



# Spatial proximity between polyploids across South American frog genera

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**Funding information**

National Science Foundation; Schneller Endowed Chair Fund

Cynthia Riginos

## Abstract

**Aim:** Polyploids have been theorized to occur more frequently in environments that are subjected to severe conditions or sudden disruptions. Here we test the expectation that polyploid taxa occur more frequently in extreme or disrupted environments than their diploid counterparts, whether due to increased adaptive potential, environmental resilience or cross-ploidy competition.

**Location:** South America.

**Taxon:** All frog genera in the area with both polyploid and diploid member species (*Ceratophrys*, *Chiasmocleis*, *Odontophrynus*, *Phylomedusa* and *Pleurodema*).

**Methods:** In all, 13,556 occurrence records of 82 frog species were collected from the Global Biodiversity Information Facility. Species distribution models, range overlap estimates, statistical tests and principal component analyses were used to estimate and compare environments between diploid and polyploid species within and across genera using several categorical and quantitative variables taken from multiple publicly available sources.

**Results:** Almost all polyploid occurrences are found within southeastern South America, largely to the exclusion of diploids. Polyploid species occur more closely with intergeneric polyploids than they do with congeneric diploids. Southeastern South America is more temperate, seasonal and less forested when compared to the tropical environments more commonly inhabited by diploids. The habitat ranges of polyploid species are subject to greater temperature fluctuations than diploid species. This region has also experienced major transformations in the modern era, owing to an agriculture boom over the last century. Polyploid occurrences are more likely to be found in areas with greater cropland usage, fertilizer application and pesticide application than diploids.

**Main Conclusions:** Across species, temperature seasonality was the only variable with strong statistical differences between diploids and polyploids. Greater annual fluctuations in temperature may lead to more established polyploid species due to reasons mentioned above; however, extreme temperature differences are also known to contribute to polyploid gamete formation, providing a possible non-selective explanation. Polyploid occurrences are also more likely to be found in areas of high agricultural impact, providing support for the hypothesis that polyploids are more resilient to environmental disruptions than diploids.

**KEY WORDS**

biogeography, frogs, polyploidy



## 1 | INTRODUCTION

Polyploids are organisms with more than two complete sets of chromosomes. Polyploids are created *via* whole genome duplication from diploids, either between separate lineages through hybridization (called allopolyploidy) or within a single lineage through the production of unreduced gametes (called autopolyploidy). The duplication of the genome is one of the most severe mutations found in nature, and polyploids are expected to experience unique evolutionary pressures and altered trajectories as a result (Comai, 2005; Otto, 2007; Otto & Whitton, 2000; Parisod et al., 2010). In particular, polyploids are often found in extreme environments, which we define as those environments which exhibit statistically greater or lower values of a given environmental variable when compared to occurrences from other species within the clade. For example, polyploids can be found under conditions that are on average colder (Adamowicz et al., 2002; Brochmann et al., 2004; Rice et al., 2019; Stebbins, 1984), drier (Diallo et al., 2016; Manzaneda et al., 2015; Thompson et al., 2014; Van de Peer et al., 2017) or more saline (Chao et al., 2013) than their diploid counterparts. This trend is best characterized in plants, but has also been observed in *Daphnia* water fleas (Adamowicz et al., 2002) and *Neobatrachus* frogs (Van de Peer et al., 2017). Polyploids are also more common in disrupted environments that are subject to radical changes, such as those that have been previously glaciated (Borgen & Hultfågård, 2003; Jørgensen et al., 2008; Novikova et al., 2018; Oberlander et al., 2016).

Several non-exclusive hypotheses have been proposed to explain this correlation, which may be the result of selective or non-selective processes. First, the formation of polyplloid gametes may be more likely within extreme or disrupted environments. Meiotic errors that lead to autopolyploids have been shown to occur more frequently under stressful conditions (Kreiner et al., 2017; Mason et al., 2011). For example, several mammalian cell types will undergo spontaneous polyploidization in response to metabolic or genotoxic stress (Pandit et al., 2013). Exposure to extreme temperatures is also known to induce autopolyploidy in a wide variety of organisms (Mable et al., 2011; Zhou & Gui, 2017), including frogs (Keller & Carl Gerhardt, 2001; Ueda, 1993). In the case of allopolyploidy, environments that are frequently disrupted also provide potential hybrid zones, allowing secondary contact between species previously separated by glaciers (Brochmann et al., 2004; Stebbins, 1984) or sea-level rise (Grismer et al., 2014). As a result, we would expect a greater incidence of allopolyploids in these areas.

