid establishment and persistence than climatic niche shifts.

MATERIALS AND METHODS

Locality data collection

Locality information was collected from the literature and publicly available herbaria databases (compilation of data is available upon request from corresponding author). Specific terms ('polyploid* distribution,' 'cytogeograph*,' and 'cytotype distribution') were used to search the *Science Citation Index Expanded* online science literature database (ISI Web of Knowledge, Web of Science, Science Citation Index Expanded, 1900–2012) for pertinent studies (details provided in Supporting Information). We surveyed plant taxa from both North America and Europe that contained either autopolyploid (genome duplication event within species) or allopolyploid (genome duplication due to hybridisation) lineages. To broaden our sampling and the generality of the results, taxa were included regardless of auto-/allopolyploid status or whether diploids and polyploids were taxonomically combined or named species. We limited our data set to studies that described precise locations and included ploidy level based on flow cytometry or chromosome counts to avoid anecdotal evidence. In some cases, we converted precise locality information into GPS coordinates using a web-based geo-reference program, ACME Mapper 2.0 (ACME Labs, www.mapper.acme.com; details in Supporting Information). All locality information was converted into decimal degrees and then we removed spatially correlated coordinates (coordinates within 1 km^2) and exact duplicate records from the database. In addition, we searched the literature for information about the approximate ages of the polyploid lineages. Studies that examined phylogeographic patterns provided information to estimate the potential age of polyploids based on biogeography.

Climate data preparation

We projected the coordinates for each cytotype individually in ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA, USA) to ensure coordinate precision and to extract climate data for analyses. We drew a polygon around the projected coordinates to outline the known delineation of the species' range that included both cytotypes. Each polygon encompassed both diploid and polyploid populations with a buffer around the coordinates that was estimated using plant dispersal ability information. These polygons were then used as a 'background region' to extract climate data from randomly selected points for the niche overlap analyses. Random points were generated in ArcGIS 9.3 (see Supporting Information) to include all potentially available habitats and accounted for heterogeneity across plant distributions. We then used DIVA-GIS v.5.4 (Hijmans *et al*. 2001) to extract climate data (Bioclim variables from WorldClim; www.worldclim.org) from the occurrence localities of diploid and polyploid populations and from the randomly generated background region points.

Calculating and statistically comparing niche overlap

Comparisons of diploid and polyploid niches were made using a recent approach described by Broennimann *et al*. (2012). In this method, an ordination approach is used to calculate the occurrence density and climatic factor density along environmental (principal component) axes and then use the density occurrences of both occurrences and climate variables to measure niche overlap along these axes. The method then builds on previous statistical tests (Warren *et al*. 2008) to evaluate niche equivalency and niche similarity. This method provides two main benefits over using previous ecological niche models to determine statistical similarity or equivalency (see Broennimann *et al*. 2012 for details). First, it separates species occurrences from the frequency of different climatic conditions that occur across a region. Second, the species densities are standardised using a kernel density smoothing function to better transition niche comparisons from observed geographical space to environmental space that is used for analysis. Kernel density smoothing alleviates any potential analytical difficulties due to spatial resolution of either occurrence data or climatic data.

In this method, species occurrences are plotted on a gridded environmental space and a kernel smoothing method is applied to the density of species occurrences and of the environmental variables along environmental axes for each cell in the data set. Niche overlap is calculated using the Schoener's *D* metric (Schoener 1970), a well-established metric of niche use (Warren *et al*. 2008) that ranges from 0 (no overlap) to 1 (complete overlap). In this approach, an unbiased estimate of *D* is calculated using a kernel density function that is applied to occurrence densities. Statistical confidence in niche overlap values is then determined using two statistical tests: niche similarity and niche equivalency (first described in Warren *et al*. 2008; built on by Broennimann *et al*. 2012). Finally, species occurrence densities in environmental niche space are plotted using a principal component analysis (PCA). These PCAs can be used to visually assess changes in niche dimensions (mean and variance) between cytotypes within a species.

