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The Role of Interspecific Competition in the Range Collapse of a Songbird After Rapid Range Expansion

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THE ROLE OF INTERSPECIFIC COMPETITION IN THE RANGE COLLAPSE OF A SONGBIRD AFTER RAPID RANGE EXPANSION

A Master's Thesis
Presented to
The Graduate College of
Missouri State University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science, Biology

By
Zachary Harrison Vickers
August 2023

THE ROLE OF INTERSPECIFIC COMPETITION IN THE RANGE COLLAPSE OF A SONGBIRD AFTER RAPID RANGE EXPANSION

Biology

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Master of Science

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ABSTRACT

There is a wealth of evidence demonstrating interspecific competition in birds, but often this evidence is localized and may or may not entirely explain range dynamics over large geographic extents. Bewick’s Wrens *(Thrymanes bewickii)* and House Wrens *(Troglodytes aedon)* are small passerine birds of the family Troglodytidae. Previous experimental evidence has demonstrated that Bewick’s Wrens suffer from asymmetric interference competition from House Wrens in Kansas, and this evidence has been cited as the likely reason for the historically recent range collapse of the Bewick’s Wren. However, I argue that localized experimental evidence is insufficient to explain abundance trends over large stretches of geographic and temporal space. By making use of several decades of climatic and count data, I applied linear modeling approaches to test the hypothesis that declines in Bewick’s Wren local abundance have corresponded spatiotemporally with increases in House Wren local abundance. I found subtle evidence for effects of competition across some time comparisons but not most time comparisons. I also found geographic variation in the relationships between the abundance trends of these two species, and support for regionally specific competition. These findings suggest that competition with House Wrens has likely been one of the drivers of Bewick’s Wrens’ range declines in the eastern United States over the past several decades. In general, this study demonstrates the utility of statistical modeling approaches in testing hypotheses related to interspecific competition.

KEYWORDS: interspecific competition, range collapse, geographic variation, climate change, linear modeling, avian ecology

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INTRODUCTION

Interspecific competition is an ecological process with a wealth of evidence from plant and animal studies (Dhondt, 2012; Gurevitch et al., 1992; Kiær et al., 2013; Schoener, 1983; Smith & Smith 2015), although the strength of the evidence provided in many studies has been questioned (Connell, 1983; Connolly et al., 2001; Connor & Simberloff, 1983; Damgaard, 2019; Tilman, 1987). Adequate evidence of interspecific competition should require the demonstration of limited and overlapping resources shared between the species, and a fitness cost to at least one of the species (Dhondt, 2012). But even when it is demonstrated that these conditions are met, such evidence still may not entirely explain population declines across a species' range via competition, as local conditions could favor competition in one area but not another (Mönkkönen et al., 2004). To extrapolate from site-specific evidence, I argue that researchers should make use of spatiotemporal data to statistically model whether the respective expansions and declines of two putative competitors' ranges are in fact concordant with experimental or observational evidence. Incorporating data from two songbird species to demonstrate this approach is the central aim of this study.

Birds constitute one of the most well-studied organismal groups in ecology, and accordingly the literature on interspecific competition in birds is robust. A recent analysis by Drury et al. (2020) found that interspecific territoriality is common and widespread among birds, particularly among those within the same taxonomic family, those that hybridize, those of similar mass, and those that nest in cavities. In fact, compelling experimental evidence of interference competition involving cavity-nesting species within the same taxonomic family, such as woodpeckers and tits, has been well-documented within study sites (Aitken & Martin, 2008;

Gustafsson, 1988; Loeb & Hooper, 1997; Slagsvold, 1978; Walters & James, 2010).

Testing hypothesized links between interspecific competition and the limits or declines of species' ranges is more difficult because of the much larger geographic extent involved, but previous studies have employed various methods to try to achieve this, both theoretically and empirically. Price & Kirkpatrick (2009) created theoretical models to mathematically demonstrate how the range of an inferior competing species could be limited by the combination of a stronger competitor and a decreasing resource base away from the center of the range. Jankowski et al. (2010) conducted a playback experiment on montane avian congeners with adjacent but non-overlapping ranges, and found in most cases that trials conducted closer to range boundaries elicited closer approaches to the speaker broadcasting the congener's vocalizations, suggesting that the elevational distributions of each species may be partly dictated by interspecific competition. McQuillan & Rice (2015) created species distribution models to show that the range of Black-capped Chickadees (*Poecile atricapillus*) is retreating as their hybrid zone with Carolina Chickadees (*Poecile carolinensis*) shifts northward in step with a warming climate; *P. carolinensis* males' dominance over *P. atricapillus* males (Bronson et al., 2003) may be a contributing factor.

However, there are at least two potential dangers to attributing seemingly correspondent avian range expansions/declines to interspecific competition. First, Simberloff & Gibbons (2004) have pointed out that often the limiting resource and mechanism of competition have not been properly demonstrated in cases where interspecific competition is offered as an explanation to the collapse of a previously expanded range, such as with Budgerigars (*Melopsittacus undulatus*) and Crested Mynahs (*Acridotheres cristatellus*). As an additional example, the population declines of Lesser Kestrels (*Falco naumanni*) were thought to be due to competition with feral pigeons (*Columbia livia*) and Jackdaws (*Coloeus monedula*) over limited nest-cavities, but a large study by Forero et al. (1996) showed that neither breeding success nor nest-site saturation was correlated with the presence of either competitor.

Secondly, and conversely, the limiting resource and mechanism of competition may be well-demonstrated in one study area, but potentially unwarranted extrapolations of such evidence are then used to explain the range expansions/declines of the two competing species across a much larger area. An example of this latter issue - which provides the impetus for the present study - involves a study on Bewick's Wrens (*Thryomanes bewickii*) and House Wrens (*Troglodytes aedon*). In Kansas, Kennedy & White (1996) constructed and monitored 152 artificial nest boxes and showed that 81% of Bewick's Wrens' nesting failures in the study area were due to nest vandalism by House Wrens, demonstrating a clear fitness cost. Tree cavities are typically considered a limited resource, because the abundance of such cavities generally depends on factors such as tree age, snag density, and the presence or absence of primary cavity-nesting birds (Newton, 1994). It should be noted however that both Bewick's and House Wrens also use non-tree cavities such as rock crevices and anthropogenic structures (Johnson, 2020; Kennedy & White, 2020) that may or may not be limited in a given area. But granting that artificial nest boxes simulate a real-world limited resource, this study provides powerful evidence of asymmetrical interference competition between the two species in their Kansas study site. This study has since been cited as a potential explanation for the large-scale range collapse of the Bewick's Wrens over the last century or so (Kennedy & White, 2020). However, aside from Kennedy and White's 1996 study, there is sparse evidence of interspecific competition between the two species that rises to the level of asymmetrical competitive exclusion. In a published observation of Bewick's Wrens and House Wrens nesting in close proximity to each other in Ohio, males of both species engaged in intense interspecific chasing and fighting, but no instances of nest vandalism were documented (Newman, 1961). In Oregon, Kroodsma (1973) found high territorial sympatry and some remarkable instances of House Wrens learning and singing Bewick's Wren songs, but few instances of aggressive interactions between the two species. Root (1969) reported displacement of Bewick's Wrens territories by House Wrens in California, but also noted the disappearance of House Wrens from one area that was subsequently occupied by Bewick's Wrens. And a multi-year California study involving point counts and spot-mapping found no evidence of competitive exclusion (Verner & Purcell, 1999). Regardless of the balance of evidence these localized studies provide, the question remains whether interspecific competition has had sufficient impact to cause population declines across the large geographic area where Bewick's Wrens' range has decreased.

Bewick's Wrens (whose current range encompasses Mexico and the western and central United States) rapidly colonized the eastern U.S. during the 19th and early 20th centuries, before experiencing an equally rapid range collapse from this colonized region over the next several decades (Kennedy & White, 2020). 'Northern' House Wrens of the U.S. and Canada have expanded their breeding range southward since the late 19th century, into many of the same states that Bewick's Wrens had previously colonized (Johnson, 2020). (House Wrens are an extremely wide-ranging species whose taxonomy is in flux (Klicka et al., 2023); for the purposes of this study, 'House Wrens' will refer to the populations of the U.S. and Canada, rather than populations inhabiting Mexico, Central America, and South America). The current range of each species is shown on Figure 1 below**.**

Both species' range expansions are thought to be a consequence of the historical conversion of forest to farmland, which presumably provided both suitable habitat and nesting opportunities within anthropogenic structures (Johnson, 2020; Kennedy & White, 2020). The House Wren expansion occurred during roughly the same time period that Bewick's Wrens began to decline in those same states (Kennedy & White, 2020). As described above, experimental evidence demonstrating that House Wrens vandalize Bewick's Wrens' nests has led to the hypothesis that interspecific competition is likely an important factor in the range collapse of Bewick's Wrens, even though populations of Bewick's Wrens in some areas of overlap have not declined (Kennedy & White, 1996; Kennedy & White, 2020).

To my knowledge, no studies have attempted to use regression approaches to determine whether increases in House Wren local abundance correspond spatiotemporally with declines of Bewick's Wren local abundance across a large geographic extent. (I will use the shorthand 'abundance' in place of 'local abundance' in the text hereafter – the total abundance across each species' entire range is not relevant to the research question). I argue that, to claim interspecific competition plays a causal role in the range decline of a given species, a synthesis of observational, experimental, and statistical modeling techniques is required. This combination of evidence could be of particular importance when the area of overlap between the two species is large, given that the effects of interspecific competition could differ regionally.

Various statistical approaches can be found in the literature that evaluate whether interspecific competition is occurring based on the population trends of two or more species, in ways that are similar yet different from my own approach described below. Taking advantage of a natural experiment derived from an avian disease outbreak wherein House Finch (*Haemorhous mexicanas*) populations decreased for several years after increasing for several years prior, Cooper et al., (2007) investigated whether putatively competitive House Sparrows (*Passer domesticus*) - which had not been affected by disease - varied in abundance inversely with *H.*

mexicanus during times of *H. mexicanus* increase and decrease. After creating linear mixed models with an interaction term denoting whether *P. domesticus* abundance was changing during a period of increased or decreased *H. mexicanus* abundance, they concluded that *P. domesticus* suffered from competition in winters during periods of increased, but not decreased, *H. mexicanus* abundance (Cooper et al., 2007). Koenig et al. (2017) created structural equation models (SEMs) to test for various effects hypothesized to have contributed to Red-headed Woodpecker (*Melanerpes erythrocephalus*) declines by combining environmental data and count data on *Accipiter* predators and putative competitors Red-bellied Woodpeckers (*Melanerpes carolinus*) and European Starlings *(Sturnus vulgaris*). While finding evidence that *Accipiter* hawk population increases have played a role in *M. carolinus* declines, predictions derived from competition hypotheses were not borne out by the data (Koenig et al., 2017). Belmaker et al. (2015) created logistic mixed-effects models using species occurrence data as well as environmental and geographic predictors to examine how scale-dependent various biological factors are in explaining species' distributions. They found that positive biological interactions were salient at both fine and coarse grains, but that the effects from negative biological interactions decreased with increasing grain size, and were not significant across all grain sizes (Belmaker et al., 2015).

In this study, I used linear regression and model selection approaches to illuminate the effects of competition between Bewick's Wrens and House Wrens across a broad spatiotemporal extent. To achieve this, I took advantage of climatic data and nation-wide Breeding Bird Survey (BBS) count data collected from 1966 to the current day. I examined whether there is geographic variation in the effects of competition, as well as whether such effects manifest themselves uniformly or unevenly across time. I included climatic predictors in my analyses in order to test alternative hypotheses that may explain Bewick's Wren range declines, namely the effects of temperature, precipitation, and humidity; the inclusion of these variables is particularly important considering that widespread changes to the climate have been observed during the range of years included in the study. I conclude the study by addressing alternative hypotheses and offering some speculations about the mechanisms underlying the results revealed by the models.

METHODS

Climate Data

Before working with the count data for each species, I downloaded monthly climatic data from the PRISM Climate Group (PRISM Climate Group, 2023) from 1961 to 2019, at a 4 km resolution and a spatial extent encompassing the entire United States. I chose three types of climate data based on their hypothesized biological importance, each of them representing a basic climatic category: temperature, precipitation, and humidity. These data were chosen to account for potential drivers of Bewick's Wrens abundance declines other than House Wren abundance increases. I summarized monthly values into annual values to create variables similar to Annual Mean Temperature and Annual Precipitation as outlined in O'Donnell & Ignizio (2012), and did the same for an additional variable called Maximum Vapor Pressure Deficit. However, because of global climate change trends, I chose to compartmentalize climatic data by decadal means, instead of using current data or the mean of all years. Additionally, I chose to use decades rather than single years in order to avoid year-by-year volatility in the data. To simplify the names of the variables as well as differentiate them from the names used in O'Donnell & Ignizio (2012), I will hereafter refer to them as Temperature, Precipitation, and Max VPD. Below is a description of how each climatic variable was created.

For Temperature, I created a raster stack using the raster package (Hijmans, 2020) in R (R Core Team, 2023) composed of each month's data of a given year, then calculated the mean for that year. Afterwards, I created a raster stack composed of each year's means in that decade, and calculated the mean of that raster stack. I repeated the same process for Precipitation, but calculated sums rather than means for each year, then calculated the mean of the decadal raster stack. Lastly, I created a raster stack of Max VPD by calculating the maximum value in a given year for each year in a decade, then took the mean of the decadal raster stack.

For each decade, this process produced a raster map for each climatic variable, composed of cells containing a single value. Decadal means were sequenced in five-year intervals beginning with 1961-1970, 1966-1975, 1971-1980…and continuing to 2011-2019 (this last decade was cut one year short to align with the Breeding Bird Survey not being conducted in 2020 as a result of the covid-19 pandemic). Raster maps for each decade were resampled in R by a factor of 2, resulting in a resolution of 0.0833 × 0.0833 decimal degrees. Because Precipitation and Max VPD had skewed distributions, I log-transformed these variables. Lastly, all three variables were scaled by the standard deviations and centered at zero.

BBS Count Data

I downloaded Breeding Bird Survey (BBS) survey datasets from the Patuxent Wildlife Research Center (Ziolkowski Jr. et al., 2022). I combined three datasets into a unified dataframe: one dataset containing information regarding any places and times Bewick's Wrens were counted over the course of 1966–2019, another containing the count totals of those routes where Bewick's Wrens were recorded as present, and another containing information about each route.

Next, I downloaded a shapefile containing a map of BBS routes (Patuxent Wildlife Research Center, 2023). Each BBS route is ~39.43 km in length and contains 50 'stops' where an observer conducts a 3-minute point count (Patuxent Wildlife Research Center, 2023). Counts of individuals were broken down into five 10-stop increments, which approximately correspond to 1/5th of the distance of the route. A custom python script was created by Gleb Zhelezov to extract from the shapefile a latitude/longitude coordinate for the start and end of each BBS route, as well as a coordinate for the midpoint of each set of 10 stops along the 50-stop BBS route. Routes from the shapefile that had less than one ten-stop segment were discarded, and only routes from the United States were included. For each route, I calculated an average count of individuals for every 10 stops along the route. I associated these averaged counts with the midpoints of each 10-stop subdivision of each route, by linking the values to distances from the start of each route (e.g., the first ten-stop midpoint of each route occurs at 3,621 meters into the route, the second at 11,668 m, etc.). The BBS data were then subsetted and averaged over five-year periods beginning with the first year of the survey (i.e., 1966–1970, 1971–1975, and so on). Each five-year period of counts was coupled with a ten-year period of climatic data: the same five years of the counts as well as the five prior years. I included these five prior years under the assumption that changes in climate do not always affect populations instantaneously (Jenouvrier, 2013; Pearce-Higgins et al., 2015). Ultimately, I decided this approach struck a balance between the volatility of yearly periods and the lower resolution of longer periods. For each midpoint of a set of 10 stops, I then extracted values from each bioclimatic variable. This entire process also was conducted with House Wren data.

Variables and Analyses

The next task involved calculating the change in each variable over time for each of 55 possible time comparisons of the overall dataset (e.g., 1966–1970 to 1991–1995). Thus, I generated the response variable (the change in Bewick's Wren abundance over time, hereafter ***Δ***BEWR) and the predictor variables (the change in House Wren abundance over time, hereafter ***Δ***HOWR; the change in Temperature, Precipitation, and Max VPD, hereafter ***Δ***Temp, ***Δ***Precip, and ***Δ***MaxVPD, respectfully; Longitude, hereafter Long; and the interaction between ***Δ***HOWR and Long, hereafter **Δ**HOWR × Long). These variables are summarized in Table 1. I decided to include the interaction term because it was apparent from the literature and initial examinations of the data that House Wren abundance might have differential effects on Bewick's Wren abundance between the western and eastern U.S., and because the eastern U.S. is the geographic area in which Bewick's Wrens' range has collapsed. Additionally, compelling evidence of competition has only been documented in the eastern part of Bewick's Wrens' range (Kennedy & White, 1996), with competitive exclusion reported to be absent in the west (Verner & Purcell, 1999). To calculate the values that populated the response and predictor variables, I subtracted values of time period *x* (e.g., 1966–1970) from time period *y* (e.g., 1971–1975). I subsetted the data to only include places where a Bewick's Wren had a non-zero value in one or both time periods.

I scaled each predictor variable, then for each time comparison I created a global linear model of all variables, then used the 'dredge' function in the R package MuMIn (Barton, 2009) to rank all 64 possible models by Akaike Information Criterion (AIC). I calculated 'importance' values, which is another term for the sums of Akaike weights for all models in the model set including a given variable, for each variable across all fitted models. An important note is that a variable with a large value is not necessarily "important" in absolute terms, but rather "important" compared to the other variables in the model. I then performed model averaging of the top-ranked models for each time comparison within 2 AIC units of the 'top' model (the model with the lowest AIC value), and summarized the effect sizes and confidence intervals of each variable.

To investigate potential geographic variation in the effects of interspecific competition between these two species, I generated predicted data based on the averaged models of each time comparison by using the ‘predict’ function in R at six different longitudinal coordinates. These longitudes approximately corresponded to the longitudes of 1) Verner & Purcell (1999)’s study site in Sierra Nevada, CA; 2) Tucson, AZ; 3) Albuquerque, NM; 4) Kennedy & White (1996)’s study site in Manhattan, KS; 5) Columbia, MO; and 6) Lexington, KY. I then plotted these model predictions using ggplot2 (Wickham, 2016) for visual analysis.

RESULTS

The importance of the HOWR × Long interaction (the primary variable of interest for this study) was fairly low overall in linear models, except in time comparisons where the ending time period was 1986–1990, 1991–1995, 1996–2000, and 2011–2015 (Fig. 2). Importance values were similar for these same time comparisons for both the **_Δ_**HOWR (Fig. 3) and Long (Fig. 4) variables. Of the climatic predictors, **_Δ_**Precip (Fig. 5) contained the most intermediate to high importance values (≥ 0.5) compared to **_Δ_**VPD (Fig. 6) and **_Δ_**Temp (Fig. 7). Table 2 summarizes all importance values for each variable, as well as median and mean importance values, and percentage of importance values above 0.5 across models for all time period comparisons. **_Δ_**HOWR × Long had the lowest median and mean importance value, but Long and **_Δ_**HOWR had the first and second highest median and mean importance values, respectively.

Table 3 displays the (conditional) results of model averaging for each time comparison, with effect sizes, adjusted standard error, and 95% confidence intervals shown for each variable. **_Δ_**HOWR × Long had almost universally negative coefficient estimates, but in 50% of the 32 time comparisons where this variable was included, the 95% confidence interval overlapped zero. All other variables were featured in at least 50 of 55 time comparisons, with coefficient estimates that varied between positive and negative values among time comparisons. Of the 53 time comparisons that included the **_Δ_**HOWR variable, only 10 (18.9%) time comparisons had confidence intervals that did not overlap zero.