Extreme environments may exhibit conditions that are conducive to the formation of polyploids, but they are also less hospitable to diploids, which may in and of itself increase the success of polyplloid populations. Although polyploids initially share their range with diploids, they are not predicted to be able to exist sympatrically for long. In a sexual polyploid population, individuals increase fitness only by mating with other polyploids, not the ancestral diploid species (Levin, 1975). The existence of a prezygotic reproduction barrier is therefore beneficial to polyplloid populations (Husband & Schemske, 2000). Diploids and polyploids must also compete for resources, a scenario in which polyploids may be outmatched. Generally, polyploids are considered

to be less fit when compared to closely related diploids for a variety of reasons. First, the diploid genome has been optimized for the environment under natural selection for far longer (Levin, 2004). Despite evidence for hundreds of genome duplication events across the animal tree of life only a minority of extant species exhibit polyploidy, suggesting that the ultimate fate for most polyploid lineages is to either evolve into diploids or become extinct. Polyploid genomes, especially for allopolyploids, are often unstable and suffer from disruptions to gene expression and cellular processes which may incur fitness costs (Comai, 2005; Doyle & Coate, 2019; Otto, 2007). Indeed, fertility and survival have been shown to be reduced in polyploids (Ramsey & Schemske, 2002). Polyploids also experience greater mutation load due to their larger gene copy number (Otto, 2007). Therefore, due to decreased competition from diploids and a reduced chance of cross-ploidy mating, polyploids are more likely to thrive in areas where diploids are less frequent (Madlung, 2013; Otto & Whitton, 2000; Parisod et al., 2010). Several studies across plants have identified niche differentiation as a significant factor in the formation and maintenance of polyploid populations (Baniaga et al., 2020; Felber, 1991; Fowler & Levin, 1984, 2016; Husband & Schemske, 2000; Levin, 1975, 1983; Rodriguez, 1996), demonstrating the importance of ecological divergence between polyploids and diploids.

Polyploid species are not predicted to survive within the environment they originated in for long; however, they may especially well-suited to life outside it, as they are often thought to possess greater environmental resilience and adaptive potential compared to diploids. Polyploids' increased genome size results in more genetic variation and a higher average mutation rate per gene (Otto, 2007; Selmecki et al., 2015). Polyploids also possess a greater capacity to mask deleterious mutations and safeguard against inbreeding depression *via* a lower incidence of homozygous genotypes (Otto, 2007; Otto & Whitton, 2000). Multiple gene copies also provide the opportunity for adaptation, as each gene now has a redundant copy that is free to specialize or evolve new function without compromising the ancestral role (Comai, 2005; Ohno, 1970). Additionally, as allopolyploids are also hybrids, heterosis may be involved as well (Comai, 2005; Otto, 2007). There have been whole genome duplications detected across many different plant lineages near the Cretaceous–Paleogene boundary (Fawcett et al., 2009; Vanneste, Baele, et al., 2014; Vanneste, Maere et al., 2014; Van de Peer et al., 2017), speaking to polyploids' ability to adapt to or resist periods of severe ecological disruption. A link has also been discovered between polyploidy and invasiveness (Te Beest et al., 2011), polyploid plants are 20% more likely to be invasive than diploids (Pandit et al., 2011), further indicating their ability to adapt to new conditions.

To test whether polyploids are more closely associated with particular environments, we collected 13,556 occurrence records of 82 species across the 5 South American frog genera with verified polyploid ( $n = 1,717$ ) and diploid ( $n = 11,839$ ) members (*Ceratophrys*, *Chiasmocleis*, *Odontophrynus*, *Phylomedusa* and *Pleurodema*) (Schmid et al., 2015). For a brief discussion of each genus, see supplemental text S1.



## 2 | MATERIALS AND METHODS

### 2.1 | Occurrence records

Each of the five genera were queried in the Global Biodiversity Information Facility (GBIF) and downloaded on 16 January 2020. GBIF is an international organization which organizes and curates biodiversity data provided by institutions from around the world. Although 78 institutions in total contributed occurrences to the dataset used in this study, the top 3 were the Bernardino Rivadavia Museum of Natural Science, Kansas University and the Smithsonian Museum, which together contributed 45.3% of occurrences. The original dataset includes 15,339 occurrences from 113 published datasets. Synonyms were updated with the Open Tree Taxonomy (Michonneau et al., 2016) and AmphibiaWeb was used to resolve discrepancies between GBIF and Open Tree. In all, 1,672 occurrences without species names were removed. Two species (three occurrences) that were no longer considered members of any of the five genera were also removed. 108 occurrences of the species *P. burmeisteri* were additionally removed as the species contains both diploid and tetraploid populations (Batistic et al., 1975) and so individual occurrences could not be classified with any certainty. All species not verified as polyploid are presumed diploid. The final dataset contains 13,556 occurrences across 82 species (Figure S1). Range maps from the International Union for the Conservation of Nature (IUCN, 2019) were also downloaded (version 2019-3) for all available species. The full record of each occurrence with all available metadata is available at <https://doi.org/10.15468/dl.akr84v>.