The first test used in this ordination approach is an extension of the niche similarity test (Warren *et al*. 2008). The test compares cytotype niche models to determine if one cytotype niche predicts the other cytotype niche better than a randomly generated niche. Consequently, this test takes into account that cytotypes have the opportunity to disperse and occupy different available habitats across a combined background region. A null distribution of niche similarity was estimated by extracting climate variables from a randomly selected set of geographic points that is equal to the number of occurrences of the other cytotype from the background region, generating a niche model, and then comparing the 'random' niche to the focal cytotype's niche to generate a *D* for the distribution. This is repeated 100 times in both directions (comparing diploid niche to random 'polyploid' niches generated from the background region and vice versa).

Observed *D*'s less than the null distribution indicates niche divergence and values greater than the null indicate that niches are more similar than random. One caveat to consider is that when the null hypothesis is accepted, this does not

necessarily mean that niches are more similar. Instead, it suggests that the two niches cannot be distinguished from each other relative to the background variation observed across the available habitat. We made 40 niche similarity comparisons: 20 compare polyploid climates with random 'diploid' climates and 20 compare diploid climates in the same manner. Using these comparisons, we could also examine whether polyploid niches were more or less similar to diploid niches than diploid niches were to polyploid niches and if polyploids were more likely to occupy novel niches or a subset of diploid niches.

The second test conducted through this ordination method is an extension of the niche equivalency test. This test was used to evaluate if niches were identical when compared directly with each other (Warren *et al.* 2008). To assess whether the observed niche overlap value (D) indicates niche equivalency, the occurrences of the two groups in question were randomly reassigned into two data sets to recalculate the niche overlap value (D). This was repeated 100 times to generate a null distribution for comparison with the observed D to determine statistical significance. If the observed D falls below the null distribution of D from randomly generated data, then the hypothesis of niche equivalency is rejected and niches are not equivalent. This is a strict test for niche conservatism and therefore, non-significant results only indicate that niches are not identical, not that the niches are dissimilar. We did not expect to find that any of the cytotypes had identical niches, given that the likelihood of two taxa having an identical niche is low (Wiens & Graham 2005).

Niche comparisons can be confounded by spatial autocorrelation of climatic variables that are associated with different populations (McCormack *et al.* 2010). For example, if two cytotypes are allopatric, there may be inherent differences in the climatic variables available to both cytotypes. Therefore, if cytotypes are allopatric, an estimate of the underlying level of background divergence of two cytotypes can be informative for niche comparisons. As an independent assessment of possible niche divergence due to allopatric distributions, we used a niche divergence test to compare diploid and polyploid niches of seven species with allopatrically distributed cytotypes. We used this approach to compare niche patterns between allopatric cytotypes of five species in North America and two European species. The niche divergence test (McCormack *et al.* 2010) alleviates spatial autocorrelation of climate variables to investigate whether cytotypes with spatially segregated distributions are more likely to differ in climatic niche conditions. The niche divergence test uses raw environmental data to test the null hypothesis that background niche variation is equal to the niche variation found between groups of interest (see McCormack *et al.* 2010 for details). Climatic variables are extracted from the occurrence locations of each cytotype independently, and the 'background region' is distinct for each cytotype. Background regions are made by extracting climatic data from random points from a polygon that encompasses a single cytotype that is spatially separated from its sister cytotype. The climatic variables for both the 'cytotype niche' and the 'background niche' are reduced using a PCA correlation matrix. These axes are used to determine niche divergence by comparing the observed difference in the mean niche value of a principal component to the difference in mean background values. If the mean divergence of the backgrounds is less than the divergence of the mean climatic niches associated with the allopatric cytotypes ($d_b < d_n$), niche divergence is supported. This test differs from methods outlined by Broennimann *et al.* (2012) in that background regions are distinct for each cytotype.