The slopes and intercepts of the predicted linear relationships between Bewick's Wren and House Wren abundances varied across time comparisons, and within time comparisons by longitude. While all 55 prediction plots are included in the supplementary material (Appendix), it is worth examining a small subset of time comparisons to see the variation in model outcomes (Fig. 8). For all models presented in Figure 8, the slopes associated with longitudes east of the Rocky Mountains were either negative or very weakly positive, whereas those west of the Rockies were clearly positive. At roughly the longitude of Verner & Purcell (1999)'s study site in California (the study which found no evidence of competitive exclusion), there was a predicted positive relationship between Bewick's Wren and House Wren abundances. At roughly the longitude of Kennedy & White (1996)'s study site in Kansas (the study which experimentally demonstrated interspecific competition), there was a mix of weakly positive and weakly negative relationships. Additionally, in the two time comparisons wherein the ΔHOWR × Long interaction had a high importance value (1966–1970 through 1986–1990 and 1966–1970 through 1996–2000), the interaction bears a strong signature of regionally specific competition, where associations between abundance changes of the two species are positive in the west but negative in the east (Fig. 8).

DISCUSSION

My findings provide subtle evidence for the effects of interspecific competition between House Wrens and Bewick's Wrens: the evidence appears strong across some time comparisons but not most, and the effects appear to be geographically variable. Bewick's Wren abundance decreases were most correlated with House Wren abundance increases in the easternmost area of the Bewick's Wren range, while the two species' abundances appear positively correlated in the western part of the range. Additionally, climatic changes over time showed a similar, but lesser, contribution to Bewick's Wren abundance declines, as evidence was unevenly distributed across time-comparison matrices, but overall importance values were lower on average. The fact that longitude was an almost universally important predictor across time comparisons reflects the fact that Bewick's Wrens abundance declines have overwhelmingly occurred in the eastern part of their range.

Since the abundance trends of both species appear to correlate in opposite directions moving from west to east, the most important variable for revealing the effects of interspecific competition is ΔHOWR × Long. This predictor yielded low importance values (none greater than 0.40) within ten-year time comparisons, but yielded high importance values for several time comparisons spanning greater temporal lengths. This is not necessarily evidence for time-lagged effects of competition, in the manner that other ecological changes such as forest fragmentation can produce (Uezu & Metzger, 2016). Rather, changes in Bewick's Wren abundance over short time periods could be of insufficient magnitude to be detected when there is a very low signal-to-noise ratio. Even so, very high importance values for ΔHOWR × Long (e.g., 0.93 between 1986-1990 and 1996-2000) occur amongst slightly longer timespans. Additionally, the idea that the effects of competition between these species simply takes time to accumulate until signal overwhelms noise is not entirely consistent with the pattern revealed by the matrix for ΔHOWR × Long (Fig. 2), which shows a clear clustering around time periods that ended with 1990, 1995, and 2000, even when comparisons span relatively short timespans.

In the west, linear models largely predicted positive relationships between Bewick's Wren and House Wren abundance, inconsistent with competition but perhaps consistent with environmental conditions having similar effects for both species due to their shared niche preferences for certain non-limited resources. Environmental conditions could even theoretically involve changes to a shared limiting resource, if said resource were to increase in availability such that abundances of both species increased in spite of competition.

It is important to reiterate that the areas in which Bewick's Wrens have declined most dramatically (i.e., states in the eastern U.S.) are areas that they only recently colonized over the past two centuries, possibly due to anthropogenic changes to the landscape that opened up nesting opportunities within anthropogenic structures. If newly favorable habitat conditions induce a species to expand its range, then the extent to which the expansion is successful likely depends in part on the competitive ability of heterospecifics with similar niche requirements. Model simulations conducted by Burton et al. (2010) indicate that 1) populations on the frontiers of a range expansion tend to be of low density, 2) that individuals in these populations are selected for dispersal ability at the expense of competitive ability, and 3) that range expansions are slowed by the presence of a competing species. In an experimental study involving artificial landscapes constructed within plastic boxes, Legault et al. (2020) compared the range expansions of a flour beetle *Tribolium casteneum* both without competition and with competition with *T. confusum*. They demonstrated that abundances of *T. casteneum* within each patch they successively colonized drastically declined in the face of increasing abundances of the competing species. However, rapid range expansions in the face of competing species have been observed in nature. For example, Western Bluebirds *(Sialia mexicana)* rapidly re-colonized their historic range in Montana after extensive artificial nest-box construction, and colonizing males were found to be more aggressive than the Mountain Bluebirds *(Sialia currucoides)* they displaced, but then Western Bluebird males' aggression was significantly reduced after just a few generations post-displacement (Duckworth & Badyaev, 2007). Often it is the case, though, that a range expansion is followed by a quick collapse. For example, the plant named 'sea-rocket' *(Cakile edentula)* expanded rapidly and became abundant after its introduction to the eastern U.S., but a portion of its range quickly collapsed, likely due to competition with another introduced species *C. maritima*, which was found to have higher reproductive fitness in the 'foredune' habitats that both species had colonized (Boyd & Barbour, 1993; Simberloff & Gibbons, 2004).

One potential explanation for the geographical discrepancy in competition effects between this study's species could be a difference between the availability of ideal nesting sites in the East compared to the West. Bewick's Wrens have likely been more reliant on anthropogenic structures for nest-sites in the East compared to the West, because some cavity tree species found in their native range - Ashe Juniper *(Juniperus ashei)*, for example (USDA, 2023) - are absent in the east. If this is the case, suitable nest sites in the east might be (1) more limited, (2) harder to defend in the presence of House Wrens, or (3) both.

Additionally, urbanized landscapes may be stimulating many novel competitive interactions between species. Recent evidence from the northwest U.S. suggests that Bewick's Wrens themselves may be limiting abundances of Pacific Wrens *(Troglodytes pacificus)* in certain areas, such as patches of forest where Pacific Wrens interact with Bewick's Wrens near edge habitat created by parks or other established development (Farwell & Marzluff, 2013), though the extent to which territorial interactions are directly causal to these simultaneous trends is unclear. Illustrating the compounding competition pressures of cavity-nesting in an urban park in southern Spain, Hernandez-Brito et al. (2014) found that the invasive and very aggressive Ring-necked Parakeet *(Psittacula krameri)* has outcompeted native birds with similar nesting preferences. While not as formidable as a mid-sized parakeet, House Wrens' propensity for nest vandalism could potentially harm Bewick's Wren populations wherever the species co-occur, but perhaps especially in areas with high amounts of anthropogenic transformation of the landscape.

Some but not all of the broad patterns found in species exhibiting interspecific territoriality (as described by Drury et al. (2020) above) are present in Bewick's Wrens and House Wrens. They are both cavity-nesting species of similar mass in the family Troglodytidae, but they are not each other's closest relatives, and intergeneric hybridization within the Troglodytidae has not been reported (Barker, 2004). An aggressive nature towards heterospecifics might be an ancient trait within Troglodytidae, as nest-destroying behavior has been documented in House Wrens, Cactus Wrens, and Marsh Wrens (e.g., Fern et al., 2019; Kennedy & White, 1996, Picman, 1984, Simons & Simons, 1990). Thus, wrens may prove to be a candidate for a model system for studying interspecific competition in birds.

The relatively less important contribution of the climatic variables in models compared to the **Δ**HOWR variable invites speculation. It may be that the similar niche preferences of House Wrens encompasses more granular and species-specific information than broad climate categories such as temperature, and thus changes in House Wren abundance may better predict changes in Bewick's Wren abundance in places where the effects of competition are not apparent, as evidenced by positive correlations between the species' abundances in the western U.S. Additionally, Bewick's Wrens are native to some very hot places in the southwestern U.S., so rising temperatures in the eastern U.S. may not harm Bewick's Wrens populations as they would with other species. A future study focused solely on the specific climatic drivers of changes in these species' abundances may be more revealing than the present study, which primarily aims to investigate effects of interspecific competition.

In conclusion, this study builds off the aforementioned experimental and observational evidence regarding Bewick's Wren and House Wren competition, by making use of decades of data to statistically test spatiotemporal correspondence of abundance changes between the two study species over a large geographic extent. While the findings of this study do not reveal a simple narrative about House Wrens outcompeting Bewick's Wrens, the statistical approaches demonstrated here could still be valuable for other studies investigating interspecific competition. Even solidly justifiable inferences about the importance of interspecific competition based on experimental or observational evidence may lead to overlooked alternative explanations when considering large range declines. For example, the edges of a range could consist of low-density populations, which theoretical modeling suggests are more vulnerable to extinction than higher-density populations near the core (Maurer & Taper, 2002). Small populations on the frontier of range expansions could have lower genetic diversity and thus be more susceptible to genetic drift that could inhibit local adaptation to heterogeneous environments (Polechová, 2018). Both of these scenarios could lead to short-lived range expansions that don't necessarily involve interspecific competition. Thus, it is helpful to pair experimental evidence of competition with other methodological approaches such as statistical modeling.

A modeling approach using temporal data may more directly test the effects of competition than other statistical approaches involving biotic interactions, such as niche modeling. Elith & Leathwick (2009) argue that the inclusion of biotic interactions in niche modeling presents a problem of potential confounding of environmental variables and biotic variables. The approach of the present study may more directly test the hypothesis that changes in the abundance of one species correspond to changes in abundance of another, which is valuable insofar as the results are paired with mechanistic evidence of interspecific competition over limited resources.

As a final note, the above discussion does not wade into issues of conservation priorities - particularly as the range loss of Bewick's Wrens appears to primarily be in areas they've only recently colonized due to human development. However, I believe that populations of this species should continue to be monitored closely, as there may be reasons beyond competition with an aggressive heterospecific underlying the rapid decline of their range.

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Table 1. Predictor variables used across candidate models to explain changes in local abundance of Bewick's Wrens (ΔBEWR) over time.[1]

Predictor Variables	Descriptions
ΔTemp	Change in annual mean temperature
ΔPrecip	Change in annual precipitation
ΔVPD	Change in maximum vapor pressure deficit
ΔHOWR	Change in House Wren abundance
Long	Longitude
ΔHOWR × Long	Interaction between Long and ΔHOWR

[1] Δ = "change in". Top-performing linear models (within 2 AIC points) were averaged; as a result some averaged models did not include every predictor variable. Refer to Methods for further descriptions of variables.

Table 2. Importance values for each predictor variable used across candidate models to explain changes in local abundance of Bewick's Wrens (ΔBEWR) over time, across each of 55 possible time comparisons.[1]

Starting Time	Ending Time	ΔTemp	ΔPrecip	ΔVPD	Long	ΔHOWR	ΔHOWR × Long
1966_1970	1971_1975	0.35	0.36	0.56	0.32	0.30	0.03
1966_1970	1976_1980	0.33	0.60	0.81	1.00	0.51	0.25
1966_1970	1981_1985	0.27	0.88	0.60	1.00	0.39	0.12
1966_1970	1986_1990	0.27	1.00	0.33	1.00	1.00	1.00
1966_1970	1991_1995	0.42	0.94	0.35	1.00	0.99	0.95
1966_1970	1996_2000	0.40	0.40	0.28	1.00	0.97	0.95
1966_1970	2001_2005	0.28	0.27	0.40	1.00	0.52	0.34
1966_1970	2006_2010	0.31	0.34	0.87	1.00	0.53	0.17
1966_1970	2011_2015	0.72	0.80	0.74	1.00	0.44	0.23
1966_1970	2016_2019	0.73	0.50	0.42	1.00	0.65	0.38
1971_1975	1976_1980	0.33	0.46	0.37	1.00	0.58	0.39
1971_1975	1981_1985	0.56	1.00	0.37	0.79	0.97	0.21
1971_1975	1986_1990	0.97	0.57	0.28	1.00	1.00	0.99
1971_1975	1991_1995	0.59	0.98	0.37	0.92	0.95	0.88
1971_1975	1996_2000	0.54	0.42	0.55	1.00	1.00	1.00
1971_1975	2001_2005	0.66	0.67	0.35	0.98	0.76	0.66
1971_1975	2006_2010	0.27	0.34	0.27	0.93	0.69	0.36
1971_1975	2011_2015	0.35	0.88	0.52	1.00	0.96	0.86
1971_1975	2016_2019	0.34	0.39	0.32	0.99	0.50	0.31
1976_1980	1981_1985	0.74	0.55	0.31	0.39	0.34	0.05
1976_1980	1986_1990	0.32	0.51	0.30	0.97	1.00	0.83
1976_1980	1991_1995	0.72	0.34	0.30	0.99	0.80	0.71
1976_1980	1996_2000	0.30	0.65	0.61	1.00	1.00	1.00

Table 2 continued

Starting Time	Ending Time	ΔTemp	ΔPrecip	ΔVPD	Long	ΔHOWR	ΔHOWR × Long
1976_1980	2001_2005	0.33	0.28	0.40	0.63	0.45	0.25
1976_1980	2006_2010	0.48	0.70	0.36	0.46	0.52	0.14
1976_1980	2011_2015	0.45	0.63	0.28	0.35	0.53	0.08
1976_1980	2016_2019	0.77	0.28	0.66	0.32	0.31	0.05
1981_1985	1986_1990	0.49	0.51	0.53	0.96	0.68	0.25
1981_1985	1991_1995	0.41	0.46	0.87	0.99	0.49	0.21
1981_1985	1996_2000	0.27	0.31	0.31	1.00	1.00	0.94
1981_1985	2001_2005	0.28	0.41	0.29	0.50	0.37	0.09
1981_1985	2006_2010	0.41	0.71	0.57	0.34	0.30	0.04
1981_1985	2011_2015	0.47	0.65	0.33	0.38	0.66	0.08
1981_1985	2016_2019	0.96	0.51	0.46	0.33	0.31	0.04
1986_1990	1991_1995	0.29	0.90	0.52	0.98	1.00	0.28
1986_1990	1996_2000	0.48	0.27	0.49	0.99	1.00	0.93
1986_1990	2001_2005	0.28	0.87	0.31	0.67	1.00	0.49
1986_1990	2006_2010	0.36	0.29	0.64	0.38	0.99	0.13
1986_1990	2011_2015	0.39	0.40	0.35	0.99	1.00	0.99
1986_1990	2016_2019	0.58	0.60	0.75	0.42	1.00	0.15
1991_1995	1996_2000	0.70	0.79	0.41	0.52	0.98	0.29
1991_1995	2001_2005	0.34	0.99	0.28	0.36	0.64	0.07
1991_1995	2006_2010	0.34	0.28	0.44	0.38	0.33	0.05
1991_1995	2011_2015	0.28	0.28	0.31	1.00	0.96	0.26
1991_1995	2016_2019	0.38	0.30	0.78	0.61	0.56	0.10
1996_2000	2001_2005	0.27	0.34	0.33	0.69	0.97	0.40
1996_2000	2006_2010	0.68	0.80	0.32	0.55	0.31	0.05

Table 2 continued

Starting Time	Ending Time	ΔTemp	ΔPrecip	ΔVPD	Long	ΔHOWR	ΔHOWR × Long
1996_2000	2011_2015	0.93	0.28	0.76	0.99	1.00	0.84
1996_2000	2016_2019	0.72	0.31	0.47	0.42	0.52	0.08
2001_2005	2006_2010	0.70	1.00	0.41	0.99	0.35	0.09
2001_2005	2011_2015	0.30	0.36	0.97	0.68	0.81	0.15
2001_2005	2016_2019	0.37	0.76	0.36	0.32	0.50	0.05
2006_2010	2011_2015	0.53	0.28	1.00	0.30	0.38	0.04
2006_2010	2016_2019	0.28	1.00	0.30	0.98	0.36	0.10
2011_2015	2016_2019	0.76	0.31	0.99	0.90	0.42	0.15
	Mean:	0.47	0.56	0.48	0.76	0.68	0.37
	Median:	0.40	0.51	0.40	0.96	0.65	0.25
	fraction ≥ 0.5	0.35	0.53	0.36	0.73	0.71	0.27

[1] For more detail on how importance values are calculated, refer to Figure 2 and Methods. Mean and median importance values are reported for each variable at the bottom of the table, as well as the % of time comparisons that featured values above 0.5.

Table 3. Summary information of model-averaged parameter estimates (Coef) for each predictor variable used across candidate models to explain changes in local abundance of Bewick's Wrens (ΔBEWR) over time, across all 55 possible time comparisons.[1]

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1966_1970	1971_1975	746	Intercept	-0.15	0.07	-0.28	-0.02
1966_1970	1971_1975		ΔVPD	0.08	0.05	-0.02	0.17
1966_1970	1971_1975		ΔTemp	-0.05	0.05	-0.15	0.06
1966_1970	1971_1975		ΔPrecip	-0.05	0.06	-0.16	0.07
1966_1970	1971_1975		ΔHOWR	0.03	0.08	-0.13	0.19
1966_1970	1971_1975		Long	0.01	0.08	-0.14	0.17
1966_1970	1976_1980	683	Intercept	-0.42	0.08	-0.58	-0.26
1966_1970	1976_1980		ΔPrecip	0.16	0.09	-0.01	0.32
1966_1970	1976_1980		ΔVPD	0.18	0.07	0.03	0.32
1966_1970	1976_1980		Long	-0.40	0.10	-0.59	-0.20
1966_1970	1976_1980		ΔTemp	0.07	0.08	-0.10	0.23
1966_1970	1976_1980		ΔHOWR	0.03	0.15	-0.28	0.33
1966_1970	1976_1980		ΔHOWR × Long	-0.17	0.13	-0.42	0.08
1966_1970	1981_1985	647	Intercept	-0.30	0.09	-0.49	-0.12
1966_1970	1981_1985		ΔPrecip	0.24	0.09	0.05	0.42
1966_1970	1981_1985		ΔVPD	0.19	0.11	-0.03	0.41
1966_1970	1981_1985		Long	-0.69	0.11	-0.91	-0.48
1966_1970	1981_1985		ΔHOWR	-0.08	0.13	-0.33	0.18
1966_1970	1986_1990	679	Intercept	-0.08	0.09	-0.25	0.09
1966_1970	1986_1990		ΔPrecip	0.33	0.08	0.17	0.49
1966_1970	1986_1990		ΔHOWR	0.09	0.10	-0.10	0.29
1966_1970	1986_1990		Long	-0.77	0.10	-0.97	-0.57
1966_1970	1986_1990		ΔHOWR × Long	-0.60	0.09	-0.78	-0.42

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1966_1970	1986_1990	679	ΔVPD	-0.07	0.09	-0.24	0.10
1966_1970	1986_1990		ΔTemp	-0.03	0.09	-0.20	0.15
1966_1970	1991_1995	706	Intercept	-0.15	0.09	-0.33	0.02
1966_1970	1991_1995		ΔPrecip	0.23	0.08	0.07	0.38
1966_1970	1991_1995		ΔHOWR	-0.14	0.12	-0.36	0.09
1966_1970	1991_1995		Long	-0.62	0.10	-0.82	-0.42
1966_1970	1991_1995		ΔHOWR × Long	-0.29	0.10	-0.48	-0.09
1966_1970	1991_1995		ΔTemp	-0.10	0.08	-0.25	0.06
1966_1970	1991_1995		ΔVPD	-0.08	0.09	-0.25	0.09
1966_1970	1996_2000	672	Intercept	0.01	0.08	-0.15	0.18
1966_1970	1996_2000		ΔHOWR	-0.15	0.10	-0.35	0.06
1966_1970	1996_2000		Long	-0.65	0.10	-0.85	-0.45
1966_1970	1996_2000		ΔHOWR × Long	-0.36	0.11	-0.58	-0.14
1966_1970	1996_2000		ΔTemp	-0.09	0.08	-0.24	0.07
1966_1970	1996_2000		ΔPrecip	-0.08	0.08	-0.23	0.07
1966_1970	1996_2000		ΔVPD	-0.04	0.11	-0.26	0.18
1966_1970	2001_2005	665	Intercept	-0.13	0.09	-0.30	0.05
1966_1970	2001_2005		Long	-0.61	0.11	-0.83	-0.38
1966_1970	2001_2005		ΔHOWR	-0.09	0.13	-0.34	0.17
1966_1970	2001_2005		ΔHOWR × Long	-0.25	0.14	-0.51	0.02
1966_1970	2001_2005		ΔVPD	-0.11	0.11	-0.31	0.10
1966_1970	2001_2005		ΔPrecip	0.03	0.10	-0.17	0.24
1966_1970	2006_2010	634	Intercept	-0.15	0.12	-0.40	0.09
1966_1970	2006_2010		ΔVPD	-0.30	0.12	-0.54	-0.06