### 2.2 | Range overlap estimation

Range estimates were performed using species distribution models (SDMs). Five climatic variables were collected from the WorldClim 2 dataset (Fick & Hijmans, 2017) at 30-s resolution ( $\geq 0.86 \text{ km}^2$ ): mean monthly temperature, mean monthly precipitation, altitude, temperature seasonality and precipitation seasonality. Seasonality describes the annual range of a variable, estimated from the standard deviation for temperature and the coefficient of variation for precipitation. SDMs were then constructed for each polyploid species using these climatic variables as predictors with a maximum entropy approach (Elith et al., 2011). From these SDMs, range overlap (Warren et al., 2008) was estimated using the age-range correlation method (Fitzpatrick & Turelli, 2006). SDMs were executed using the R package *dismo* 1.1.5 (Hijmans et al., 2017) and range overlap was estimated using the R package *phyloclim* 0.9.5 (Heibl & Calenge, 2013).

Estimation of range overlap between  $>2$  lineages requires a phylogenetic tree (Figure S2). To achieve this, a concatenated multiple species alignment of the 12S and 16S mitochondrial gene from 57 frog species (including all polyploids) was generated using T-Coffee (Di Tommaso et al., 2011). A maximum likelihood tree was then constructed in IQ-TREE 2.0.3 (Nguyen et al., 2015) under the GTR+F+I+G4 substitution model, the best-fitting model as determined by ModelFinder

(Kalyaanamoorthy et al., 2017). Neither genes nor sites were partitioned. The tree was then time calibrated using a penalized likelihood method (Kim & Sanderson, 2008) using the chronos function as implemented in the R package *ape* 5.3 (Paradis et al., 2004). Lower and upper age bounds for each genus were taken from the available literature (Table S1) and used to time-calibrate the maximum likelihood tree. All files required to evaluate and reproduce the tree building steps are available at [use doi.org/10.5281/zenodo.4536106](https://doi.org/10.5281/zenodo.4536106) for an archived version.

### 2.3 | Categorical environmental variables

Three main data sources were used to categorize environments across South America. The first was the Köppen–Geiger climate classification (Geiger, 1954; Köppen, 1900), which categorizes the earth's landmass into five groups on the basis of climate (Tropical, Arid, Temperate, Continental and Polar), and then further into 30 total subgroups on the basis of seasonal temperature and precipitation trends. Herein, we use an updated digital version of the original classification system (Kottek et al., 2006). Environmental regions were also categorized into one of 10 biomes, and further divided into a specific ecoregion (defined as a 'large unit of land or water containing a geographically distinct assemblage of species, natural communities, and environmental conditions') as defined by the World Wildlife Fund (Olson et al., 2001). Each individual occurrence was given a climate, biome and ecoregion classification based on geographical location.

### 2.4 | Quantitative environmental variables

In addition to categorical data, we collected several continuous environmental variables where we had some *a priori* expectation they would influence frog habitability, and where data were available throughout South America. As previously mentioned, five climatic variables (mean monthly temperature, mean monthly precipitation, altitude, temperature seasonality and precipitation seasonality) were collected from the WorldClim 2 dataset (Fick & Hijmans, 2017). Additionally, five anthropogenic variables (pasture usage, cropland usage, fertilizer application, manure application and pesticide application) were taken from the Socioeconomic Data and Applications Center. Inputs from fertilizer and manure were collected from Global Agricultural Inputs v1 dataset (Potter et al., 2010), land usage from pastures and croplands were collected from the Global Agricultural Lands dataset (Ramankutty et al., 2008), and pesticide application was collected from the Global Pesticide Grids dataset (Maggi et al., 2019).

Quantitative environmental variables were analysed in several ways. Wilcoxon rank-sum tests were used to directly compare quantitative environmental variables between diploid and polyploid occurrences. As many occurrences were observed from the same species (and all species share some degree of common ancestry), occurrences cannot be said to be truly independent, and so violate an assumption of the test. We hope that by sampling polyploid and diploid species across several different genera, the



impact of this violation is reduced; however, we cannot discount the possibility that observed differences are the result of shared ancestry between occurrences rather than ploidy alone. To explicitly incorporate evolutionary history into our analyses, we also performed a phylogenetic ANOVA (Garland et al., 1993) using the R package geiger 2.0.7 (Pennell et al., 2014), though with only nine polyploid species statistical power is limited. To explore polyploid and diploid distributions in higher-dimensional space, principal component analysis (PCA) employing singular value decomposition was conducted on all occurrences using every quantitative environmental variable. As all the same caveats apply as with the Wilcoxon rank-sum tests, a phylogenetic PCA (Revell, 2009) was also performed using the R package phytools 0.7.47 (Revell, 2012).