Because niche evolution is inherently linked to the ability of an organism to disperse (Wiens & Donoghue 2004), we surveyed the literature to identify primary dispersal mechanisms for the 20 species of interest to examine the potential relationship between dispersal mechanism and niche patterns. From the identified sources, we recorded whether dispersal occurred via wind, animal or ballistic mechanisms. In addition, we classified seed dispersal as long- or short-range dispersal according to the recorded mechanism. For example, if a plant was known to have ballistic seed dispersal (seeds drop from the capsule near the maternal plant), we classified this species as a short-range disperser, as the probability of short-range dispersal is greater than long-range dispersal. Species were divided into categories based on niche pattern (e.g. expansion, contraction) and dispersal (long range vs. short range). A chi-squared test was used to examine whether niche outcome was associated with long- or short-range dispersal.

RESULTS

The PCAs showed how cytotypes were distributed along principal climate niche axes, given the possibility that there may be simultaneous shifts in both mean and variance of the climatic conditions associated with each cytotype pair. This approach revealed three patterns of diploid and polyploid niche patterns (Fig. 2). First, niche expansion was evident in four of 20 species (20%), where polyploids had the same mean climatic conditions as diploids, but exhibited significantly greater variance in climate conditions than diploids (Fig. 2a). Second, eight polyploid lineages (40%) were restricted to a subset of the diploid climatic niche (Fig. 2b), and therefore exhibited niche contraction, or a reduced variance in conditions relative to diploids despite similar mean conditions. Finally, the remaining eight species (40%) had patterns suggesting climatic niche conservatism (stasis) with no detectable difference in mean or variance of climate conditions. For four of these eight static species, diploids and polyploids had niches that were judged identical by the previous analyses (Table 1, Table 2, Fig. 2c). Interestingly, the occurrence densities of diploids and polyploids differed across similar climatic conditions for the other four static species (Fig. 2d).

Results from the test of niche similarity did not strongly support frequent or dramatic climate-based niche shifts by polyploids. Of the 40 comparisons, 14 showed that the pairs of diploid–polyploid niches were more similar than random (Table 1). Two species had polyploid niches that were similar to diploid niches, but the diploid niches were not similar to the corresponding polyploid niches (Table 1; *Virgulus oblongfolius, Knautia arvenis*). For the remaining comparisons, the cytotype niche overlap values were not significantly different from the null expectation (Table 1). Failure to reject the null indicates that the environmental conditions associated