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1966_1970	2006_2010	634	Long	-0.76	0.15	-1.06	-0.46
1966_1970	2006_2010		ΔHOWR	-0.21	0.17	-0.55	0.13
1966_1970	2006_2010		ΔPrecip	0.11	0.14	-0.18	0.39
1966_1970	2006_2010		ΔTemp	0.07	0.11	-0.14	0.29
1966_1970	2011_2015	614	Intercept	-0.30	0.10	-0.49	-0.11
1966_1970	2011_2015		ΔPrecip	0.26	0.11	0.05	0.48
1966_1970	2011_2015		ΔTemp	0.20	0.09	0.02	0.38
1966_1970	2011_2015		ΔVPD	-0.25	0.11	-0.48	-0.03
1966_1970	2011_2015		Long	-0.84	0.13	-1.10	-0.58
1966_1970	2011_2015		ΔHOWR	-0.03	0.16	-0.34	0.27
1966_1970	2011_2015		ΔHOWR × Long	-0.20	0.14	-0.48	0.07
1966_1970	2016_2019	614	Intercept	-0.08	0.10	-0.28	0.11
1966_1970	2016_2019		ΔPrecip	0.19	0.13	-0.06	0.45
1966_1970	2016_2019		ΔHOWR	-0.22	0.18	-0.57	0.12
1966_1970	2016_2019		ΔTemp	0.20	0.10	0.00	0.39
1966_1970	2016_2019		Long	-0.64	0.16	-0.95	-0.34
1966_1970	2016_2019		ΔHOWR × Long	-0.34	0.21	-0.74	0.06
1966_1970	2016_2019		ΔVPD	-0.12	0.10	-0.31	0.06
1971_1975	1976_1980	961	Intercept	-0.27	0.06	-0.39	-0.15
1971_1975	1976_1980		Long	-0.28	0.06	-0.39	-0.16
1971_1975	1976_1980		ΔHOWR	-0.11	0.15	-0.39	0.18
1971_1975	1976_1980		ΔHOWR × Long	-0.18	0.09	-0.36	0.01
1971_1975	1976_1980		ΔPrecip	0.05	0.04	-0.02	0.12
1971_1975	1976_1980		ΔVPD	0.05	0.06	-0.07	0.16

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1971_1975	1976_1980	961	ΔTemp	-0.04	0.07	-0.17	0.10
1971_1975	1981_1985	922	Intercept	0.02	0.10	-0.17	0.21
1971_1975	1981_1985		ΔPrecip	0.22	0.06	0.11	0.33
1971_1975	1981_1985		ΔHOWR	-0.26	0.09	-0.44	-0.08
1971_1975	1981_1985		ΔTemp	0.15	0.09	-0.03	0.33
1971_1975	1981_1985		Long	-0.21	0.11	-0.42	0.00
1971_1975	1981_1985		ΔVPD	0.05	0.10	-0.16	0.25
1971_1975	1981_1985		ΔHOWR × Long	-0.04	0.09	-0.21	0.14
1971_1975	1986_1990	976	Intercept	0.16	0.08	-0.01	0.32
1971_1975	1986_1990		ΔPrecip	0.08	0.05	-0.02	0.19
1971_1975	1986_1990		ΔHOWR	-0.04	0.10	-0.23	0.16
1971_1975	1986_1990		ΔTemp	0.23	0.07	0.09	0.37
1971_1975	1986_1990		Long	-0.12	0.08	-0.28	0.04
1971_1975	1986_1990		ΔHOWR × Long	-0.26	0.07	-0.41	-0.12
1971_1975	1986_1990		ΔVPD	0.03	0.10	-0.16	0.22
1971_1975	1991_1995	1017	Intercept	0.15	0.08	-0.01	0.31
1971_1975	1991_1995		ΔPrecip	0.14	0.05	0.05	0.24
1971_1975	1991_1995		ΔHOWR	-0.25	0.12	-0.49	-0.01
1971_1975	1991_1995		ΔTemp	0.11	0.07	-0.03	0.25
1971_1975	1991_1995		Long	-0.06	0.09	-0.24	0.12
1971_1975	1991_1995		ΔHOWR × Long	-0.26	0.09	-0.42	-0.09
1971_1975	1991_1995		ΔVPD	0.09	0.10	-0.10	0.27
1971_1975	1996_2000	924	Intercept	0.16	0.10	-0.03	0.35
1971_1975	1996_2000		ΔHOWR	-0.27	0.13	-0.52	-0.03

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1971_1975	1996_2000	924	ΔVPD	0.17	0.10	-0.03	0.37
1971_1975	1996_2000		Long	-0.23	0.11	-0.45	-0.02
1971_1975	1996_2000		ΔHOWR × Long	-0.40	0.09	-0.58	-0.22
1971_1975	1996_2000		ΔTemp	0.11	0.07	-0.03	0.25
1971_1975	1996_2000		ΔPrecip	-0.06	0.05	-0.17	0.04
1971_1975	2001_2005	920	Intercept	0.08	0.08	-0.07	0.23
1971_1975	2001_2005		ΔPrecip	-0.11	0.06	-0.22	0.00
1971_1975	2001_2005		ΔHOWR	-0.16	0.13	-0.41	0.08
1971_1975	2001_2005		ΔTemp	0.12	0.07	0.00	0.25
1971_1975	2001_2005		Long	-0.21	0.09	-0.38	-0.05
1971_1975	2001_2005		ΔHOWR × Long	-0.24	0.10	-0.44	-0.05
1971_1975	2006_2010	880	Intercept	0.17	0.10	-0.02	0.37
1971_1975	2006_2010		ΔHOWR	-0.28	0.17	-0.60	0.05
1971_1975	2006_2010		Long	-0.25	0.10	-0.45	-0.04
1971_1975	2006_2010		ΔHOWR × Long	-0.20	0.13	-0.45	0.05
1971_1975	2006_2010		ΔPrecip	0.07	0.09	-0.10	0.24
1971_1975	2011_2015	867	Intercept	-0.10	0.09	-0.29	0.08
1971_1975	2011_2015		ΔPrecip	0.16	0.07	0.03	0.30
1971_1975	2011_2015		ΔHOWR	-0.06	0.14	-0.34	0.22
1971_1975	2011_2015		Long	-0.40	0.10	-0.60	-0.19
1971_1975	2011_2015		ΔHOWR × Long	-0.27	0.11	-0.48	-0.06
1971_1975	2011_2015		ΔVPD	-0.13	0.09	-0.30	0.05
1971_1975	2011_2015		ΔTemp	0.05	0.06	-0.07	0.18
1971_1975	2016_2019	847	Intercept	0.12	0.09	-0.05	0.30

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1971_1975	2016_2019	847	Long	-0.33	0.09	-0.50	-0.16
1971_1975	2016_2019		ΔPrecip	-0.09	0.08	-0.24	0.06
1971_1975	2016_2019		ΔHOWR	-0.17	0.16	-0.48	0.13
1971_1975	2016_2019		ΔHOWR × Long	-0.20	0.12	-0.43	0.03
1971_1975	2016_2019		ΔVPD	0.07	0.08	-0.08	0.22
1971_1975	2016_2019		ΔTemp	0.07	0.07	-0.07	0.21
1976_1980	1981_1985	828	Intercept	0.23	0.08	0.07	0.38
1976_1980	1981_1985		ΔTemp	0.13	0.06	0.00	0.25
1976_1980	1981_1985		ΔPrecip	0.07	0.05	-0.03	0.18
1976_1980	1981_1985		Long	0.11	0.11	-0.11	0.33
1976_1980	1981_1985		ΔHOWR	-0.05	0.08	-0.21	0.12
1976_1980	1981_1985		ΔVPD	0.06	0.07	-0.08	0.20
1976_1980	1986_1990	880	Intercept	0.55	0.08	0.38	0.71
1976_1980	1986_1990		ΔPrecip	-0.07	0.05	-0.17	0.03
1976_1980	1986_1990		ΔHOWR	-0.05	0.12	-0.29	0.19
1976_1980	1986_1990		Long	0.19	0.08	0.04	0.34
1976_1980	1986_1990		ΔHOWR × Long	-0.20	0.08	-0.37	-0.04
1976_1980	1986_1990		ΔTemp	0.05	0.07	-0.09	0.18
1976_1980	1986_1990		ΔVPD	-0.05	0.07	-0.19	0.10
1976_1980	1991_1995	925	Intercept	0.57	0.09	0.40	0.75
1976_1980	1991_1995		ΔHOWR	-0.42	0.19	-0.80	-0.05
1976_1980	1991_1995		ΔTemp	-0.13	0.07	-0.26	0.00
1976_1980	1991_1995		Long	0.27	0.09	0.10	0.44
1976_1980	1991_1995		ΔHOWR × Long	-0.32	0.13	-0.57	-0.07

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1976_1980	1991_1995	925	ΔPrecip	0.03	0.06	-0.08	0.13
1976_1980	1996_2000	837	Intercept	0.68	0.09	0.50	0.86
1976_1980	1996_2000		ΔPrecip	-0.11	0.06	-0.23	0.01
1976_1980	1996_2000		ΔHOWR	-0.49	0.19	-0.87	-0.12
1976_1980	1996_2000		Long	0.16	0.10	-0.02	0.35
1976_1980	1996_2000		ΔHOWR × Long	-0.52	0.13	-0.77	-0.27
1976_1980	1996_2000		ΔVPD	0.16	0.10	-0.03	0.35
1976_1980	1996_2000		ΔTemp	-0.07	0.08	-0.22	0.09
1976_1980	2001_2005	821	Intercept	0.38	0.10	0.19	0.57
1976_1980	2001_2005		Long	0.14	0.09	-0.03	0.31
1976_1980	2001_2005		ΔHOWR	-0.29	0.21	-0.70	0.11
1976_1980	2001_2005		ΔHOWR × Long	-0.29	0.15	-0.58	0.00
1976_1980	2001_2005		ΔVPD	0.09	0.09	-0.09	0.27
1976_1980	2001_2005		ΔTemp	-0.10	0.07	-0.24	0.05
1976_1980	2001_2005		ΔPrecip	-0.03	0.05	-0.14	0.07
1976_1980	2006_2010	773	Intercept	0.45	0.10	0.26	0.64
1976_1980	2006_2010		ΔPrecip	0.19	0.09	0.01	0.37
1976_1980	2006_2010		ΔHOWR	-0.20	0.17	-0.54	0.13
1976_1980	2006_2010		ΔTemp	-0.10	0.09	-0.27	0.06
1976_1980	2006_2010		ΔVPD	0.14	0.13	-0.12	0.39
1976_1980	2006_2010		Long	0.07	0.13	-0.18	0.33
1976_1980	2011_2015	770	Intercept	0.23	0.09	0.07	0.40
1976_1980	2011_2015		ΔPrecip	0.12	0.07	-0.01	0.26
1976_1980	2011_2015		ΔHOWR	0.21	0.15	-0.09	0.51

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1976_1980	2011_2015	770	ΔTemp	-0.09	0.07	-0.21	0.04
1976_1980	2011_2015		Long	-0.05	0.10	-0.26	0.15
1976_1980	2011_2015		ΔVPD	-0.03	0.09	-0.20	0.14
1976_1980	2016_2019	759	Intercept	0.52	0.09	0.34	0.70
1976_1980	2016_2019		ΔTemp	-0.21	0.09	-0.38	-0.04
1976_1980	2016_2019		ΔVPD	0.20	0.10	0.01	0.40
1976_1980	2016_2019		ΔPrecip	-0.03	0.08	-0.19	0.14
1976_1980	2016_2019		ΔHOWR	-0.06	0.18	-0.41	0.30
1981_1985	1986_1990	771	Intercept	0.32	0.09	0.13	0.50
1981_1985	1986_1990		ΔPrecip	-0.07	0.05	-0.17	0.02
1981_1985	1986_1990		ΔHOWR	0.03	0.11	-0.18	0.24
1981_1985	1986_1990		ΔVPD	-0.10	0.06	-0.22	0.03
1981_1985	1986_1990		Long	0.28	0.11	0.06	0.50
1981_1985	1986_1990		ΔTemp	-0.14	0.10	-0.33	0.06
1981_1985	1986_1990		ΔHOWR × Long	-0.09	0.09	-0.27	0.08
1981_1985	1991_1995	840	Intercept	0.34	0.13	0.09	0.59
1981_1985	1991_1995		ΔVPD	-0.21	0.08	-0.37	-0.04
1981_1985	1991_1995		Long	0.38	0.12	0.15	0.61
1981_1985	1991_1995		ΔPrecip	-0.10	0.07	-0.24	0.05
1981_1985	1991_1995		ΔHOWR	-0.01	0.19	-0.39	0.36
1981_1985	1991_1995		ΔTemp	-0.08	0.09	-0.26	0.09
1981_1985	1991_1995		ΔHOWR × Long	-0.19	0.17	-0.52	0.14
1981_1985	1996_2000	785	Intercept	0.54	0.12	0.31	0.77
1981_1985	1996_2000		ΔHOWR	-0.33	0.25	-0.83	0.16

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1981_1985	1996_2000	785	Long	0.32	0.10	0.12	0.53
1981_1985	1996_2000		ΔHOWR × Long	-0.47	0.17	-0.80	-0.13
1981_1985	1996_2000		ΔPrecip	-0.05	0.08	-0.21	0.10
1981_1985	1996_2000		ΔVPD	0.07	0.10	-0.13	0.26
1981_1985	2001_2005	776	Intercept	0.22	0.11	0.00	0.44
1981_1985	2001_2005		Long	0.14	0.10	-0.06	0.34
1981_1985	2001_2005		ΔPrecip	0.09	0.07	-0.06	0.24
1981_1985	2001_2005		ΔVPD	-0.07	0.09	-0.24	0.10
1981_1985	2001_2005		ΔHOWR	0.10	0.16	-0.21	0.40
1981_1985	2001_2005		ΔTemp	-0.03	0.07	-0.16	0.10
1981_1985	2006_2010	739	Intercept	0.26	0.12	0.02	0.50
1981_1985	2006_2010		ΔPrecip	0.19	0.09	0.00	0.37
1981_1985	2006_2010		ΔVPD	-0.18	0.12	-0.41	0.05
1981_1985	2006_2010		ΔTemp	-0.10	0.08	-0.26	0.07
1981_1985	2006_2010		Long	-0.13	0.19	-0.51	0.25
1981_1985	2011_2015	718	Intercept	0.00	0.10	-0.19	0.19
1981_1985	2011_2015		ΔPrecip	0.13	0.07	-0.01	0.27
1981_1985	2011_2015		ΔHOWR	0.29	0.17	-0.04	0.62
1981_1985	2011_2015		ΔTemp	-0.10	0.07	-0.23	0.04
1981_1985	2011_2015		ΔVPD	-0.06	0.10	-0.27	0.14
1981_1985	2011_2015		Long	-0.08	0.15	-0.38	0.22
1981_1985	2016_2019	711	Intercept	0.32	0.11	0.12	0.53
1981_1985	2016_2019		ΔPrecip	0.13	0.09	-0.04	0.29
1981_1985	2016_2019		ΔTemp	-0.27	0.10	-0.46	-0.07

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1981_1985	2016_2019	711	ΔVPD	0.14	0.11	-0.07	0.35
1981_1985	2016_2019		Long	0.10	0.12	-0.14	0.34
1981_1985	2016_2019		ΔHOWR	-0.08	0.18	-0.43	0.27
1986_1990	1991_1995	973	Intercept	0.27	0.10	0.08	0.46
1986_1990	1991_1995		ΔPrecip	-0.15	0.06	-0.26	-0.04
1986_1990	1991_1995		ΔHOWR	-0.29	0.12	-0.51	-0.06
1986_1990	1991_1995		ΔVPD	-0.11	0.07	-0.26	0.04
1986_1990	1991_1995		Long	0.31	0.09	0.12	0.49
1986_1990	1991_1995		ΔTemp	0.03	0.07	-0.11	0.18
1986_1990	1991_1995		ΔHOWR × Long	0.05	0.12	-0.19	0.30
1986_1990	1996_2000	932	Intercept	0.30	0.10	0.10	0.51
1986_1990	1996_2000		ΔHOWR	0.22	0.20	-0.17	0.61
1986_1990	1996_2000		ΔVPD	0.15	0.11	-0.06	0.37
1986_1990	1996_2000		Long	0.22	0.10	0.02	0.42
1986_1990	1996_2000		ΔHOWR × Long	-0.37	0.13	-0.63	-0.11
1986_1990	1996_2000		ΔTemp	0.12	0.09	-0.06	0.31
1986_1990	1996_2000		ΔPrecip	-0.02	0.06	-0.14	0.10
1986_1990	2001_2005	938	Intercept	0.00	0.11	-0.21	0.21
1986_1990	2001_2005		ΔPrecip	0.15	0.06	0.03	0.26
1986_1990	2001_2005		ΔHOWR	0.51	0.24	0.05	0.97
1986_1990	2001_2005		Long	0.08	0.10	-0.12	0.28
1986_1990	2001_2005		ΔHOWR × Long	-0.29	0.14	-0.57	-0.01
1986_1990	2001_2005		ΔVPD	-0.05	0.10	-0.26	0.15
1986_1990	2001_2005		ΔTemp	-0.03	0.08	-0.19	0.13

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1986_1990	2006_2010	889	Intercept	0.15	0.09	-0.03	0.33
1986_1990	2006_2010		ΔHOWR	0.60	0.17	0.26	0.93
1986_1990	2006_2010		ΔVPD	-0.18	0.10	-0.38	0.01
1986_1990	2006_2010		ΔTemp	-0.04	0.09	-0.23	0.14
1986_1990	2006_2010		ΔPrecip	0.01	0.08	-0.14	0.16
1986_1990	2011_2015	882	Intercept	-0.32	0.12	-0.56	-0.09
1986_1990	2011_2015		ΔHOWR	0.35	0.20	-0.03	0.73
1986_1990	2011_2015		Long	-0.23	0.12	-0.47	0.02
1986_1990	2011_2015		ΔHOWR × Long	-0.48	0.14	-0.75	-0.20
1986_1990	2011_2015		ΔTemp	-0.08	0.07	-0.23	0.06
1986_1990	2011_2015		ΔPrecip	0.10	0.09	-0.08	0.29
1986_1990	2011_2015		ΔVPD	-0.10	0.10	-0.28	0.09
1986_1990	2016_2019	874	Intercept	0.32	0.13	0.07	0.58
1986_1990	2016_2019		ΔPrecip	0.18	0.11	-0.03	0.39
1986_1990	2016_2019		ΔHOWR	0.52	0.15	0.24	0.81
1986_1990	2016_2019		ΔTemp	-0.23	0.12	-0.46	0.01
1986_1990	2016_2019		ΔVPD	0.29	0.14	0.02	0.57
1986_1990	2016_2019		Long	0.03	0.15	-0.26	0.32
1991_1995	1996_2000	1443	Intercept	0.27	0.08	0.13	0.42
1991_1995	1996_2000		ΔPrecip	0.10	0.04	0.02	0.18
1991_1995	1996_2000		ΔHOWR	0.04	0.16	-0.28	0.37
1991_1995	1996_2000		ΔTemp	0.13	0.06	0.01	0.24
1991_1995	1996_2000		ΔVPD	-0.07	0.06	-0.18	0.05
1991_1995	1996_2000		Long	0.05	0.10	-0.14	0.24

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1991_1995	1996_2000	1443	ΔHOWR × Long	-0.19	0.12	-0.41	0.04
1991_1995	2001_2005	1423	Intercept	0.03	0.07	-0.10	0.16
1991_1995	2001_2005		ΔPrecip	0.15	0.04	0.07	0.23
1991_1995	2001_2005		ΔHOWR	0.11	0.06	-0.02	0.23
1991_1995	2001_2005		ΔTemp	0.05	0.06	-0.06	0.16
1991_1995	2001_2005		Long	-0.06	0.09	-0.24	0.11
1991_1995	2001_2005		ΔVPD	0.03	0.08	-0.12	0.19
1991_1995	2006_2010	1395	Intercept	0.01	0.09	-0.16	0.19
1991_1995	2006_2010		ΔVPD	0.11	0.09	-0.06	0.29
1991_1995	2006_2010		Long	-0.10	0.11	-0.31	0.11
1991_1995	2006_2010		ΔTemp	-0.06	0.06	-0.18	0.07
1991_1995	2006_2010		ΔPrecip	-0.03	0.06	-0.14	0.09
1991_1995	2006_2010		ΔHOWR	0.03	0.07	-0.11	0.18
1991_1995	2011_2015	1334	Intercept	-0.59	0.09	-0.78	-0.41
1991_1995	2011_2015		ΔHOWR	0.16	0.10	-0.03	0.35
1991_1995	2011_2015		Long	-0.45	0.09	-0.62	-0.28
1991_1995	2011_2015		ΔVPD	0.05	0.07	-0.10	0.19
1991_1995	2011_2015		ΔTemp	0.02	0.05	-0.09	0.13
1991_1995	2011_2015		ΔPrecip	-0.02	0.06	-0.13	0.09
1991_1995	2011_2015		ΔHOWR × Long	-0.02	0.15	-0.31	0.26
1991_1995	2016_2019	1290	Intercept	-0.01	0.13	-0.26	0.24
1991_1995	2016_2019		ΔVPD	0.21	0.10	0.02	0.40
1991_1995	2016_2019		Long	-0.17	0.11	-0.38	0.04
1991_1995	2016_2019		ΔHOWR	0.12	0.13	-0.13	0.38

Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1991_1995	2016_2019	1290	ΔTemp	0.07	0.08	-0.10	0.23
1991_1995	2016_2019		ΔPrecip	0.03	0.07	-0.11	0.17
1991_1995	2016_2019		ΔHOWR × Long	0.04	0.21	-0.38	0.45
1996_2000	2001_2005	1475	Intercept	-0.33	0.07	-0.48	-0.18
1996_2000	2001_2005		ΔHOWR	0.06	0.17	-0.27	0.39
1996_2000	2001_2005		Long	-0.10	0.07	-0.23	0.04
1996_2000	2001_2005		ΔHOWR × Long	-0.18	0.11	-0.40	0.03
1996_2000	2001_2005		ΔPrecip	-0.03	0.04	-0.11	0.05
1996_2000	2001_2005		ΔVPD	0.05	0.06	-0.07	0.18
1996_2000	2001_2005		ΔTemp	0.01	0.04	-0.08	0.09
1996_2000	2006_2010	1427	Intercept	-0.14	0.13	-0.39	0.12
1996_2000	2006_2010		ΔPrecip	-0.14	0.07	-0.27	-0.01
1996_2000	2006_2010		ΔTemp	-0.11	0.06	-0.22	0.00
1996_2000	2006_2010		Long	0.23	0.14	-0.04	0.51
1996_2000	2006_2010		ΔVPD	0.08	0.09	-0.09	0.25
1996_2000	2011_2015	1358	Intercept	-0.71	0.09	-0.89	-0.53
1996_2000	2011_2015		ΔHOWR	-0.17	0.22	-0.61	0.26
1996_2000	2011_2015		ΔTemp	-0.15	0.05	-0.25	-0.05
1996_2000	2011_2015		ΔVPD	0.16	0.08	0.01	0.31
1996_2000	2011_2015		Long	-0.24	0.09	-0.41	-0.07
1996_2000	2011_2015		ΔHOWR × Long	-0.35	0.15	-0.64	-0.06
1996_2000	2016_2019	1307	Intercept	-0.14	0.10	-0.33	0.06
1996_2000	2016_2019		ΔTemp	-0.15	0.08	-0.31	0.00
1996_2000	2016_2019		ΔVPD	0.14	0.09	-0.04	0.32

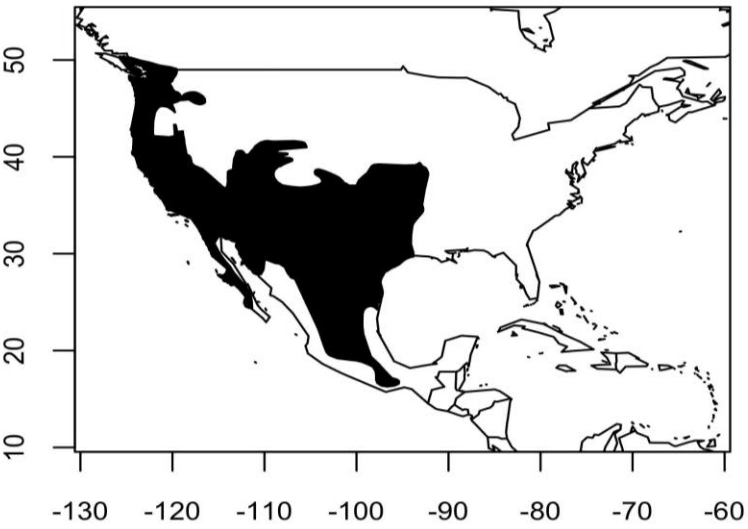
Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
1996_2000	2016_2019	1307	ΔHOWR	0.15	0.11	-0.07	0.38
1996_2000	2016_2019		Long	-0.12	0.11	-0.33	0.10
1996_2000	2016_2019		ΔPrecip	-0.06	0.07	-0.19	0.08
2001_2005	2006_2010	1425	Intercept	0.28	0.10	0.09	0.48
2001_2005	2006_2010		ΔPrecip	-0.21	0.06	-0.32	-0.10
2001_2005	2006_2010		ΔTemp	-0.09	0.05	-0.19	0.00
2001_2005	2006_2010		Long	0.45	0.13	0.19	0.70
2001_2005	2006_2010		ΔVPD	0.07	0.06	-0.04	0.18
2001_2005	2006_2010		ΔHOWR	0.03	0.07	-0.11	0.18
2001_2005	2011_2015	1326	Intercept	-0.34	0.10	-0.54	-0.14
2001_2005	2011_2015		ΔHOWR	0.19	0.09	0.01	0.36
2001_2005	2011_2015		ΔVPD	-0.20	0.07	-0.33	-0.07
2001_2005	2011_2015		Long	-0.15	0.10	-0.34	0.03
2001_2005	2011_2015		ΔPrecip	0.05	0.05	-0.06	0.16
2001_2005	2011_2015		ΔTemp	0.03	0.05	-0.08	0.13
2001_2005	2016_2019	1305	Intercept	-0.02	0.09	-0.19	0.15
2001_2005	2016_2019		ΔPrecip	-0.13	0.06	-0.26	-0.01
2001_2005	2016_2019		ΔHOWR	0.13	0.10	-0.06	0.31
2001_2005	2016_2019		ΔTemp	-0.08	0.07	-0.23	0.06
2001_2005	2016_2019		ΔVPD	-0.06	0.06	-0.19	0.06
2001_2005	2016_2019		Long	0.05	0.10	-0.15	0.24
2006_2010	2011_2015	1312	Intercept	-0.26	0.07	-0.39	-0.12
2006_2010	2011_2015		ΔTemp	0.13	0.09	-0.04	0.30
2006_2010	2011_2015		ΔVPD	-0.34	0.06	-0.46	-0.23

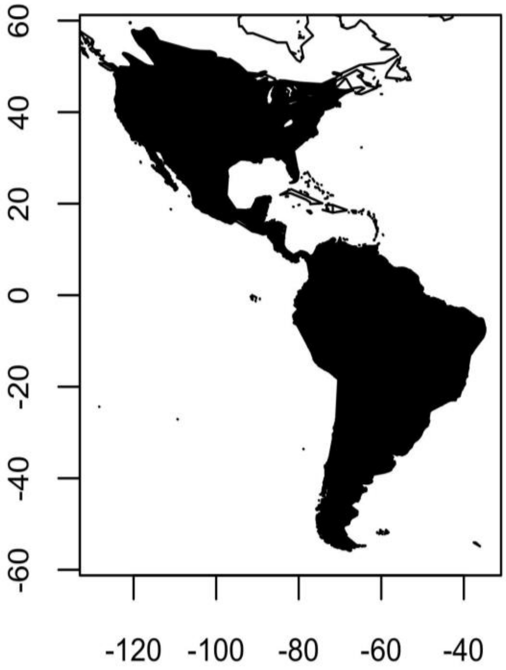
Table 3 continued

Starting Time	Ending Time	n	Parameter	Coef	SE	CI (low)	CI (high)
2006_2010	2011_2015	1312	ΔHOWR	0.09	0.10	-0.11	0.28
2006_2010	2011_2015		ΔPrecip	0.04	0.06	-0.08	0.15
2006_2010	2016_2019	1290	Intercept	-0.70	0.17	-1.04	-0.36
2006_2010	2016_2019		ΔPrecip	-0.50	0.08	-0.66	-0.34
2006_2010	2016_2019		Long	-0.50	0.14	-0.78	-0.21
2006_2010	2016_2019		ΔHOWR	0.06	0.13	-0.18	0.31
2006_2010	2016_2019		ΔVPD	-0.04	0.08	-0.20	0.12
2011_2015	2016_2019	1215	Intercept	0.54	0.11	0.34	0.75
2011_2015	2016_2019		ΔTemp	-0.15	0.08	-0.30	-0.01
2011_2015	2016_2019		ΔVPD	0.25	0.07	0.12	0.39
2011_2015	2016_2019		Long	0.30	0.12	0.07	0.53
2011_2015	2016_2019		ΔHOWR	0.06	0.07	-0.09	0.20

[1] Sample size (n) represents the number of 10-stop midpoints where Bewick's Wrens were present in at least one of the time periods (starting and/or ending) of the time comparison. Coef = Coefficient, SE = Standard Error (adjusted), CI = Confidence Interval; the lower and upper bounds of 95% confidence intervals are presented.



(a) Bewick's Wren



(b) House Wren

Figure 1. Range maps depicting the ranges of (a) Bewick's Wren and (b) House Wren. Shaded areas denote present ranges. As described in the Introduction, House Wrens are an extremely widespread group whose taxonomy is in flux; the House Wrens of the United States and Canada are the primary group of interest for this study. Data taken from IUCN Red List (Birdlife International and Handbook of the Birds of the World 2016; 2021).

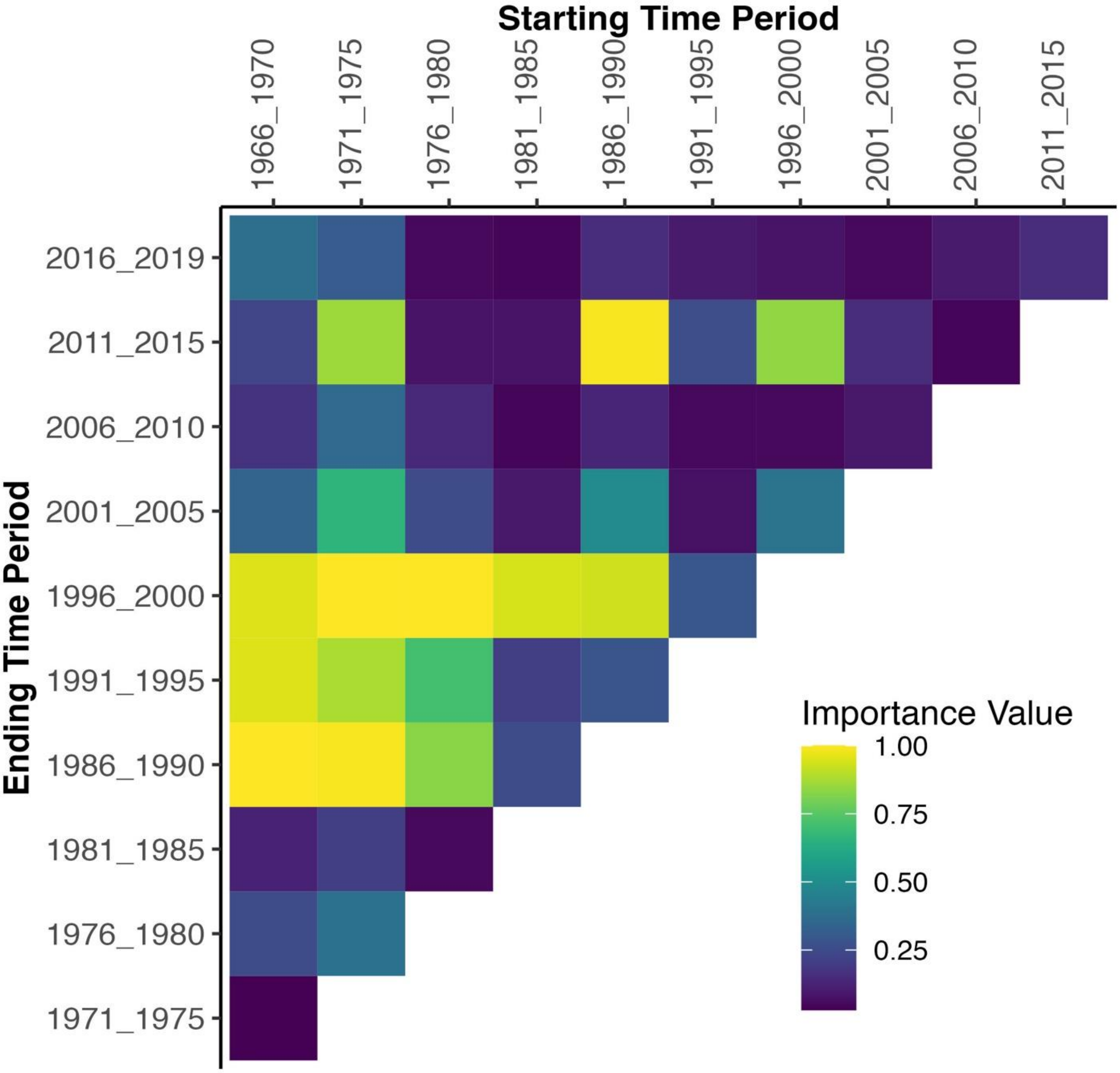


Figure 2. After constructing linear models to test whether changes in predictor variables over time explained changes in Bewick's Wren local abundance (ΔBEWR) over time (using every potential combination of predictor variables), I outputted an 'importance' value for each predictor variable - i.e., the sum of Akaike weights of all models containing a given variable. This matrix designates an 'importance' value of the interaction between changes in House Wren local abundance and longitude (***Δ***HOWR × Long) for every possible time comparison in our dataset. For example, in models assessing whether the changes in predictor variables over the period of 1986-2000 explained ΔBEWR over the same time period, the ***Δ***HOWR × Long interaction was a highly important variable to include in models. The other predictor variables included in analyses were ΔHOWR, Long, ΔVPD, ΔPrecip, and ΔTemp. Refer to Table 1 for abbreviations of predictor variables as described in Methods.

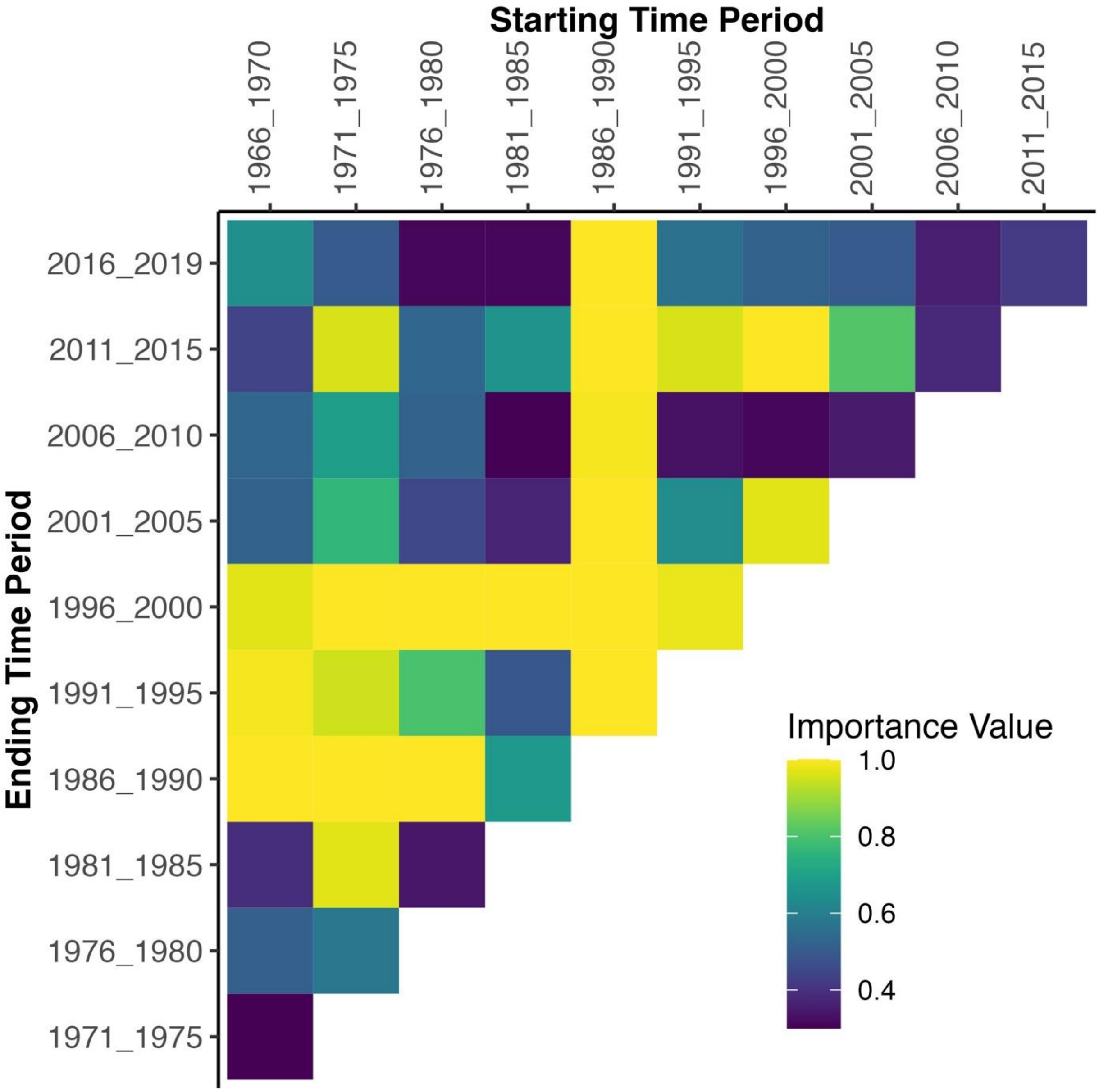


Figure 3. This matrix designates an 'importance' value of the variable denoting changes in House Wren local abundance over time (***Δ***HOWR) for every possible time comparison in our dataset. The response variable is ΔBEWR and the other predictor variables included in analyses were ΔHOWR × Long, Long, ΔVPD, ΔPrecip, and ΔTemp. For more detail on this process, refer to Figure 2.

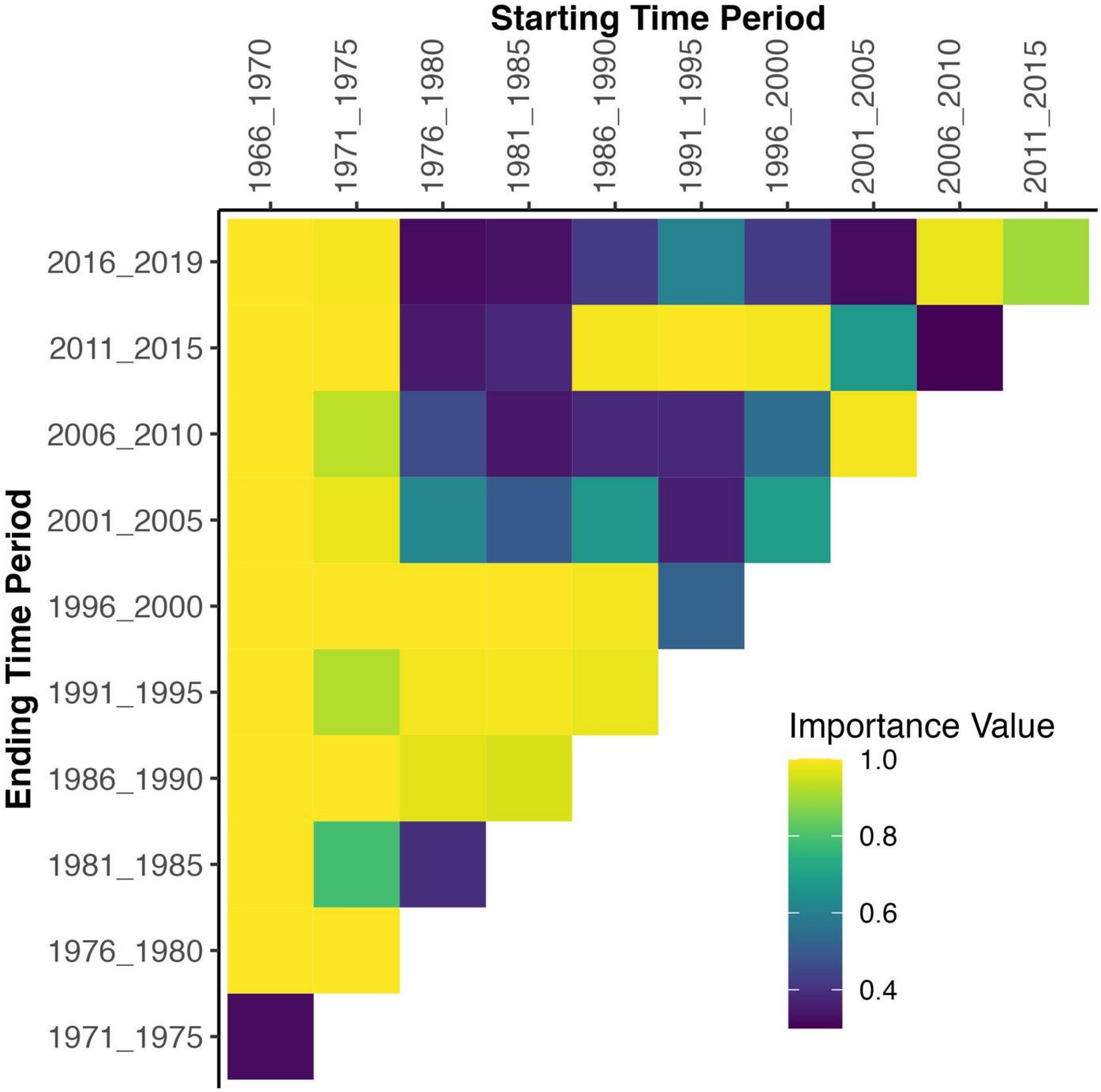


Figure 4. This matrix designates an ‘importance’ value of the longitude variable (Long) for every possible time comparison in our dataset. The response variable is ΔBEWR and the other predictor variables included in analyses were ΔHOWR × Long, ΔHOWR, ΔVPD, ΔPrecip, and ΔTemp. For more detail on this process, refer to Figure 2.