### 3 | RESULTS

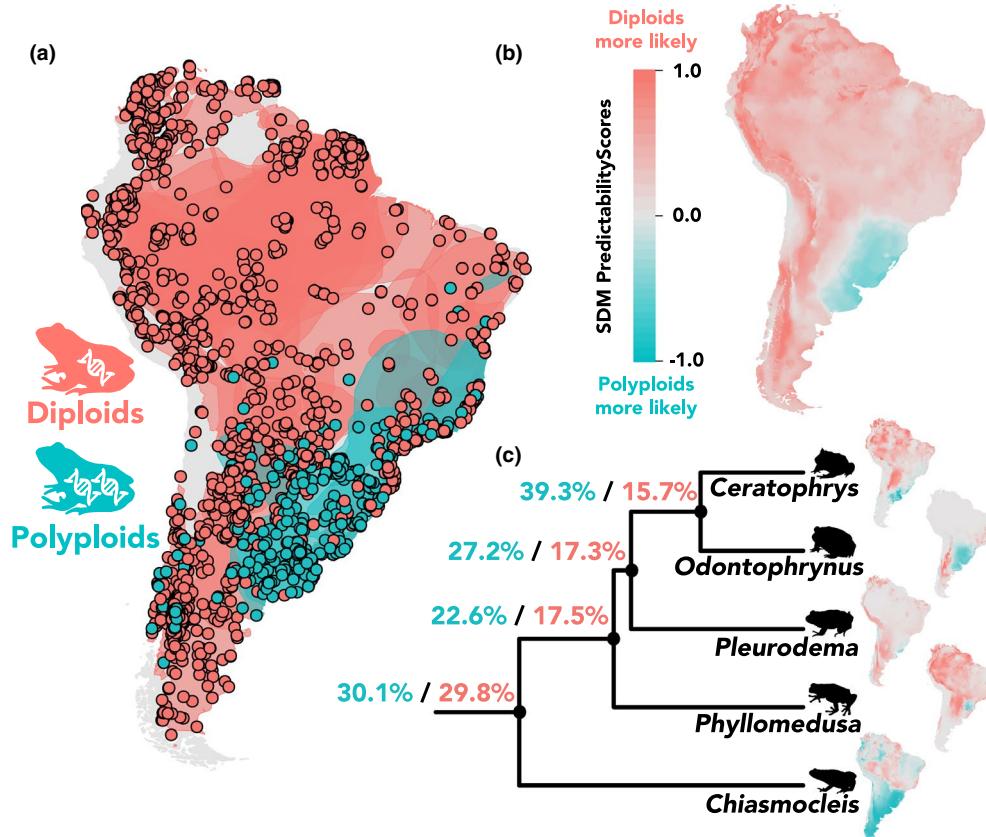
#### 3.1 | Distribution of diploid and polyploid frogs

For South American frogs, ploidy appears to be strongly correlated with species range. Range maps of diploid species collectively cover most of the continent (Figure 1A, Figure S1). Noticeable