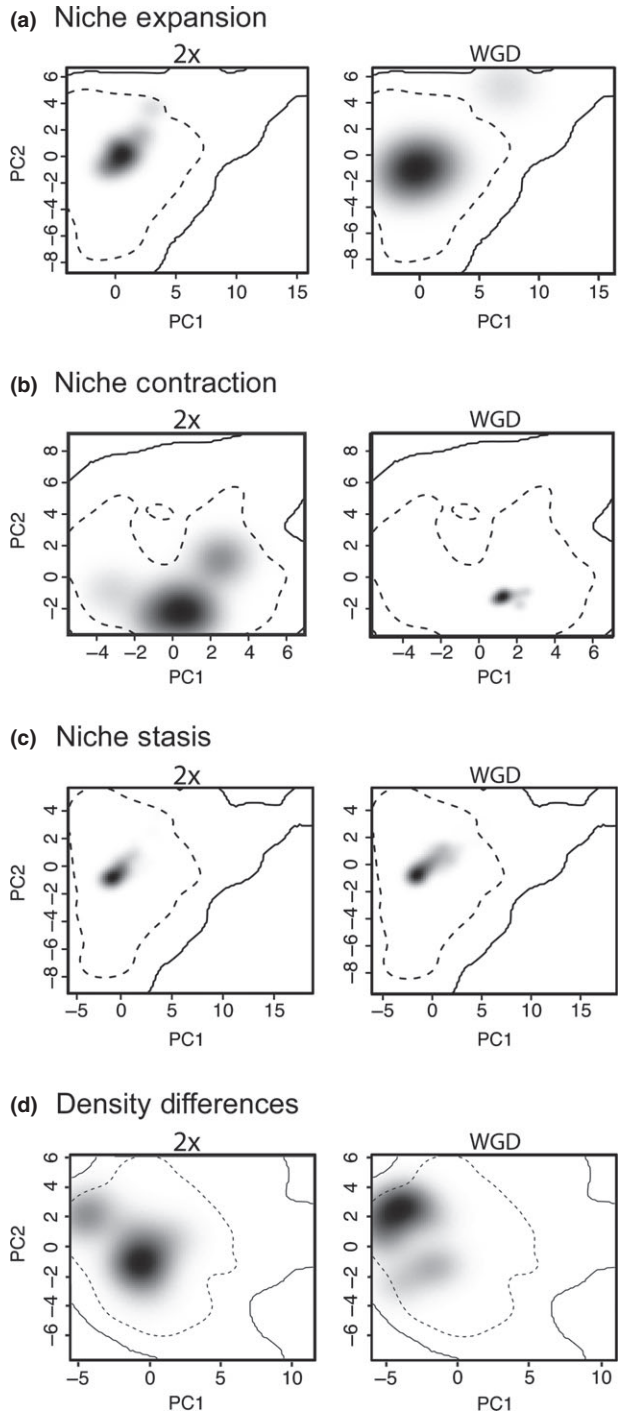

Figure 2 Examples of PCA niche patterns of four species in climatic niche space. (a) Polyploid niches of *Centauria stoebe* expand to include new climatic conditions. (b) The climatic niche of *Melampodium cinereum* polyploids is significantly contracted relative to the diploids. (c) *Knautia arvensis* polyploids exhibit stasis, or the maintenance of the same climatic niche as the diploids. There may be multiple explanations of niches that are stable or contracted relative to diploid progenitors. For instance, such results could indicate that after a polyploid event, new polyploid individuals may not have had enough time to expand into novel habitats, or may live in a subset of the ancestral diploid's niche. Lastly, in (d), diploid and polyploid populations of *Larrea tridentata* seem to occupy the same climatic conditions, but the densities of each cytotype differ across the climatic niche. This may be a result of limited dispersal of the cytotypes.

Table 1 Results from the niche similarity test that compares niche overlap between diploid and polyploid plant lineages. Significant *P*-values are in bold and indicate significant similarity of niches between cytotypes

Diploid–polyploid pair	Niche overlap (D)	Similarity test 4x → 2x *P*-value	Similarity test 2x → 4x *P*-value
Allium oleracum	0.633	**0.0198**	**0.0198**
Artemisa tridentata	0.562	0.0792	0.0594
Centauria stoebe	0.140	0.7920	0.2772
Claytonia perfoliata	0.554	0.0990	0.3168
Claytonia virginica	0.258	0.9310	0.9310
Dianthus broteri	0.704	**0.0396**	**0.0198**
Galium pumilum	0.091	0.2772	0.3168
Heuchera cylindrica	0.347	0.6732	0.9901
Knautia arvenis	0.547	**0.0396**	0.0990
Larrea tridentata	0.639	**0.0198**	**0.0198**
Melampodium cinereum	0.091	0.7128	0.4356
Melampodium leucanthum	0.280	0.8712	0.5346
Pilosella officinarum	0.251	0.3564	0.3366
Ranunculus adoneus	0.560	**0.0198**	**0.0198**
Ranunculus kuepferi	0.162	0.4752	0.0990
Senecio carniolius	0.694	**0.0198**	**0.0198**
Solidago gigantea	0.622	**0.0198**	**0.0198**
Tolmiea menziesii	0.236	0.1980	0.5148
Vicia cracca	0.456	0.1980	0.1782
Virgulus oblongfolius	0.357	**0.0198**	0.3366