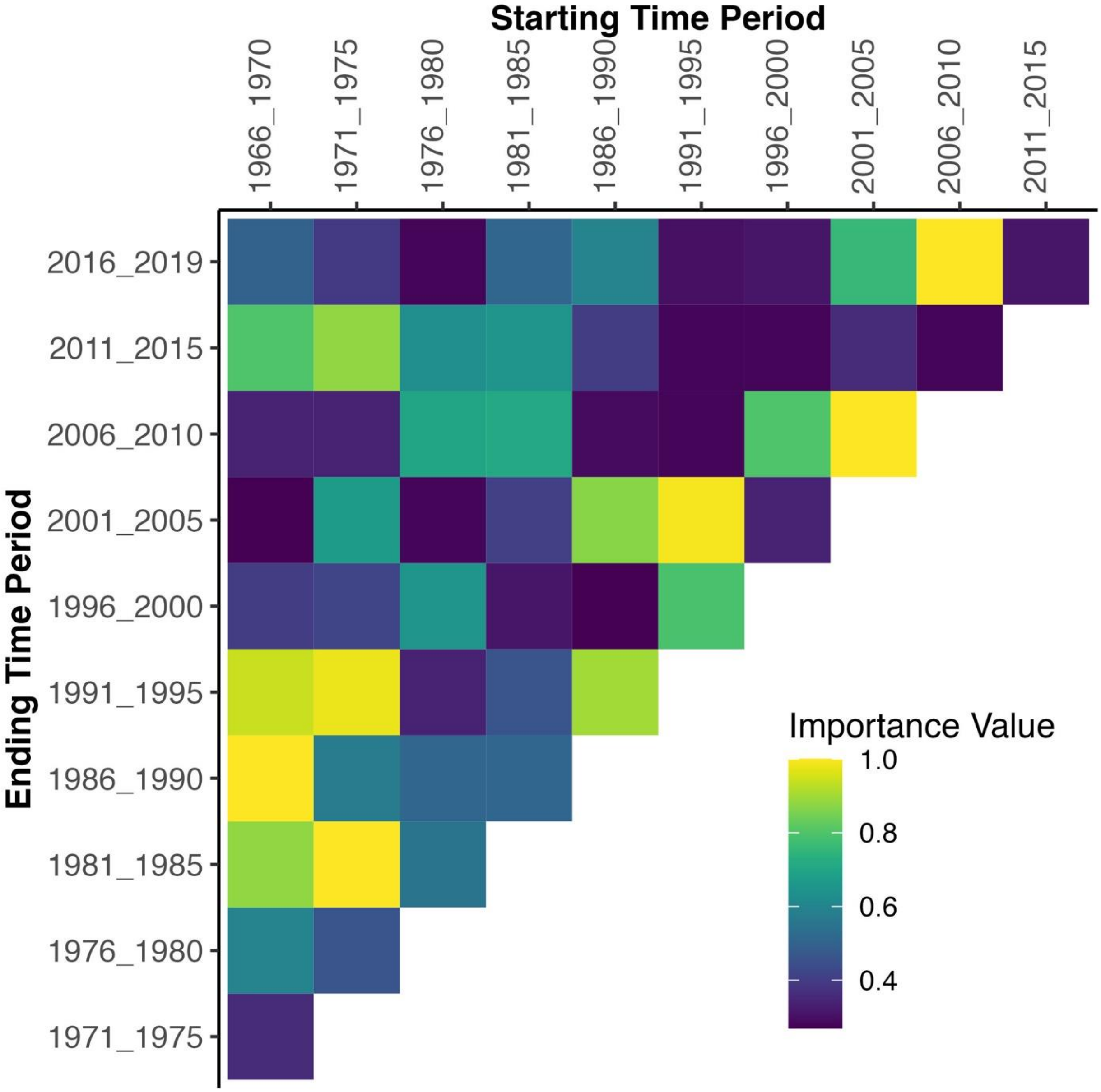


Figure 5. This matrix designates an 'importance' value of the variable denoting changes in Annual Precipitation over time (**Δ**Precip) for every possible time comparison in our dataset. The response variable is ΔBEWR and the other predictor variables included in analyses were ΔHOWR × Long, ΔHOWR, Long, ΔVPD, and ΔTemp. For more detail on this process, refer to Figure 2.

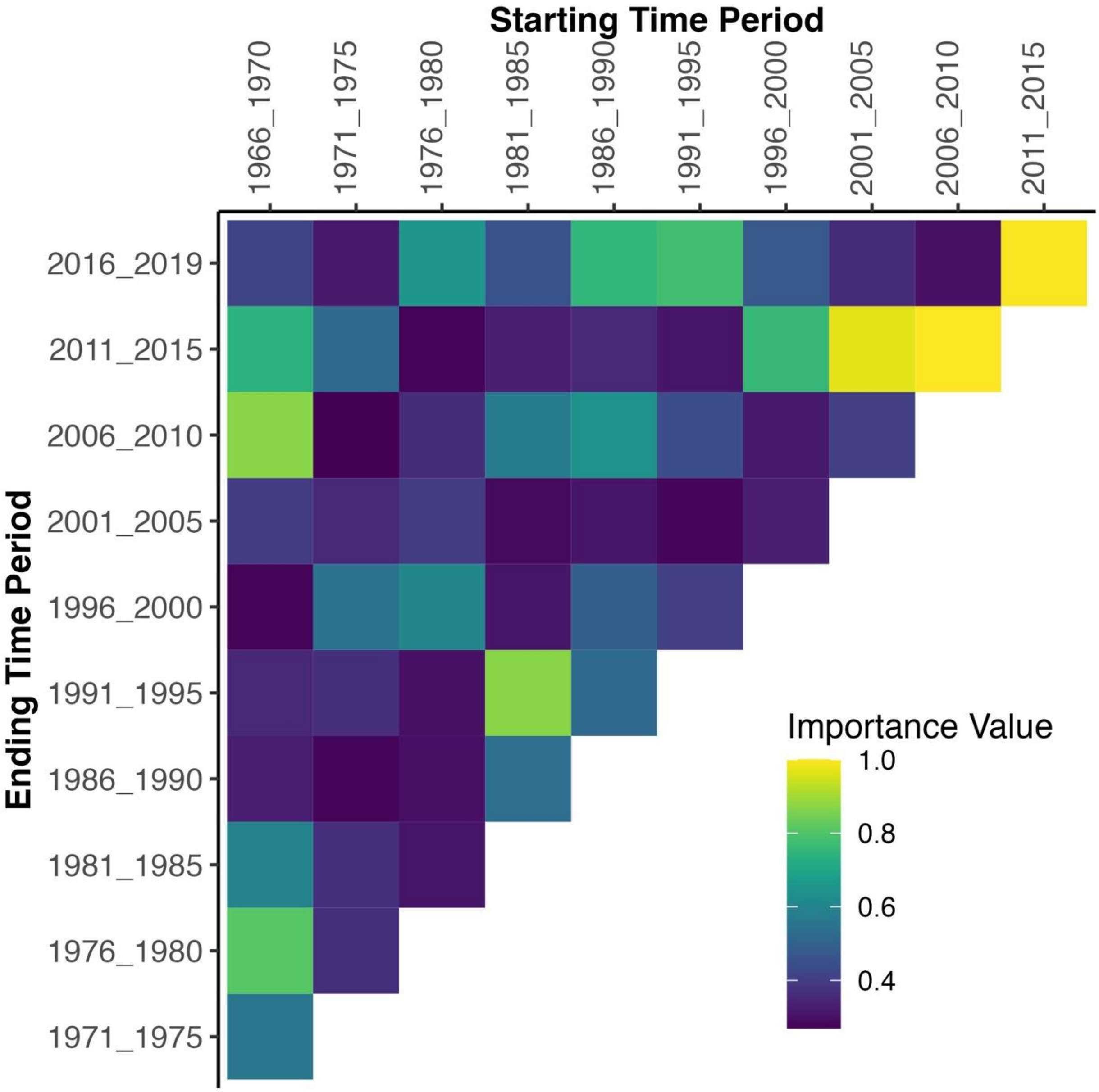


Figure 6. This matrix designates an 'importance' value of the variable denoting changes in Maximum Vapor Pressure Deficit over time (***Δ***VPD) for every possible time comparison in our dataset. The response variable is ΔBEWR and the other predictor variables included in analyses were ΔHOWR × Long, ΔHOWR, Long, ΔPrecip, and ΔTemp. For more detail on this process, refer to Figure 2.

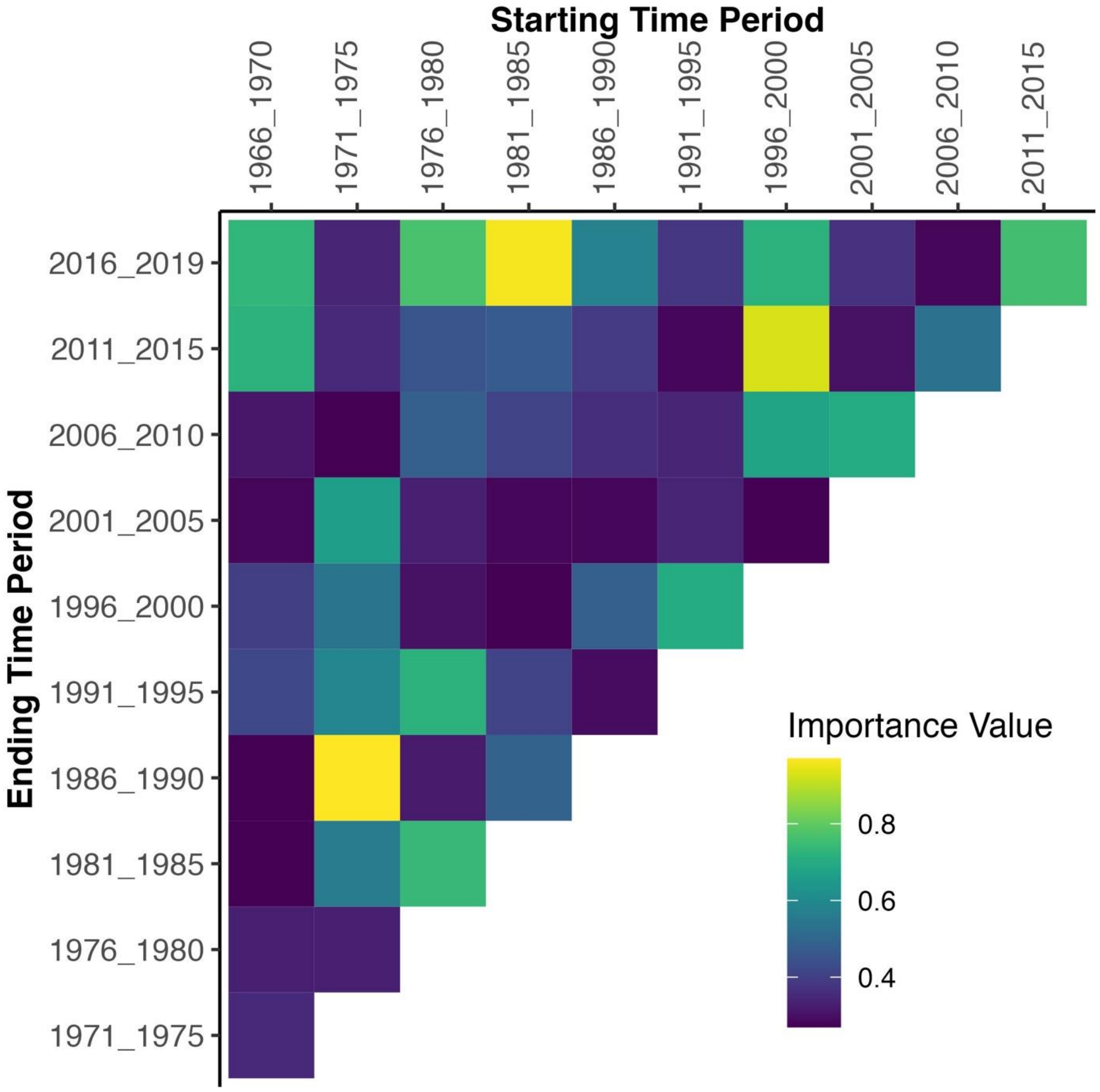


Figure 7. This matrix designates an 'importance' value of the variable denoting changes in Annual Mean Temperature over time (***Δ***Temp) for every possible time comparison in our dataset. The response variable is ΔBEWR and the other predictor variables included in analyses were ΔHOWR × Long, ΔHOWR, Long, ΔVPD, and ΔPrecip. For more detail on this process, refer to Figure 2.

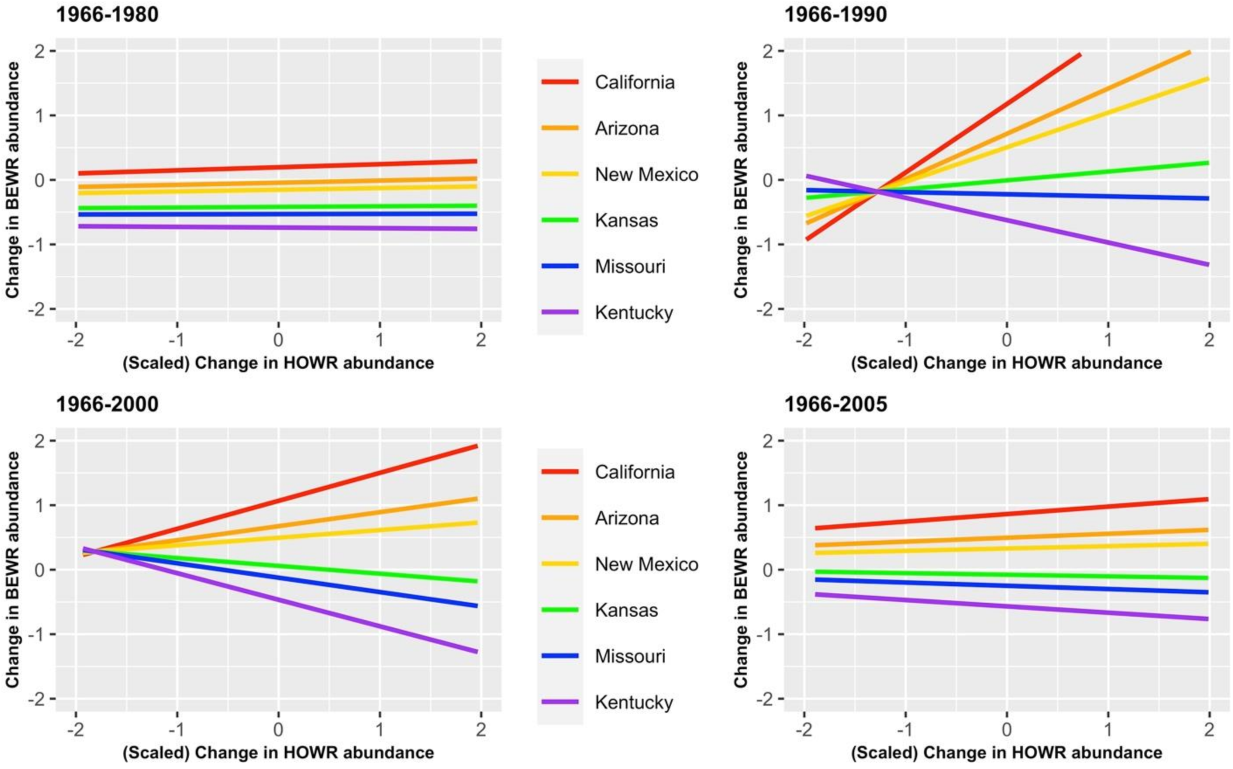
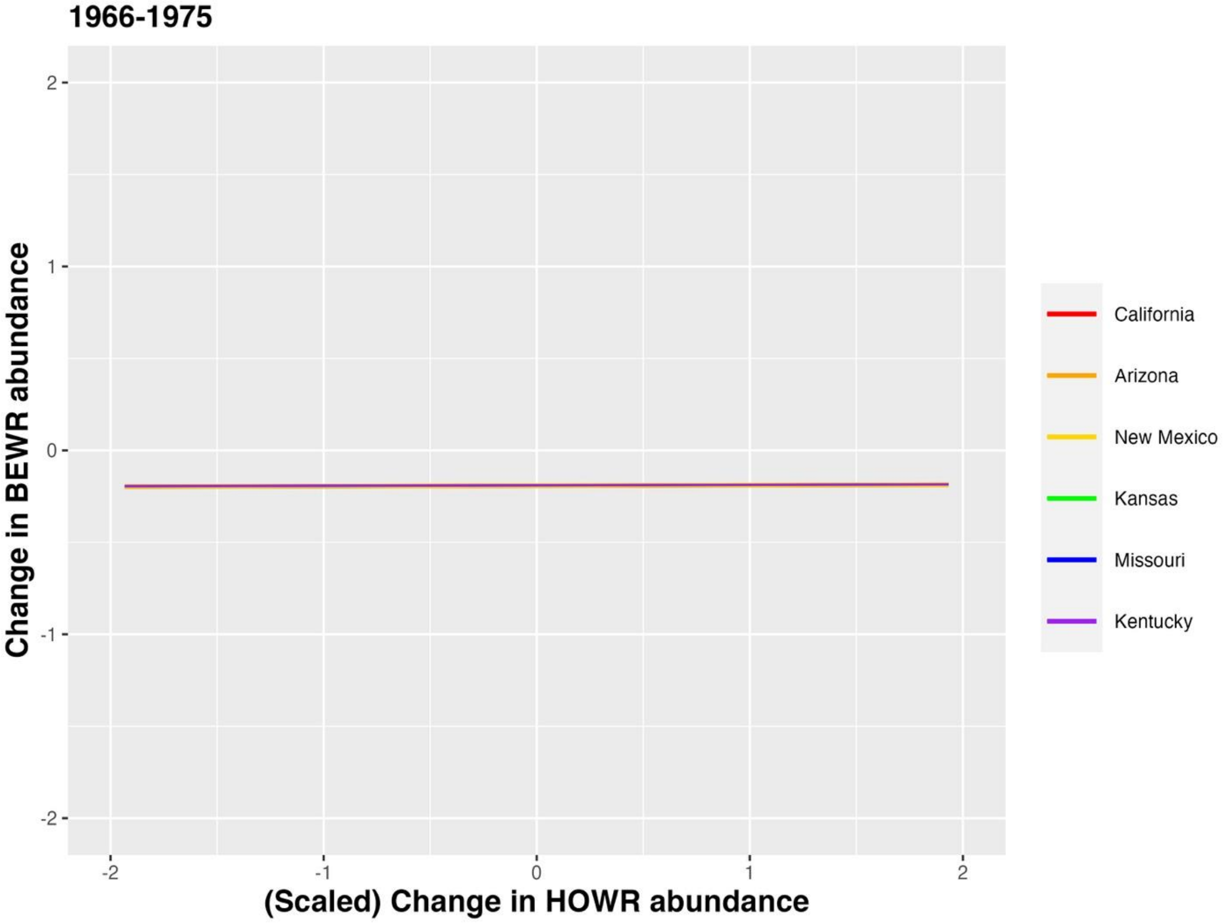
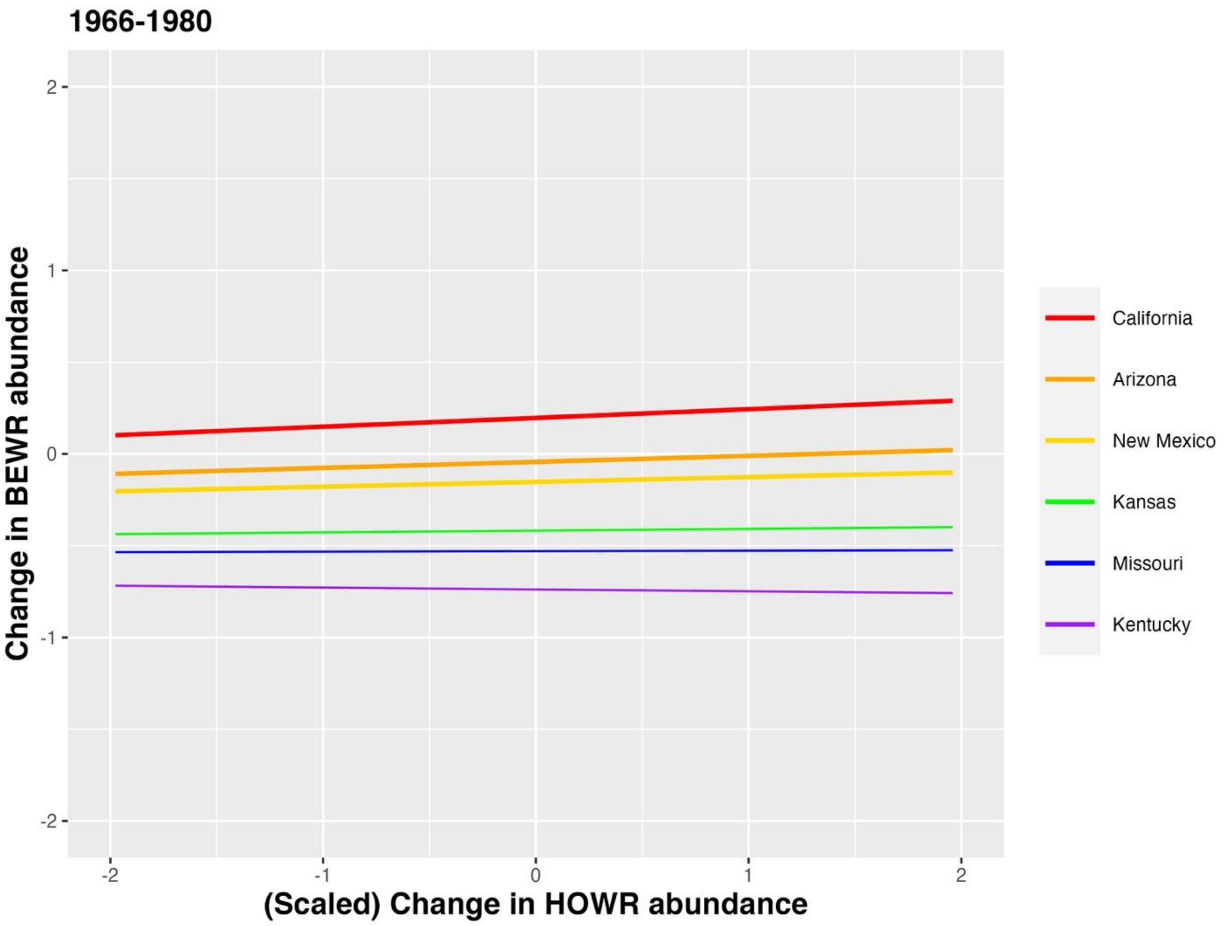