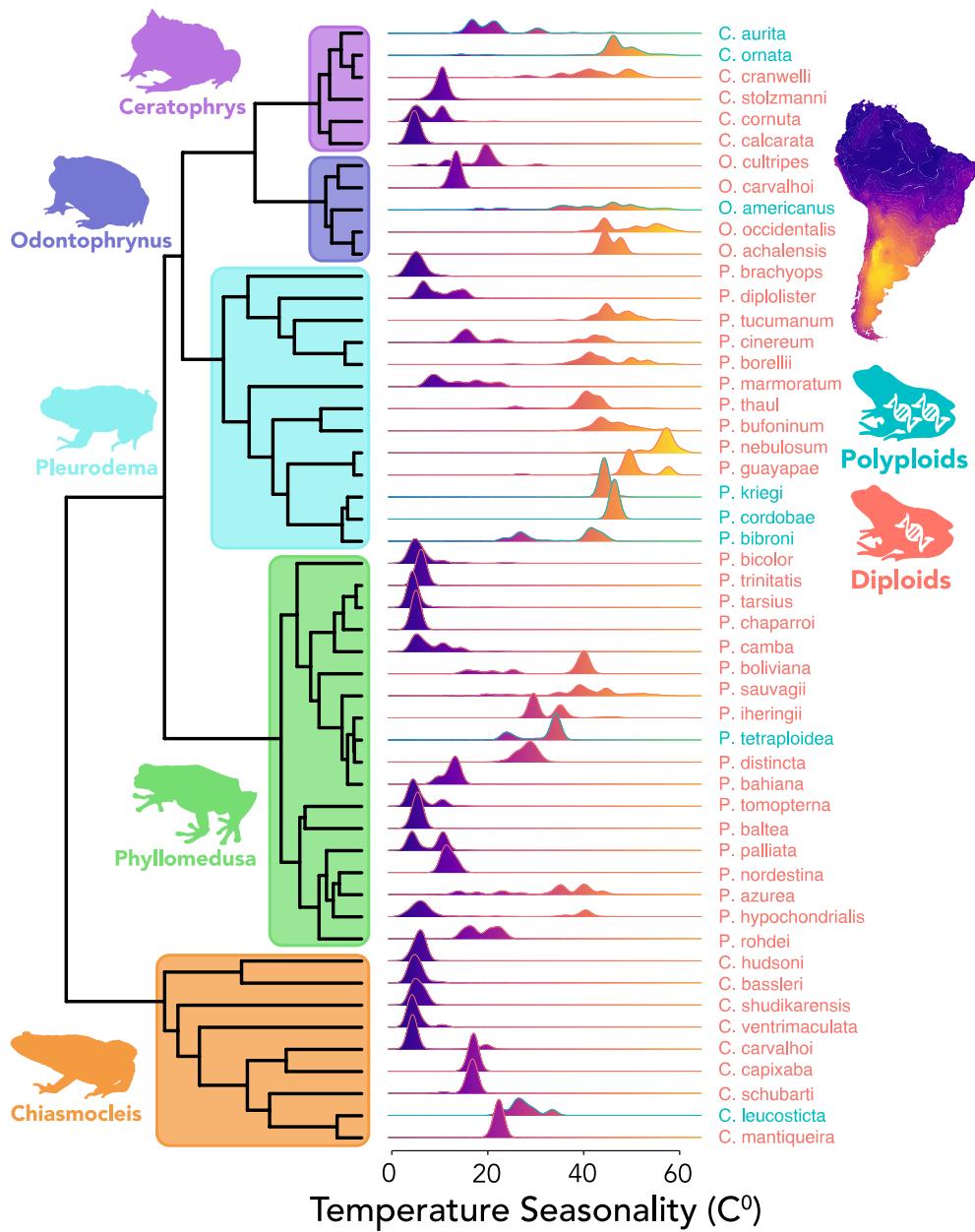
exceptions to this are much of the Andes Mountains along the western coast and part of the Guiana Highlands in southeastern Venezuela. Diploids are also largely absent from a region in the southeast which encompasses southern Brazil, southern Paraguay, parts of Uruguay and northeastern Argentina. Unlike the Andes or Guiana Highlands, there are no clear topographical features that would prevent frogs from becoming established in this region. Indeed, this is where most of the polyploid species are located. The area south of 25°S and east of 65°W contains 64.8% of polyploid occurrences but only 7.1% of diploids (Figure 1A, Figure S1). SDMs of polyploid and diploid taxa also reveal tighter spatial associations between polyploids. Diploids are more likely to be present throughout 88.4% of South America, with the exception of the southeastern region (Figure 1B). Ancestral reconstructions of range overlap are also greater between polyploids than diploids across genera (Figure 1C).

#### 3.2 | Characterizing the polyploid environment

In addition to geographical range, distributions across climate, biome and ecoregion were also different between diploids and



**FIGURE 1** (a) GBIF occurrences and IUCN range maps of the 82 frog species included in this study, coloured by ploidy. (b) Predictability scores generated from SDMs for diploids, subtracted by those for polyploids. Positive values (red) indicate areas where diploids are more likely to be present, whereas negative values (blue) indicate areas where polyploids are more likely to be present. (c) Range overlap between polyploid (blue) and diploid (red) species across genera, as estimated by age range correlation. Interpretation for genera-specific maps is the same in Figure 1B.