Table 2 Results from the niche equivalency test. The niche equivalency test is a strict test for niche conservatism; therefore, although significant *P*-values (bold) reject the hypothesis of identical niches between cytotypes, they do not necessarily indicate that niches are strongly divergent

Cytotype comparison	Equivalency test *P*-value
Allium oleracum	**0.0198**
Artemisa tridentata	**0.0198**
Centauria stoebe	**0.0198**
Claytonia perfoliata	**0.0198**
Claytonia virginica	**0.0198**
Dianthus broteri	0.5742
Galium pumilum	**0.0198**
Heuchera cylindrica	**0.0198**
Knautia arvenis	**0.0198**
Larrea tridentata	0.5148
Melampodium cinereum	**0.0198**
Melampodium leucanthum	**0.0198**
Pilosella officinarum	**0.0198**
Ranunculus adoneus	**0.0396**
Ranunculus kuepferi	**0.0198**
Senecio carniolius	0.0594
Solidago gigantea	0.2772
Tolmiea menziesii	**0.0198**
Vicia cracca	**0.0198**
Virgulus oblongfolius	**0.0198**

with habitats are distributed in such a way that conclusions cannot be drawn about niche differentiation; thus, non-significance does not indicate divergence (Warren *et al.* 2008). Substantial variation in climate across the background region can ultimately lead to a non-significant result when using the niche similarity test to compare two niches because this test compares overlap in niche means, not niche variances (Fig. 1). The highly conser-

vative niche equivalency test indicated that four of the 20 species had equivalent (identical) niches (Table 2).

The results of the niche divergence tests showed that the cytotypes' climatic conditions were not as divergent as the climatic conditions of the allopatric background regions for six of the seven diploid–polyploid comparisons, thus indicating that niches were generally conserved between allopatrically distributed diploids and polyploids (Table 3). Chi-square analysis showed that dispersal was associated with the different types of niche patterns ($\chi^2 = 6.67$, d.f. = 2, $P < 0.05$). Species that showed evidence of niche contraction or conservatism generally had short-range dispersal mechanisms (observed = 14 vs. 2 species with long-distance dispersal), whereas species that exhibited niche expansion were capable of long-range dispersal (wind, animals) and were mostly outcrossers (observed = 14).

DISCUSSION

Upon formation, polyploid individuals face a number of challenges to successfully establish and persist as a novel lineage. The niche shift hypothesis (NSH) suggests that shifts in climatic niche habitats are a prerequisite for successful establishment and subsequent existence of these novel lineages (Levin 2003). Although studies have examined niche divergence between cytotypes of a single species or species complex, consistent evidence for niche shifts has not been shown. We tested whether niche shifts consistently occurred across 20 plant species that are distributed in North America or Europe. The data show a variety of niche patterns, therefore, we interpreted our results based on how cytotype niches differed in mean, variance or both, which aided in developing hypotheses about the processes behind the observed niche patterns (e.g. Fig. 3). In addition, we evaluated whether additional factors, like dispersal, could explain the observed niche patterns.

While shifts in climatic tolerances provide one possible mechanism to establishment under the NSH, we did not find evidence for climatic niche shifts between many diploid–polyploid pairs of North American and European plant species. Instead, the results indicated that the polyploids in this study often occupied similar climatic conditions as their diploid counterparts, suggesting that climatic niche differentiation may not be a requirement of polyploid establishment and persistence. For instance, the results from the niche similarity, divergence and equivalency tests showed that polyploids rarely shift climatic niches relative to diploids in ways that are statistically identifiable (Tables 1, 2 and 3), and for two species, polyploids may be occupying a subset of the diploids' climatic niche (Table 1; *Virgulus oblongfolius, Knautia arvenis*). Collectively, the results support the idea that polyploids often share similar mean climatic conditions with diploid progenitors, despite some differences in climatic niche variance (niche breadth).