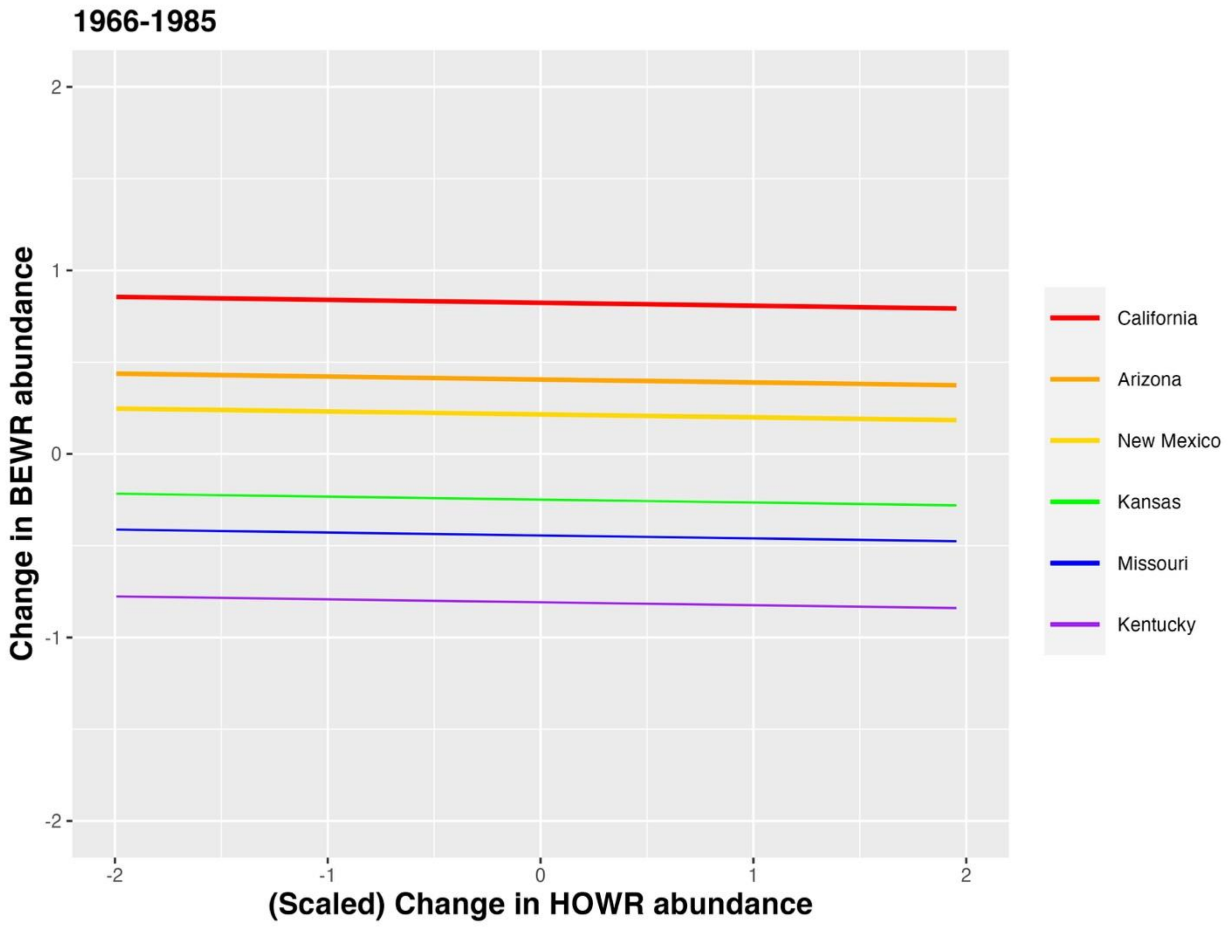
Figure 8. Predicted change in Bewick's Wren local abundance in response to changes in House Wren local abundance at various longitudes as described in Methods. ΔHOWR is scaled. Each line represents predictions made for that particular longitude (color-coded by state). Four different time-comparisons show variation in predictions.

APPENDIX

The graphs below show predicted changes in Bewick's Wren local abundance in response to changes in House Wren local abundance at various longitudes as described in Methods. ΔHOWR is scaled. Each line represents predictions made for that particular longitude (color-coded by state). All 55 time-comparisons included in the study are shown.




1966-1980
2
1
0
-1
-2
Change in BEWR abundance
-2
-1
0
1
2
(Scaled) Change in HOWR abundance
California
Arizona
New Mexico
Kansas
Missouri
Kentucky


1966-1985
Change in BEWR abundance
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1
0
-1
-2
(Scaled) Change in HOWR abundance
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-1
0
1
2
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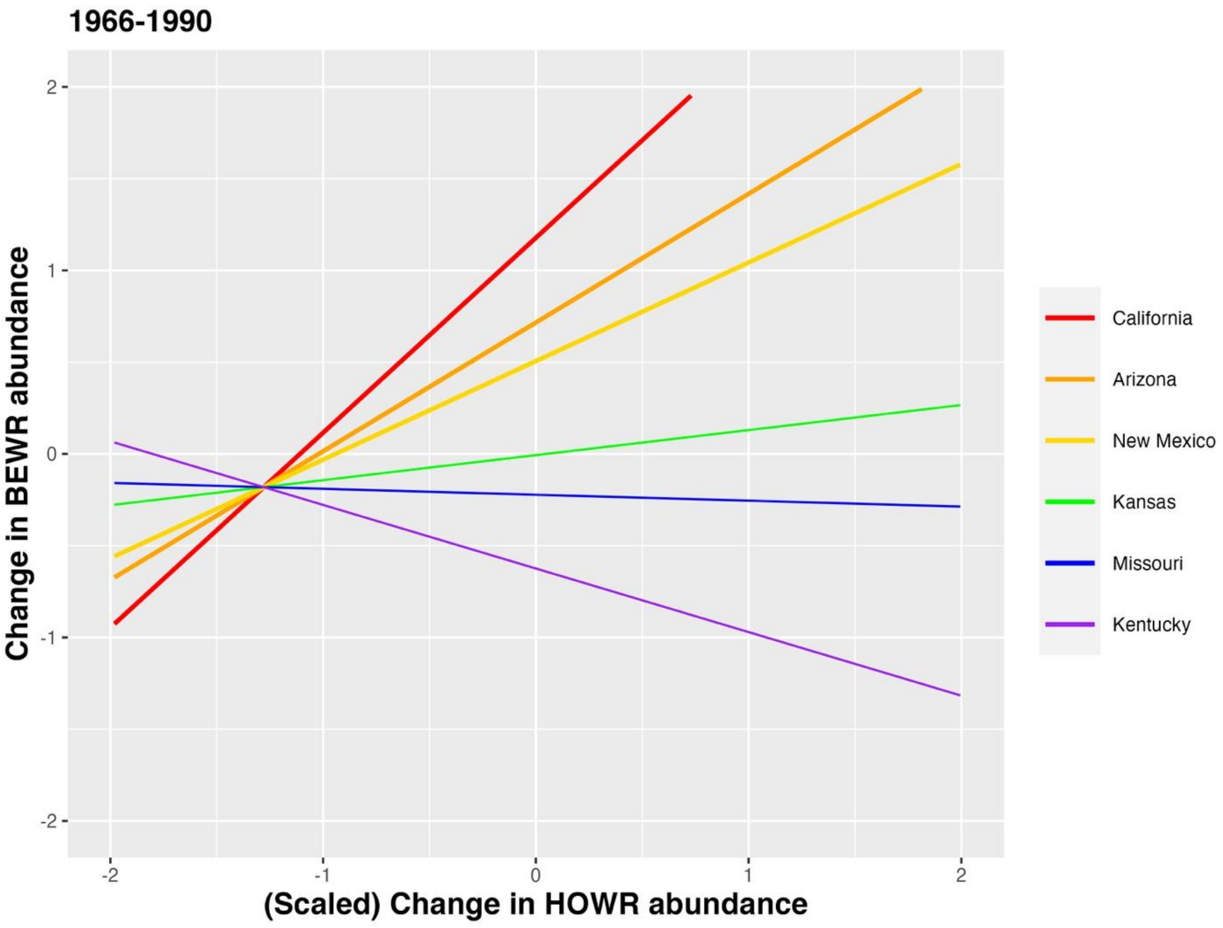
Kansas
Missouri
Kentucky


1966-1990
Change in BEWR abundance
(Scaled) Change in HOWR abundance
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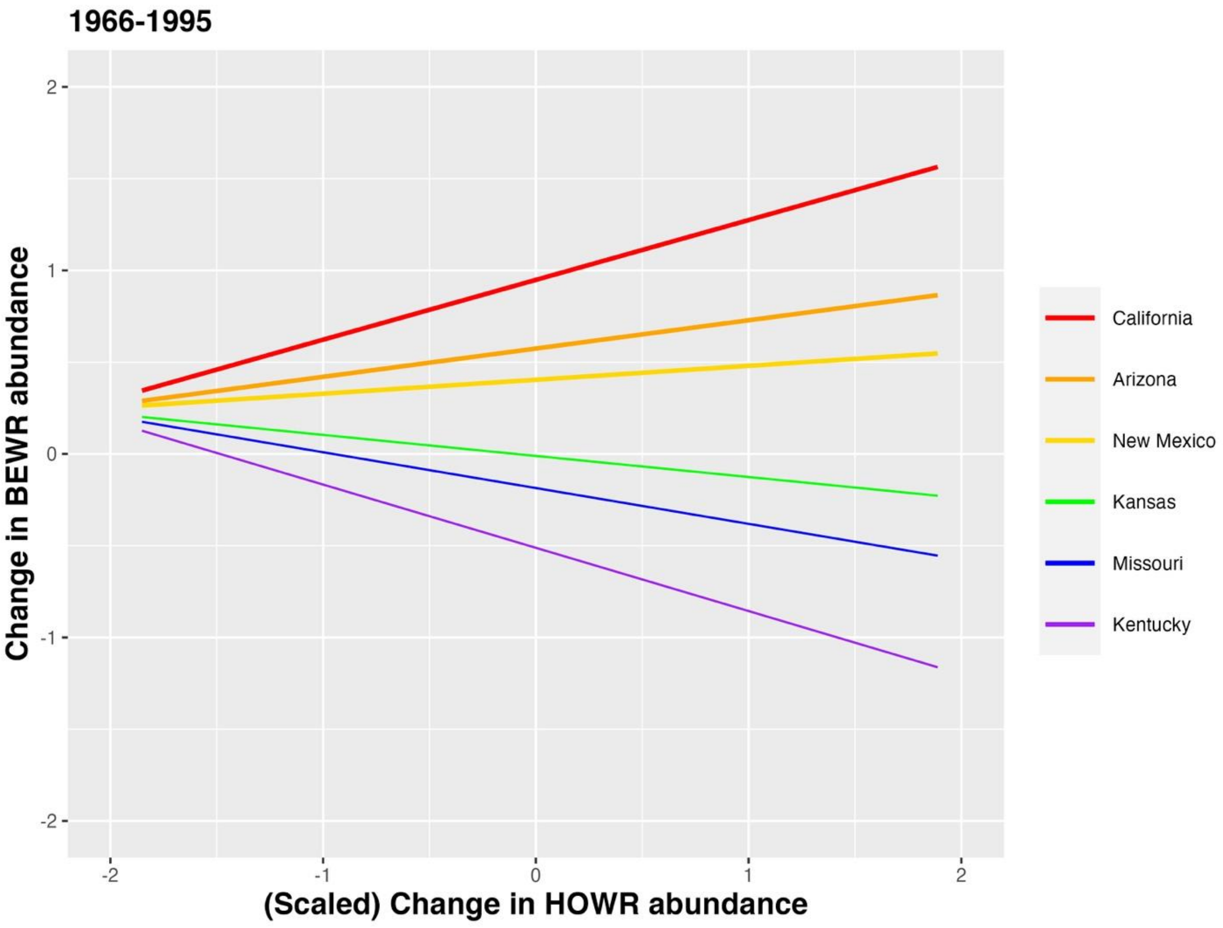
New Mexico
Kansas
Missouri
Kentucky