**FIGURE 2** Density plots of temperature seasonality for each species with greater than two occurrences and available genetic data. Polyploid species on average occur in areas with greater temperature seasonality than diploid species ( $p < 0.05$ ).

polyploids (Figure S3). Polyploids are associated with temperate climates, with 84.7% of occurrences located within temperate regions, compared to 40.9% for diploids. This disparity is particularly true of the humid temperate climate, containing 49.5% of all polyploid occurrences but just 5.2% of diploids. Conversely, diploid occurrences are most likely to be located within tropical climates (44.3%). The most common of these is the tropical rainforest climate (17.3%) for which only two polyploid occurrences have ever been reported (0.1%). Similarly, polyploids have less than half the relative frequency in forested biomes (31.1%) than diploids (63.2%). Instead, polyploid occurrences are more common in grasslands, savannas and shrublands (58.7%).

Generally, polyploids appear more common throughout temperate grasslands and similar environments and are largely absent from the more tropical forested regions to the north.

Occupying more temperate climates indicates that polyploids likely experience more seasonality, rather than the binary wet and dry seasons of the tropics. Indeed, temperature seasonality was the only variable with significant ( $p < 0.05$ ) differences between diploid and polyploid species across the phylogeny, though the strength of this trend varies across genera (Figure 2).

In addition to being more temperate, seasonal and less forested than the surrounding area, southeastern South America is subjected to unique anthropogenic inputs as well, having undergone an



agricultural boom since the turn of the 20<sup>th</sup> century. Polyploid occurrences are more likely to be found in areas with large human impacts than diploids. In each of the sampled genera, polyploids were more frequent in areas with higher cropland usage, fertilizer application and pesticide application compared to diploids between every comparison with statistical significance ( $p < 0.05$ ) (Figure 3).

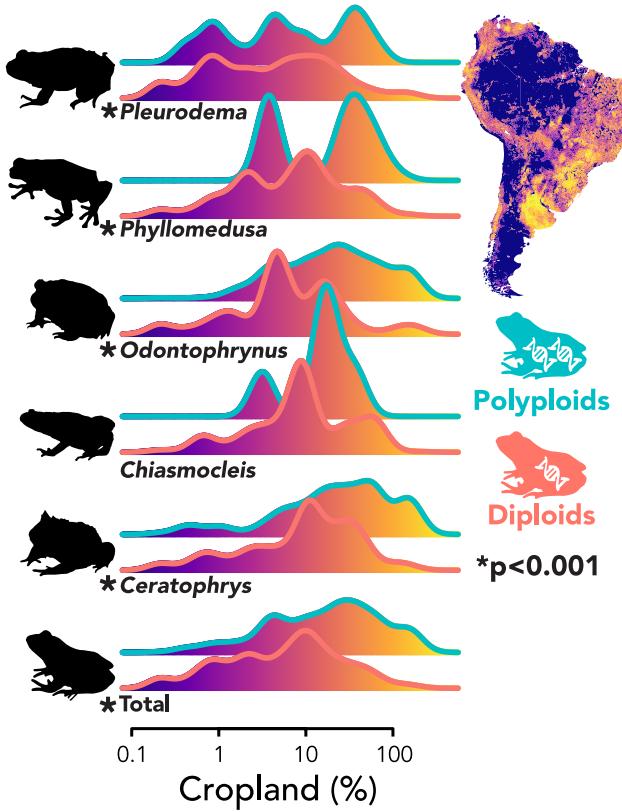
#### 4 | DISCUSSION

As opposed to diploids, which are dispersed throughout most of South America, polyploids appear to occur almost exclusively within the southeastern region, regardless of genus. Occurrence data reveal a striking pattern between environment and ploidy. On average, polyploids are nearer to other polyploid species of different genera than they are to diploids of their own genus. This close spatial affinity between polyploids across genera suggests a particular region or environment that is conducive for polyploidy. We identify several unique features of southeastern South America that may have non-exclusively contributed to the exceptionally high occurrence of polyploids in the area.

First, the unique geological history of the region is worth briefly noting. The Paranese seaway was a marine incursion into the Paraná Basin (encompassing modern-day west Brazil as well as northern Argentina and Uruguay) during the Mid to Late Miocene (~7–15 Ma) (Candela et al., 2012; Gross et al., 2016; Ruskin et al., 2011). The subsequent retreat of the Paranese seaway would have provided new terrestrial environments for polyploid species to take advantage of. The retreat of the Paranese seaway as a geographical barrier may also have created new hybrid zones, leading to increased allopolyploid formation. According to phylogenetic analyses, all polyploid species diverged from their closest sampled relative during or after this period (<11.1 Ma) (Figure S2). However, the Paranese seaway is not the only marine incursion to have occurred in South America, with the Tethys waterspout and Amazonian sea hypothesized to have existed at around the same time (Ortiz-Jaureguizar & Cladera, 2006), so geological transformations alone are not sufficient to explain the occurrence of polyploids.