Although the data presented here suggest that polyploids can survive in diploid climates, the possibility remains that young polyploid lineages may not have had sufficient time to disperse and subsequently diverge in climatic niche use from

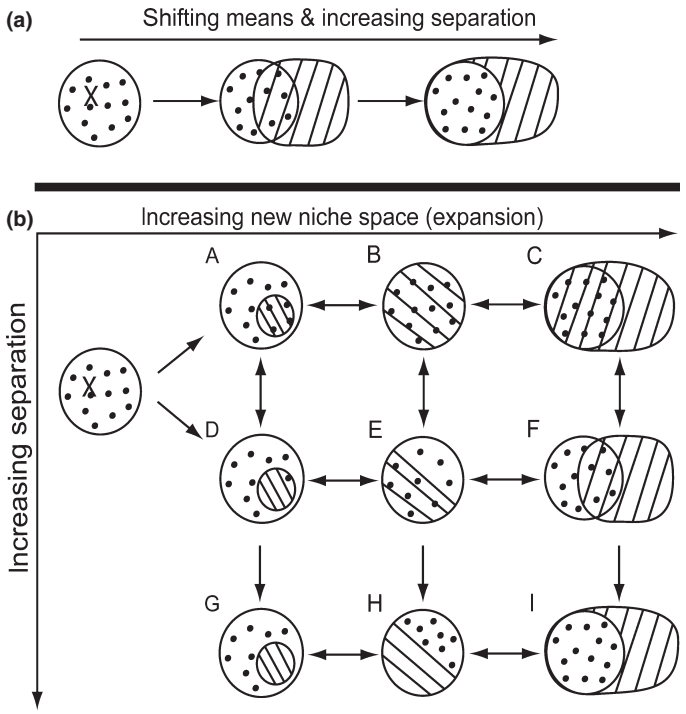

Figure 3 A two-dimensional framework that describes climatic niche evolution (outlined shapes) of polyploid persistence that is independent of geographic space. Panel a illustrates a two-step process (Levin 2003) of niche differentiation when a polyploid (X) forms within an ancestral diploid niche (dots). Polyploids first share the diploid niche (dots and dashes), then colonises new climatic niches, establishes and locally adapts to novel climates (dashes), moving along a 'separation' axis. Panel b illustrates nine polyploid niche evolution scenarios on two axes. The horizontal axes depict niche expansion; polyploids expand to novel climates, without changing the mean between cytotypes. The vertical axis (separation) denotes how polyploids can partition similar niches by shifting means, but not variance, and specialises on climatic subsets to various degrees (e.g. d, e and f vs. g, h and i). Notably, neither option is static, as niches are dynamic and evolve as indicated by the double-headed arrows.

Table 3 Results from the niche divergence test for seven species with allopatric diploid and polyploid geographic distributions. Values lower than the null distribution indicate conservatism (C), whereas values greater than the null distribution indicate differentiation (D)

	Niche axes		
Pairwise comparison	PC1	PC2	PC3
Heuchera cylindrica	0.456 C (2.46–2.47)	1.576 C (1.83–1.84)	0.008 C (0.931–0.936)
Knautia arvensis	1.34 D (1.23–1.24)	0.25 C (0.577–0.587)	0.64 C (1.30–1.31)
Larrea tridentata	1.72 C (2.62–2.63)	1.00 C (1.27–1.28)	0.406 C (0.214–0.211)
Melampodium cinereum	0.759 C (4.23–4.24)	0.439 D (0.262–0.269)	0.233 C (0.331–0.336)
Melampodium leucanthum	3.76 C (4.27–4.28)	0.547 D (0.085–0.093)	0.439 C (1.12–1.13)
Ranunculus kuepferi	2.91 D (1.90–1.91)	1.42 D (0.89–0.91)	0.35 C (1.49–1.50)
Tolmeia menziesii	1.40 C (4.54–4.55)	1.76 D (0.505–0.510)	0.42 C (0.609–0.617)