1966-1995
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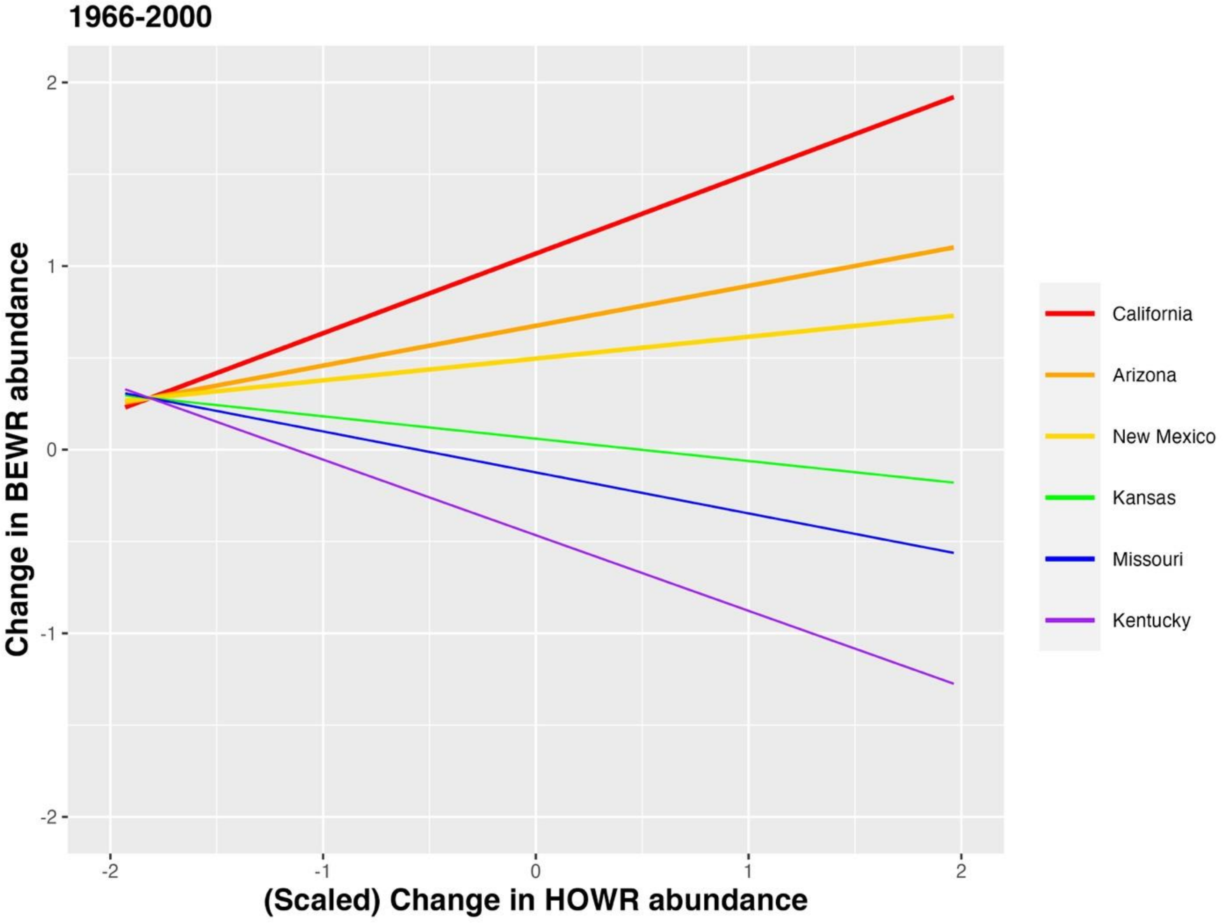
Kentucky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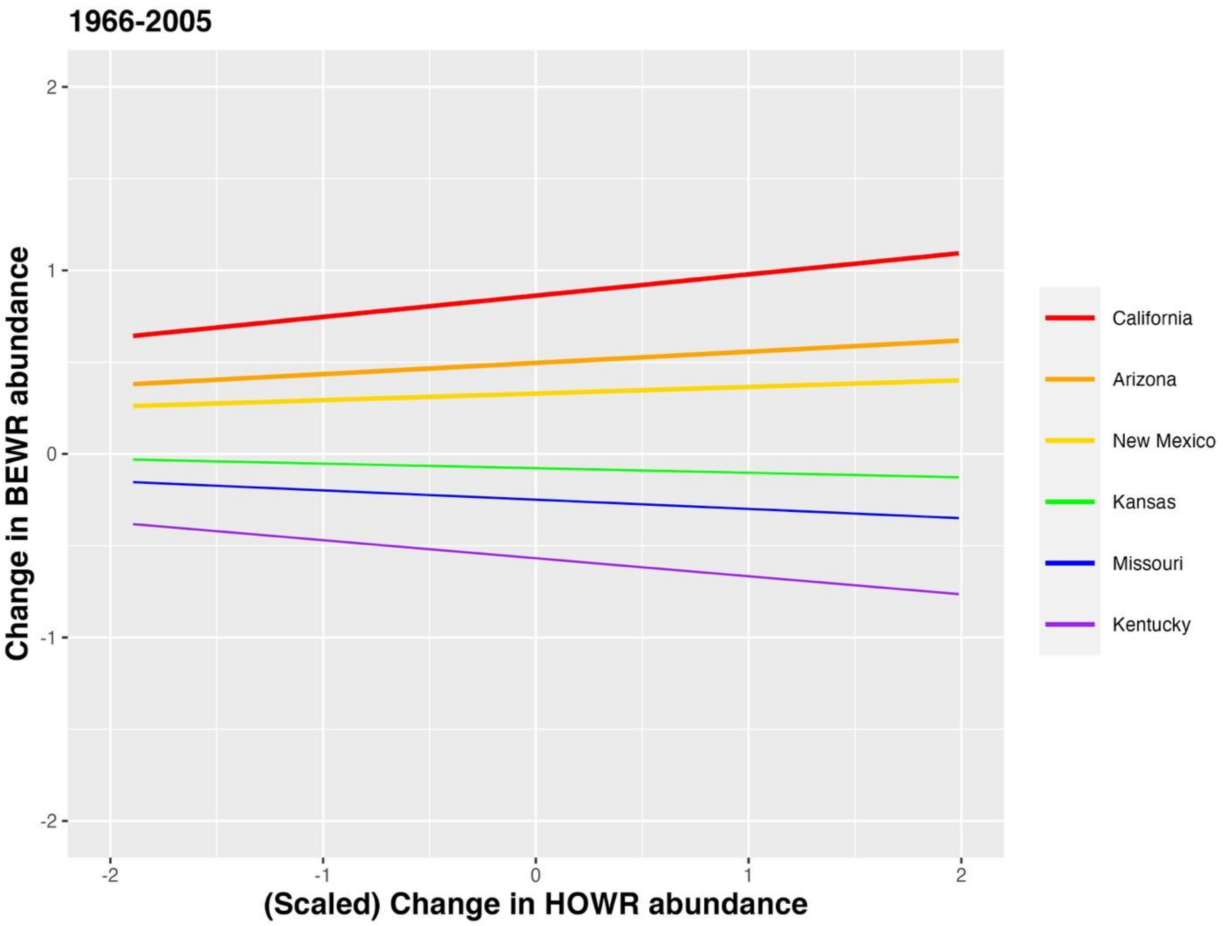
1966-2005
Change in BEWR abundance
2
1
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-1
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(Scaled) Change in HOWR abundance
-2
-1
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1
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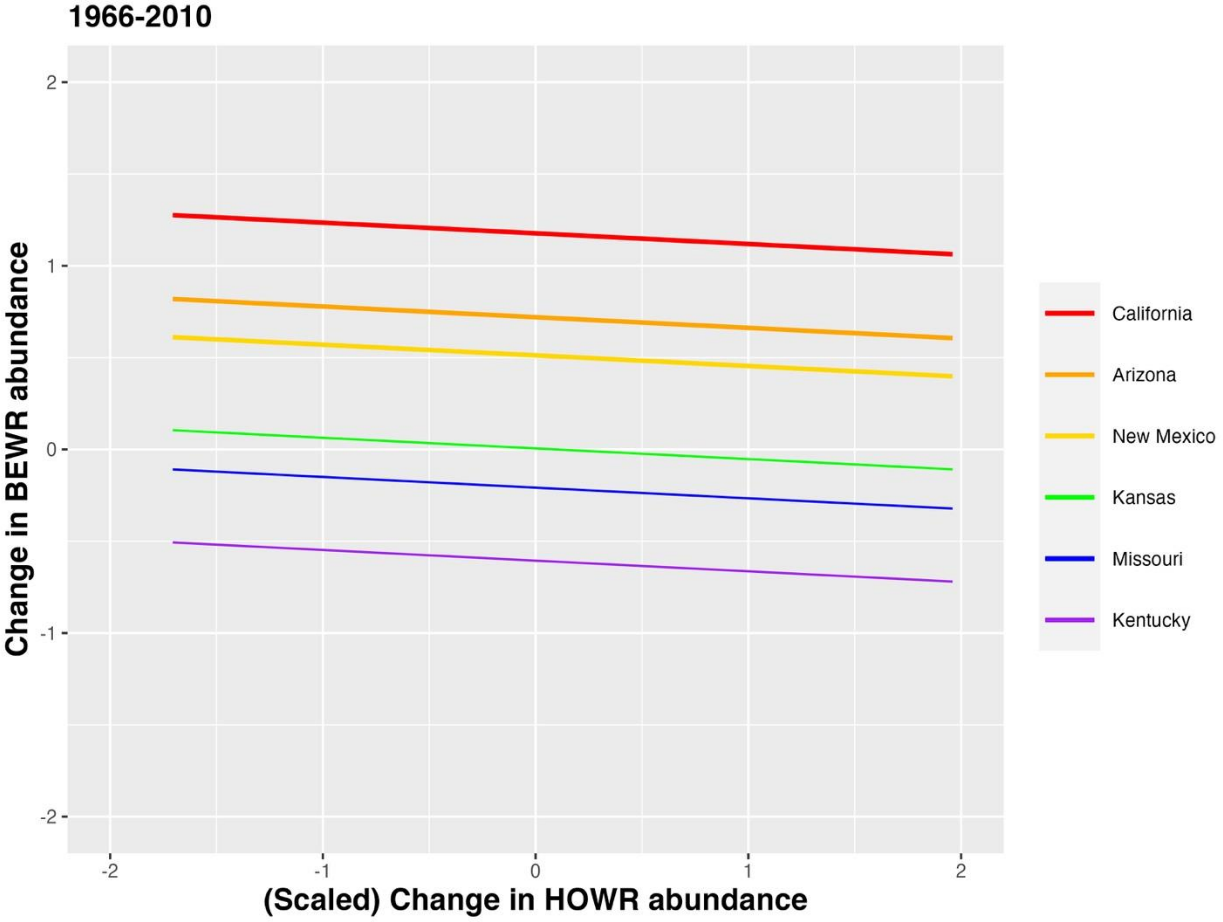
New Mexico
Kansas
Missouri
Kentucky