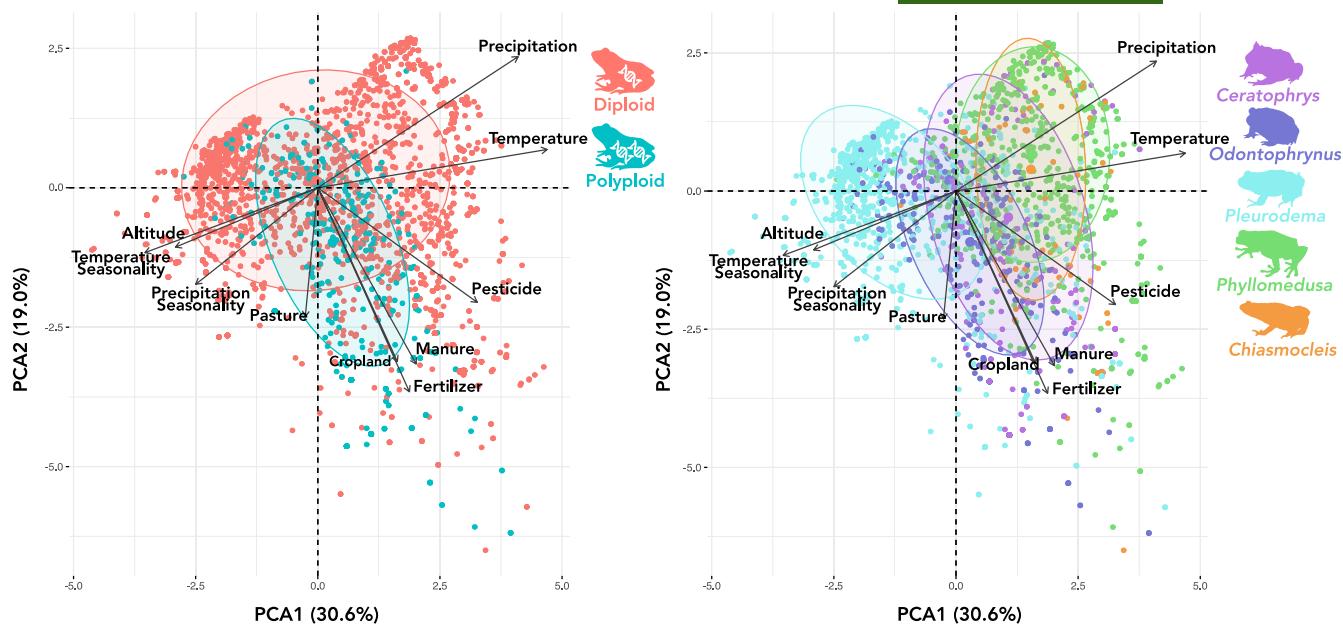
Another notable characteristic of southeastern South America is its seasonality, subject to fluctuations in temperature rather than precipitation compared to the surrounding area. Temperature seasonality was significant ( $p < 0.05$ ) between polyploid and diploid species across genera (Figure 2). Temperature fluctuations have been previously identified as a condition common to fish and amphibian polyploids (Mable et al., 2011), possibly related to their resilience to disrupted environments. However, temperature changes could also lead to an increase in polyploids through a non-selective process, as temperature shocks are a well-documented method for inducing autoploidy in many aquaculture species (Zhou & Gui, 2017), as well as frogs (Keller & Carl Gerhardt, 2001; Ueda, 1993).

Lastly, we consider relatively recent transformations to the region. Over the past century, southeastern South America has experienced one of the largest upward precipitation trends in the world



**FIGURE 3** Cropland usage density plots for diploids and polyploids across and within genera. For all comparisons with statistical significance ( $p < 0.001$ ), polyploid occurrences are on average greater than diploid occurrences. Similar results were also recovered for fertilizer and pesticide application.

(Gonzalez et al., 2010; Liebmann et al., 2004), linked to sea surface temperature anomalies (Barros et al., 2008; Haylock et al., 2006; Seager et al., 2010) and ozone depletion (Gonzalez et al., 2014). This increased wetting has resulted in a farming boom (Barros et al., 2008; Gonzalez et al., 2014; Seager et al., 2010), creating the most agriculturally productive region of South America (Ramankutty et al., 2008). Unfortunately, this has also resulted in widespread habitat destruction and pollution, with southeastern South America suffering one of the largest biodiversity declines in the world (Newbold et al., 2016). Contamination from agrochemical inputs is of special concern to the conservation of amphibians, who can absorb deleterious chemicals through their permeable skin (Baker et al., 2013; Ortiz et al., 2004). The Pampas ecoregion in particular has undergone two periods of ecological collapse over the last century as a result of unsustainable land management (Viglizzo & Frank, 2006). Notably, the Pampas is the most common ecoregion for polyploid occurrences (27.0%), where they have 54 times more relative frequency than diploids (0.5%) (Figure S3). In addition to possessing increased adaptive potential to extreme or novel environments, polyploids are also theorized to be more resilient to sudden or severe disruptions (Schoenfelder & Fox, 2015; Van de Peer et al., 2017), such as those caused by anthropogenic intervention