their diploid progenitors. This seems unlikely given that most of these polyploids originated within the last glacial period and, as glaciers retreated, available habitat would have opened up for polyploids to occupy. The availability of these new habitats would likely have facilitated niche divergence from diploids, reducing time needed for divergence. Alternatively, but less parsimoniously, polyploid lineages may have diverged initially to facilitate persistence and then later recolonised diploid climate conditions. Such reversion to niche conservatism from initial niche divergence seems unlikely. In addition, another possibility is that the full extent of polyploid ranges was not included in cytogeographic studies used in this analysis, given that young polyploids may be cryptic. The exclusion of these cryptic populations could potentially underrepresent novel habitats occupied by polyploids, thus underestimate the extent of niche shifts. However, given that none of the included taxa are endemic or rare and that, for some species, the geographic ranges are large, it is likely that we were able to sample from the possible range of climatic habitats where these lineages occur.

Findings from other studies also suggest that niche conservatism may be more common between cytotypes than previously recognised. A literature review (details provided in Supporting Information) revealed that studies examining niche segregation showed evidence for niche divergence in 11 of 23 species and niche similarity (conservatism) in ten species. For two species, the evidence presented was inconclusive, but suggested niche similarity (Table S1). Some studies report marked spatial segregation as evidence for niche shifts (Lumaret *et al.* 1987) or that ploidy and environment are only weakly related, if at all (Sampoux & Huyghe 2009). Results from the most direct tests of niche differentiation, reciprocal transplant experiments, showed only weak or no niche differentiation (Table S1). In addition, our results are consistent with previous observations that niches of autopolyploids (polyploids formed by a within-species genome duplication) are similar to niches of their diploid progenitors, a finding further corroborated by recent experimental results showing that close relatives are ecologically similar (Burns & Strauss 2011).

The results also highlight the difficulties in examining niche evolution when using the niche similarity and equivalency tests (Fig. 1). The classic niche conservatism/divergence dichotomy only determines if niches are different, a question that is perhaps of less interest than how and under what circumstances do we observe conservatism vs. divergence (Wiens & Graham 2005). Comparing climatic conditions between diploids and polyploids requires an understanding of both the mean and variance of the climatic conditions that each cytotype inhabits. To address this, we propose a two-dimensional framework for polyploid niche evolution that provides a context in which to compare niches and develop hypotheses regarding the processes that may have initiated the observed niche patterns. In this framework, we outline a conventional view of polyploid establishment and persistence (Fig. 3a) and then show nine alternative scenarios that could explain observed niche patterns (Fig. 3b). In the conventional view of polyploid establishment (Fig. 3a), a polyploid event occurs and the newly formed polyploid individual necessarily and rapidly occupies a niche that is different in its mean climate conditions from its diploid progenitor and is sometimes driven by rapid changes in physiological and morphological traits (Levin 2003). Polyploids would exhibit 'separation' when the ancestral diploid niche mean differs from that of polyploids. However, the conventional approach only examines niche divergence from the perspective of a single dimension (i.e. separation) and a second dimension (i.e. expansion) is necessary to fully describe alternative patterns.

Instead of strictly niche shifts between cytotypes, alternative niche patterns may arise via a change in the niche variance, and examining such differences are necessary for building a comprehensive view of niche evolution and speciation (Fig. 3b). For instance, a polyploid may exploit more extreme conditions, and thus a greater range of climate conditions by simply expanding its climatic niche variance ('expansion'), without any change in mean conditions as compared with the diploid progenitor (Fig. 3b, Panel c). In our data set, the *Centauria stoebe* (Fig. 2, Panel a) diploid niche and polyploid niche appear to have similar means, but the niche variance of the polyploid cytotype is greater than that of the diploid. Instead of only considering whether niche means have shifted (separation), investigating the climatic niche variance provides an additional dimension to examine processes that may lead to niche divergence or conservatism. This expansion axis further enables hypotheses to be generated about the evolutionary processes that affect speciation in general. For example, the results suggest that climate may not be a primary factor driving the spatial segregation of *Larrea tridentata* cytotypes because cytotypes appear to occupy a similar climatic niche, but effectively partition these conditions which are observable in the differences in occurrence density (Fig. 2d). This may be a result of limited dispersal or that *L. tridentata* cytotypes may be currently competing for niche space and that a conclusion of niche evolution cannot be determined at this time. By considering these two axes together, we are able to better interpret niche dynamics as polyploids evolve from their diploid ancestors and generate hypotheses for polyploid niche evolution.

By using this two-dimensional framework in the context of this study, we hypothesised that polyploid persistence can occur under a number of other circumstances, such as when cytotypes occupy the same set of climatic conditions, but are found in different spatial locations due to alternative mechanisms, like limited dispersal (e.g. Baack & Stanton 2005; Sampoux & Huyghe 2009). Given the diversity of niche patterns observed across 20 species and that dispersal can play a key role in how often plants encounter novel habitats, we explored whether dispersal mechanisms could explain the observed niche patterns. Long-distance dispersal might facilitate niche divergence because propagules may more readily migrate into new climatic conditions, whereas short-distance dispersal might be associated with niche conservatism or contraction (Levin 1975; Wiens & Graham 2005). Indeed, we found that dispersal mode was associated with the different types of niche patterns. Species that had conserved or contracted niches generally had short-range dispersal mechanisms, whereas long-range dispersal and outcrossing was associated with species that exhibited niche expansion. Recent work suggests that limited dispersal may lead to increased polyploid

establishment in the absence of niche shifts or expansion (Baack 2005) because polyploids are locally maintained by the absence of gene flow from diploids. Limited dispersal might also explain why diploids and polyploids appear to be spatially segregated on local scales within the same climatic niche. Therefore, for some species, limited dispersal and frequency-dependent mating may be more responsible for the success of polyploid persistence in a primarily diploid habitat than climatic niche shifts (Felber 1991; Rodriguez 1996; Baack 2005). We acknowledge that the resolution of the climate data (1 km^2) may be too coarse to identify microhabitat climatic differences that may influence plants with limited dispersal mechanisms; however, the diversity of niche patterns presented in this study suggests that broad-scale climatic niche shifts may only rarely assist polyploid establishment and speciation.

Thus, this two-dimensional framework that includes niche mean and variance more completely describes the suite of possible climatic niche dynamics, especially those that may shape polyploid speciation. Furthermore, we found this framework useful for developing hypotheses about the processes that may have shaped the observed niche patterns, like limited dispersal. As climatic niches of polyploids can change through time (as indicated by the double-headed arrows in Fig. 3b), simply analysing whether niches have diverged would overlook the potential role of limited dispersal or local adaptation in diploid–polyploid niche dynamics of established polyploids. Consequently, the 'obligatory allopatry' (Kay 1969) between cytotypes may instead be a result of competitive exclusion between cytotypes, limited dispersal and drift or local selection, rather than climatic niche shifts.

ACKNOWLEDGEMENTS

The authors thank N. Romero for help compiling the cytotype distribution data set and D. Althoff, J. Apodaca, M. Geber, and two anonymous reviewers for comments on an earlier draft. This material is based on work supported by the National Science Foundation under Award No. 1002589 to KLG and DEB 0743101 to KAS.

AUTHORSHIP

All authors designed the study, KLG collected and analysed data, KLG wrote first draft of manuscript and all authors contributed substantially to revisions.

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Editor, Richard Bardgett
Manuscript received 4 November 2013
First decision made 14 December 2013
Second decision made 12 January 2014
Manuscript accepted 21 January 2014