**FIGURE 4** PCA biplot of all quantitative variables and occurrences across South America, coloured by ploidy (left) and genera (right). Arrows indicate how each variable influences a principal component. Generally, arrows aligned to one another are correlated, positively if pointing in the same direction and negatively if pointing in opposite directions. Similarly, arrows orthogonal to one another are uncorrelated. Each point represents an occurrence. Ellipses are drawn around points within one standard distribution.

(Levin, 2020; Otto, 2018). However, empirical evidence remains controversial. A recent study comparing the effects of agrichemicals on the polyploid *O. americanus* and diploid *O. cordobae* found that although the polyploid species exhibited more micronucleases and cytotoxic effects, possibly due to their increased genome or cell size, they showed significantly less nuclear abnormalities, indicating diploids may be more sensitive to pollutants (Pollo et al., 2019). This sensitivity may be why polyploid occurrences on average exhibit greater degrees of cropland usage as well as fertilizer and pesticide application than diploids (Figure 3).

PCA results show a similar trend (Figure 4). Whereas diploid occurrences are distributed throughout feature space, polyploids align more narrowly along the correlated anthropogenic variables. Furthermore, polyploid occurrences typically occur further along this 'anthropogenic axis' than diploids. Phylogenetic PCAs reveal a similar pattern with regard to temperature seasonality (Figure S4). Taken together, these results seem to suggest that polyploids are more closely associated with areas with greater temperature fluctuations as well as those more highly impacted by human activities than diploids.

## 5 | CONCLUSION

Occurrences of polyploid frog species reveal a pattern of significant clustering across genera. The tight spatial relationship between polyploids, and absence of diploids, suggests the environment of southeastern South America may be particularly conducive to polyploidy. This region is characterized by a temperate climate and dominated primarily by grassland, in contrast to the tropical rainforests in the north.

Southeastern South America is also more seasonal than the surrounding region, experiencing higher temperature fluctuations as a result, which may lead to a higher incidence of polyploidization. The region has also experienced radical changes over just the past century, further influencing the occurrences and species ranges we observe today. Southeastern South America has recently been subjected to large agricultural transformations, resulting in a steep decline in biodiversity. This radical shift may provide new opportunities to polyploid populations who are more resilient and/or better able to adapt to changing environments previously occupied by diploids. These non-exclusive scenarios are supported by previous studies which indicate polyploids are more resilient and adaptable to extreme conditions, as well as more likely to take advantage of new environments (Comai, 2005; Otto, 2007; Van de Peer et al., 2017). Southeastern South America is also noteworthy for its lack of diploid occurrences, possibly related to the environmental differences we described. This absence may also provide opportunities for polyploids as they would have less competition and chance for cross-ploidy mating with diploids. Clearly, more work is required to distinguish between each of these hypotheses explicitly and may require genomic sampling to look for evidence of population expansions and/or migrations.

## ACKNOWLEDGEMENTS

The authors would like to thank Dr. Joseph Fan, Coral Halanych and Jamie Oaks for their invaluable discussions and feedback as well members of the Molette Lab for their support in particular: Damien Waits, Viktoria Bogantes, Michael Tassia, Caitlin Redak, Oluchi Oyekwe and Yu Sun. This work was supported by the National Science Foundation Graduate Research Fellowship Program and the Schneller Endowed



Chair Fund. This is Molette Biology Laboratory contribution #104. No collecting permits were required for this research.

## AUTHORS' CONTRIBUTIONS

KTD devised and performed the analyses, wrote and revised the manuscript. KMH contributed meaningful discussion and revised the manuscript.

## DATA AVAILABILITY STATEMENT

All code required to rerun and update analyses are available at use doi.org/10.5281/zenodo.4536106 for an archived version.

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## BIOSKETCH

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Author contributions: KTD devised and performed the analyses, wrote and revised the manuscript. KMH contributed meaningful discussion and revised the manuscript.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** David KT, Halanych KM. Spatial proximity between polyploids across South American frog genera. *J Biogeogr*. 2021;00:1–10. <https://doi.org/10.1111/jbi.14067>