1966-2010
Change in BEWR abundance
(Scaled) Change in HOWR abundance
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New Mexico
Kansas
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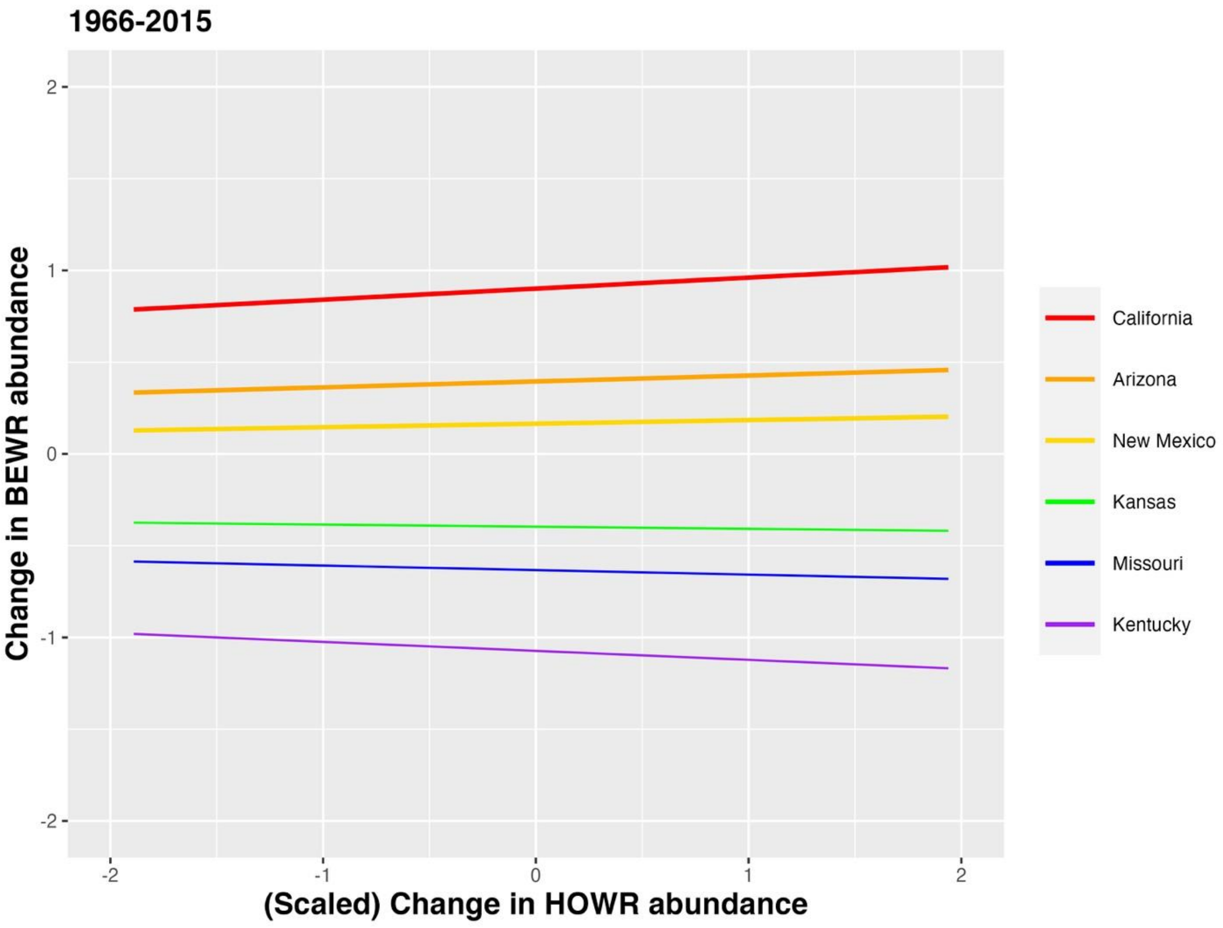
1966-2015
Change in BEWR abundance
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1
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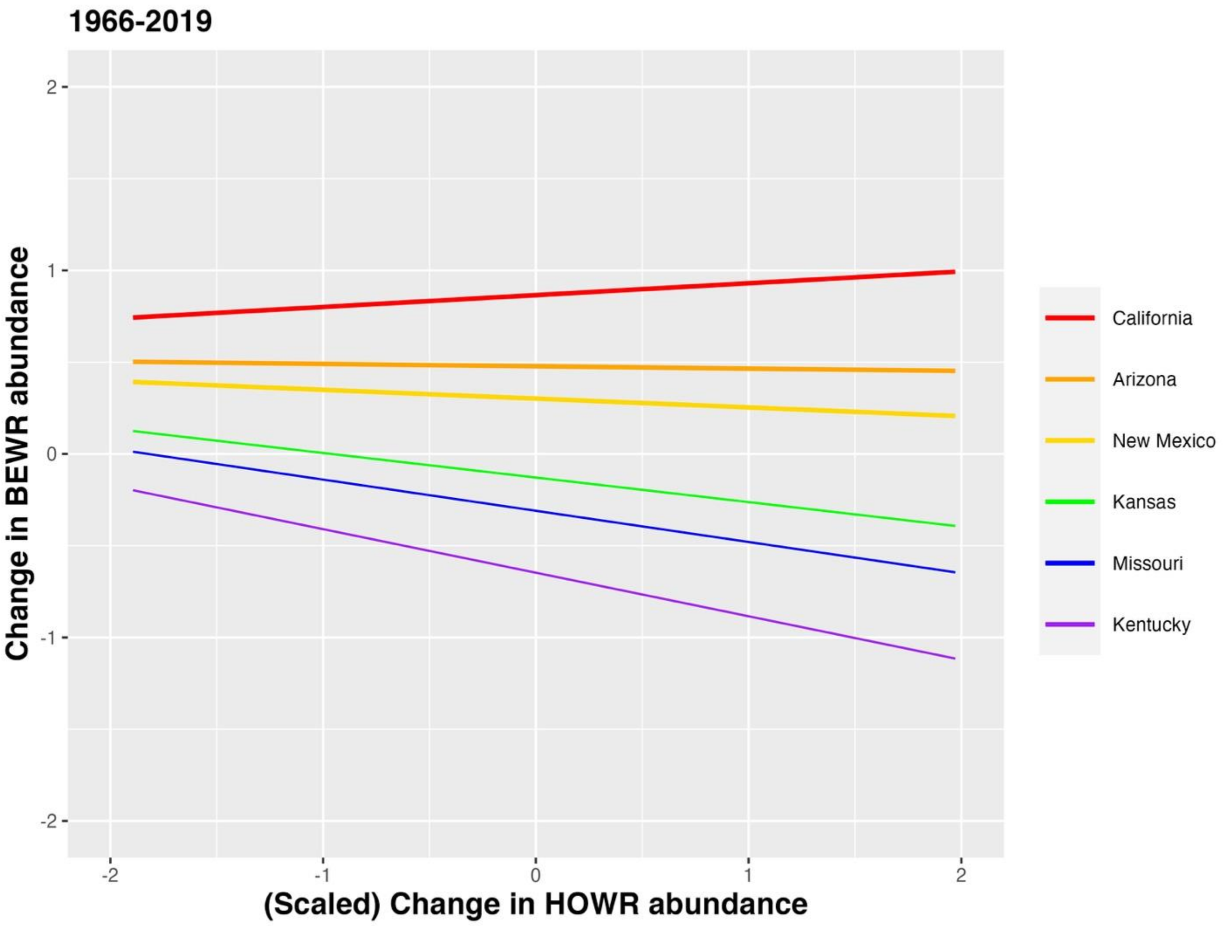
1966-2019
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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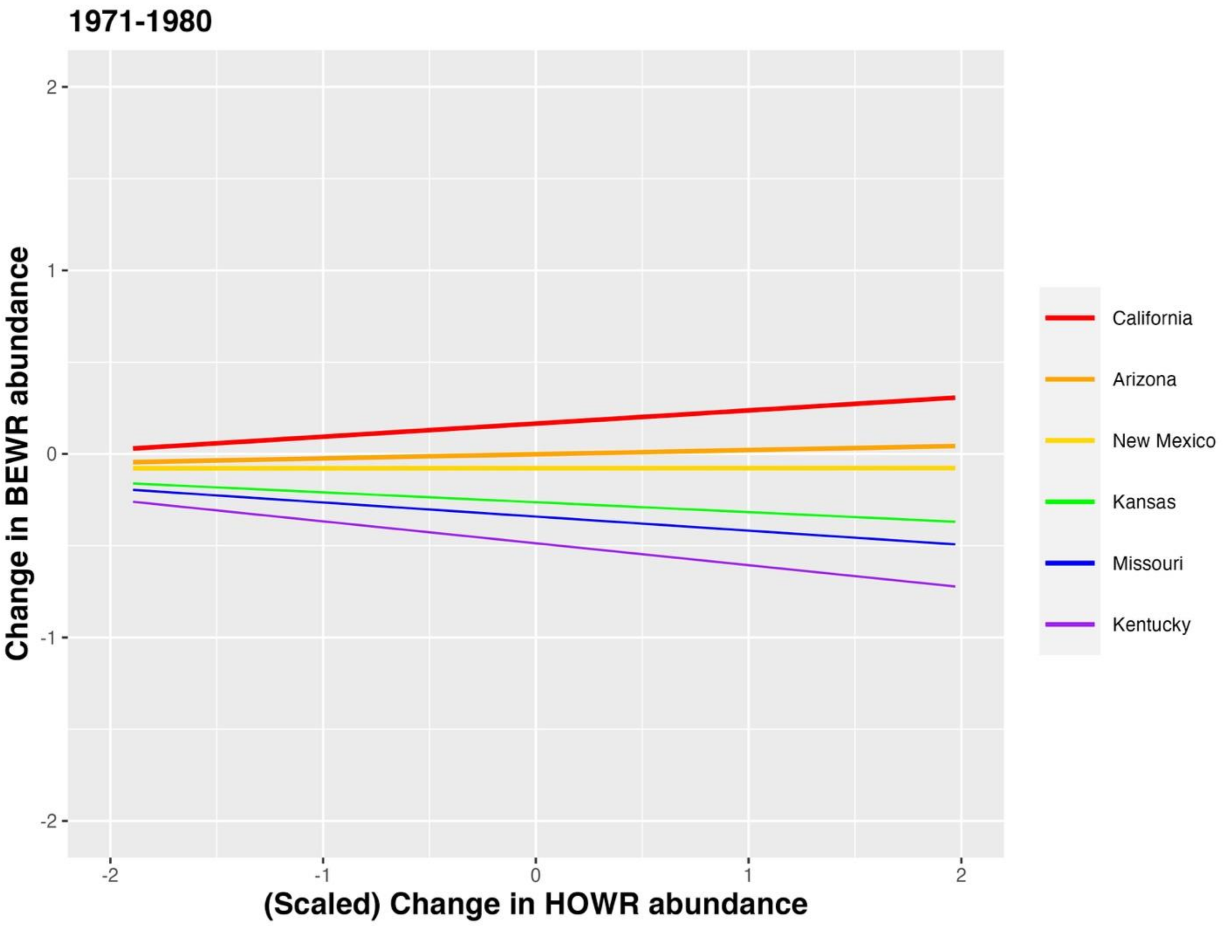
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Change in BEWR abundance
(Scaled) Change in HOWR abundance
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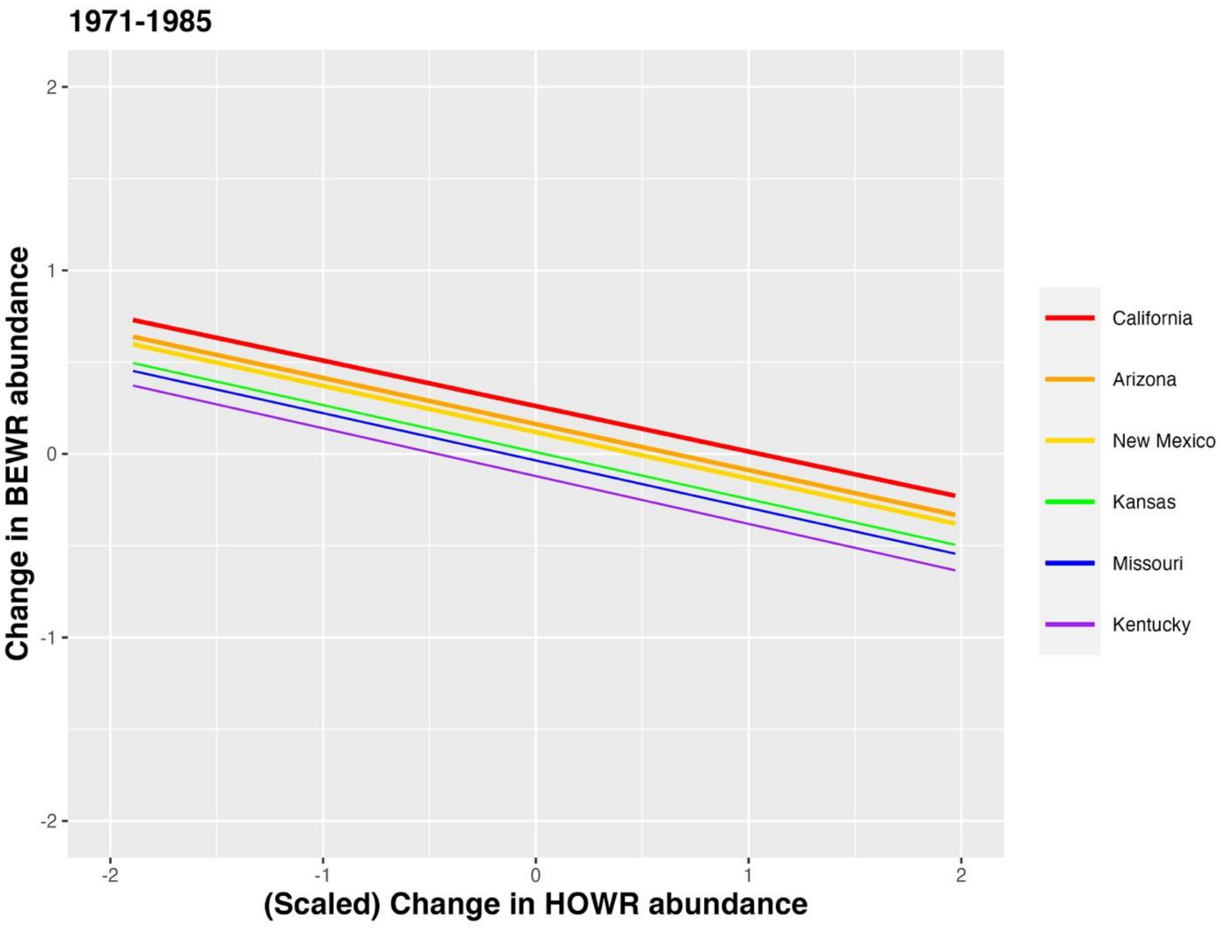
Kentucky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Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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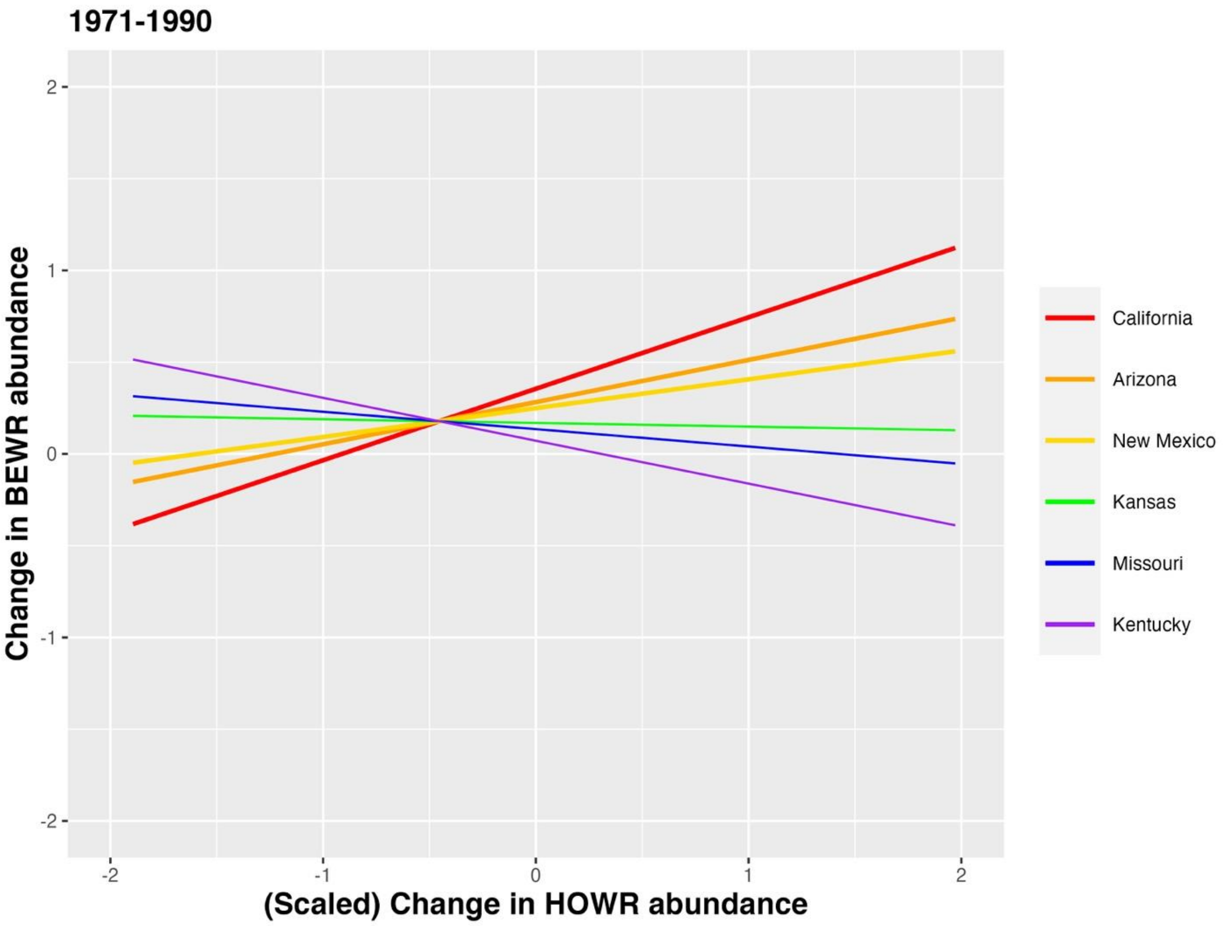
Kansas
Missouri
Kentucky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Change in BEWR abundance
(Scaled) Change in HOWR abundance
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-1
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1
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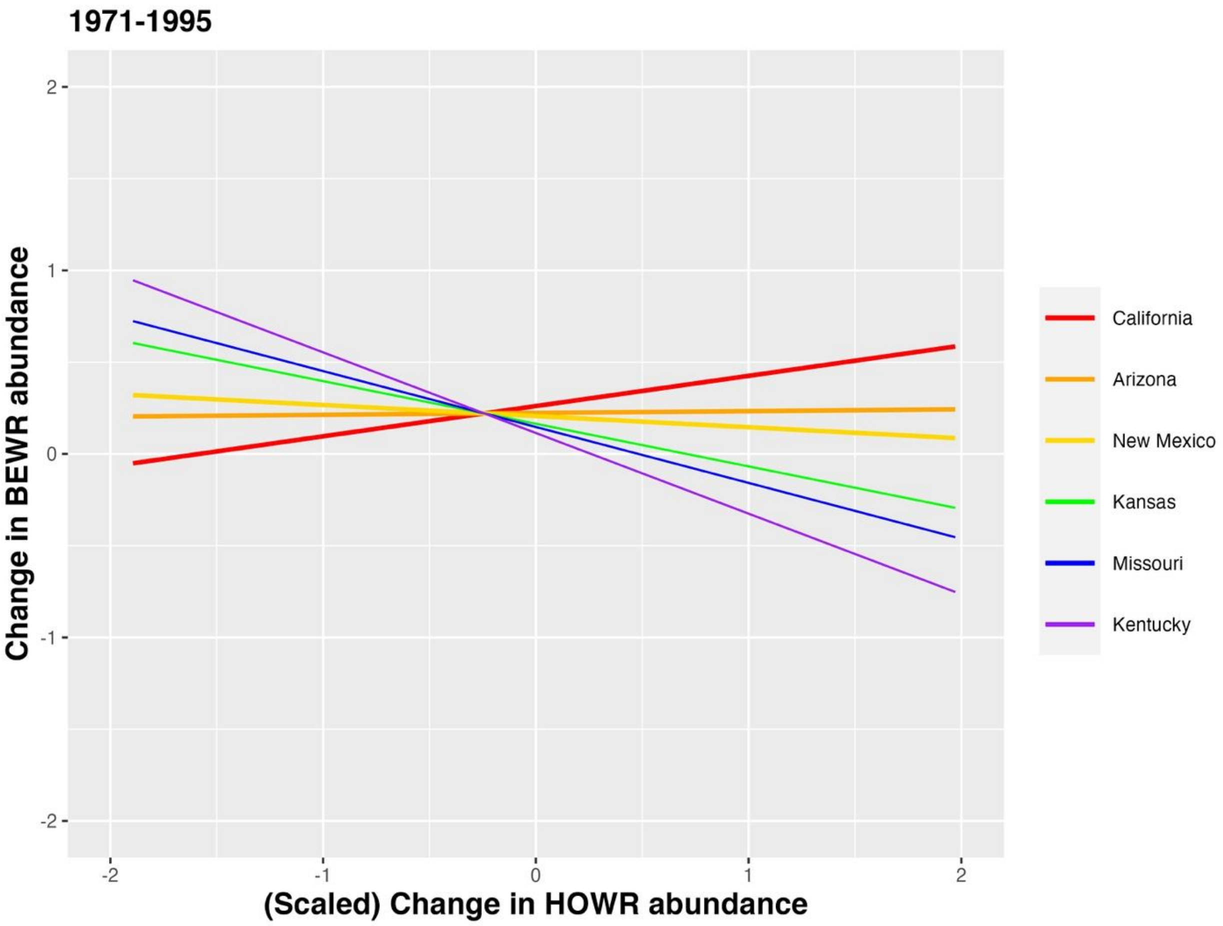
Kansas
Missouri
Kentucky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Change in BEWR abundance
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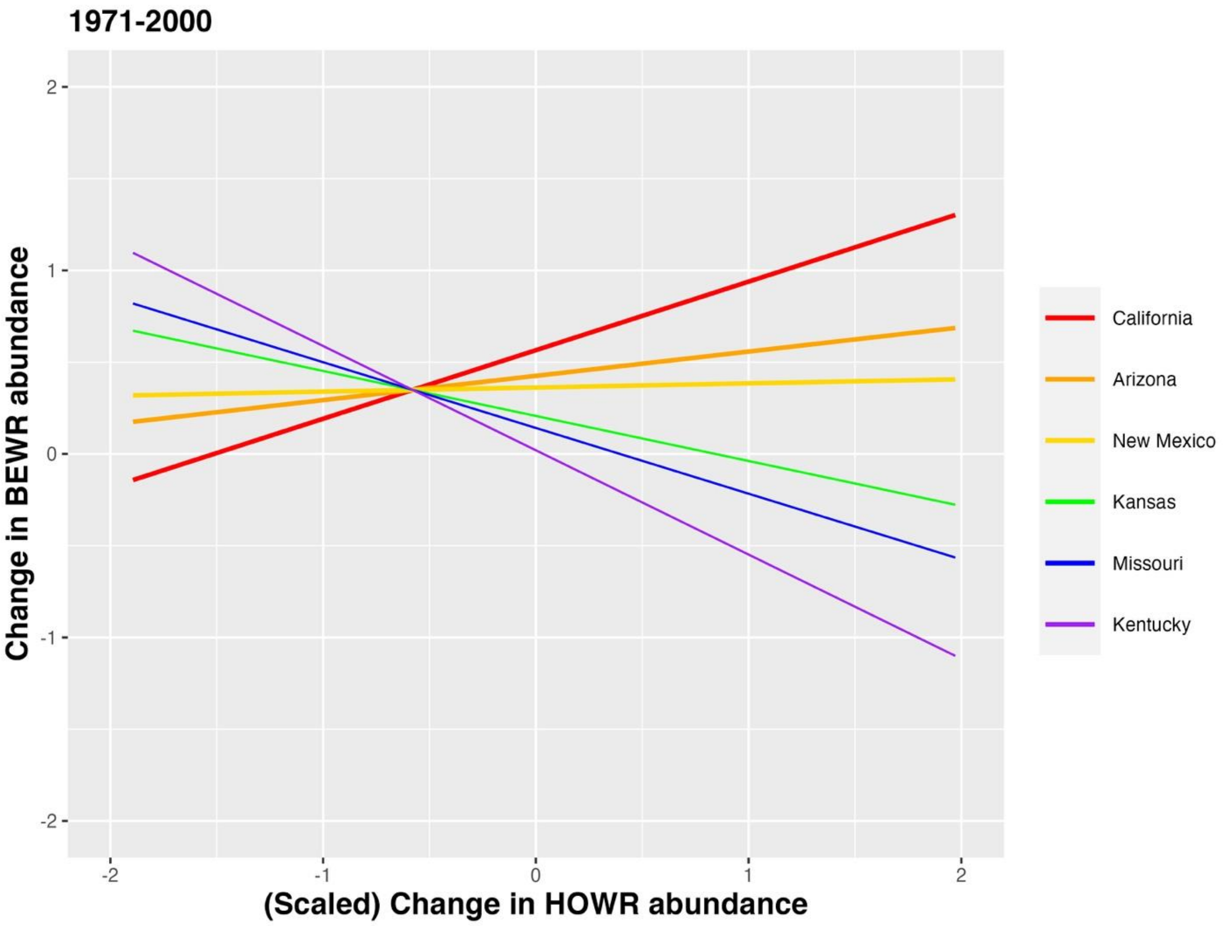
Missouri
Kentucky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Change in BEWR abundance
(Scaled) Change in HOWR abundance
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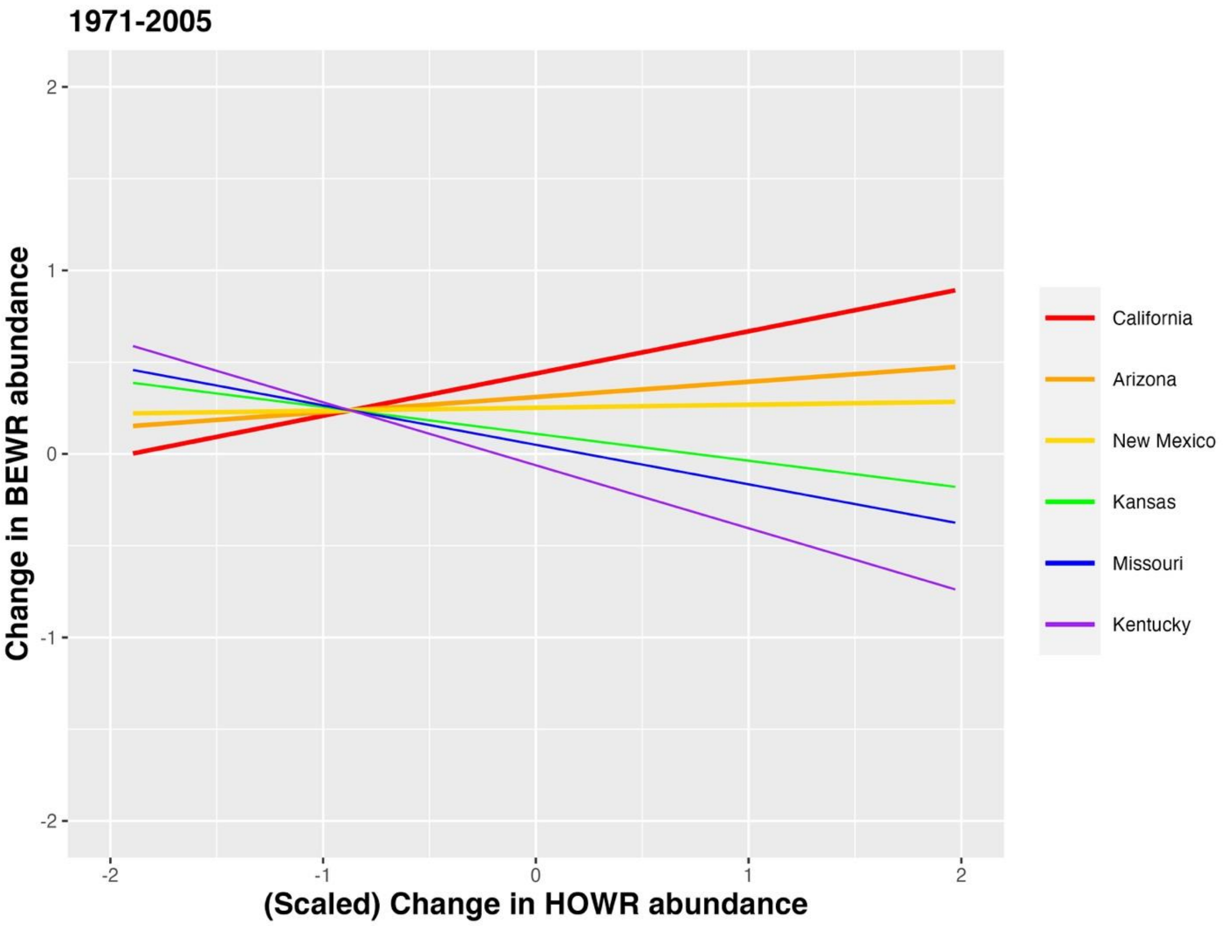
Kansas
Missouri
Kentucky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Change in BEWR abundance
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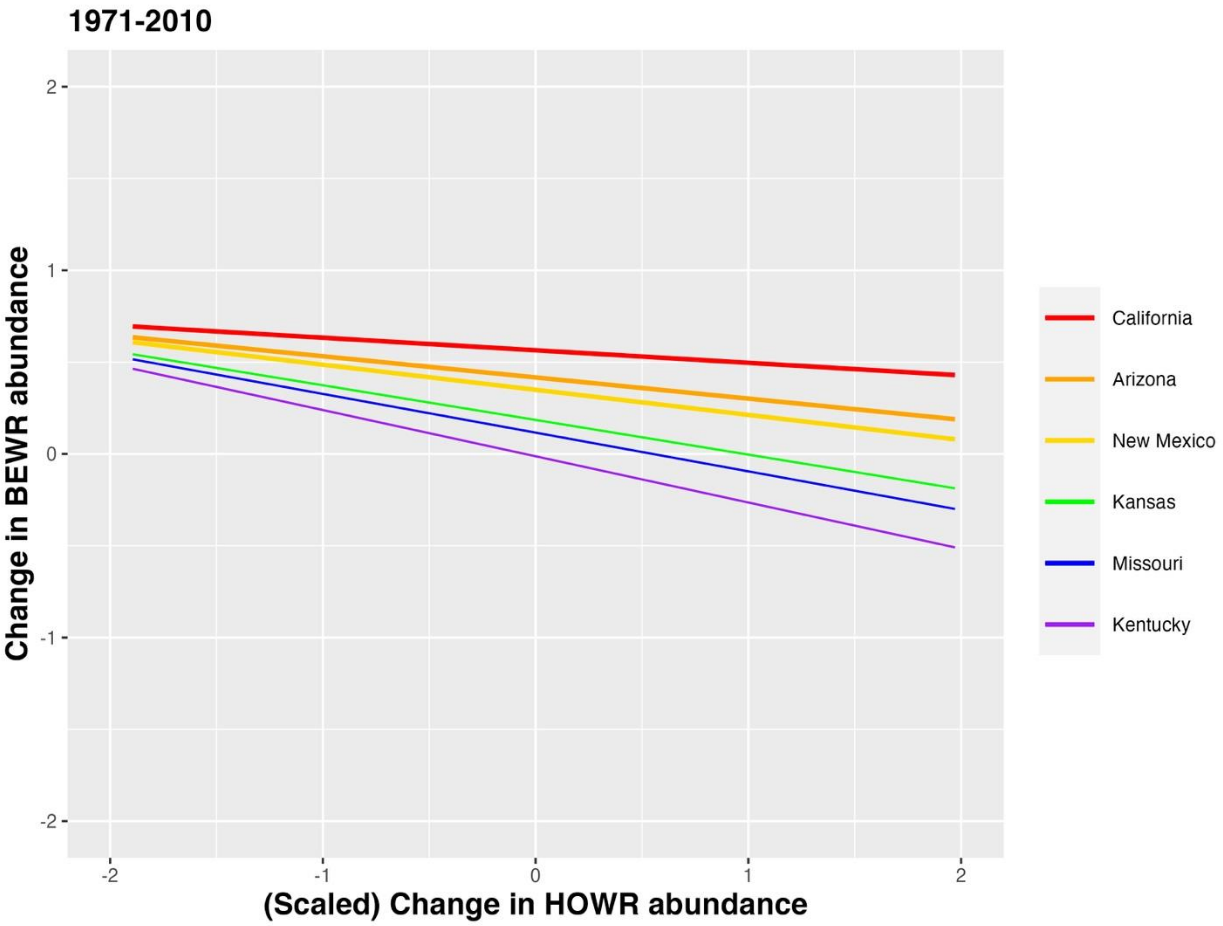
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Change in BEWR abundance
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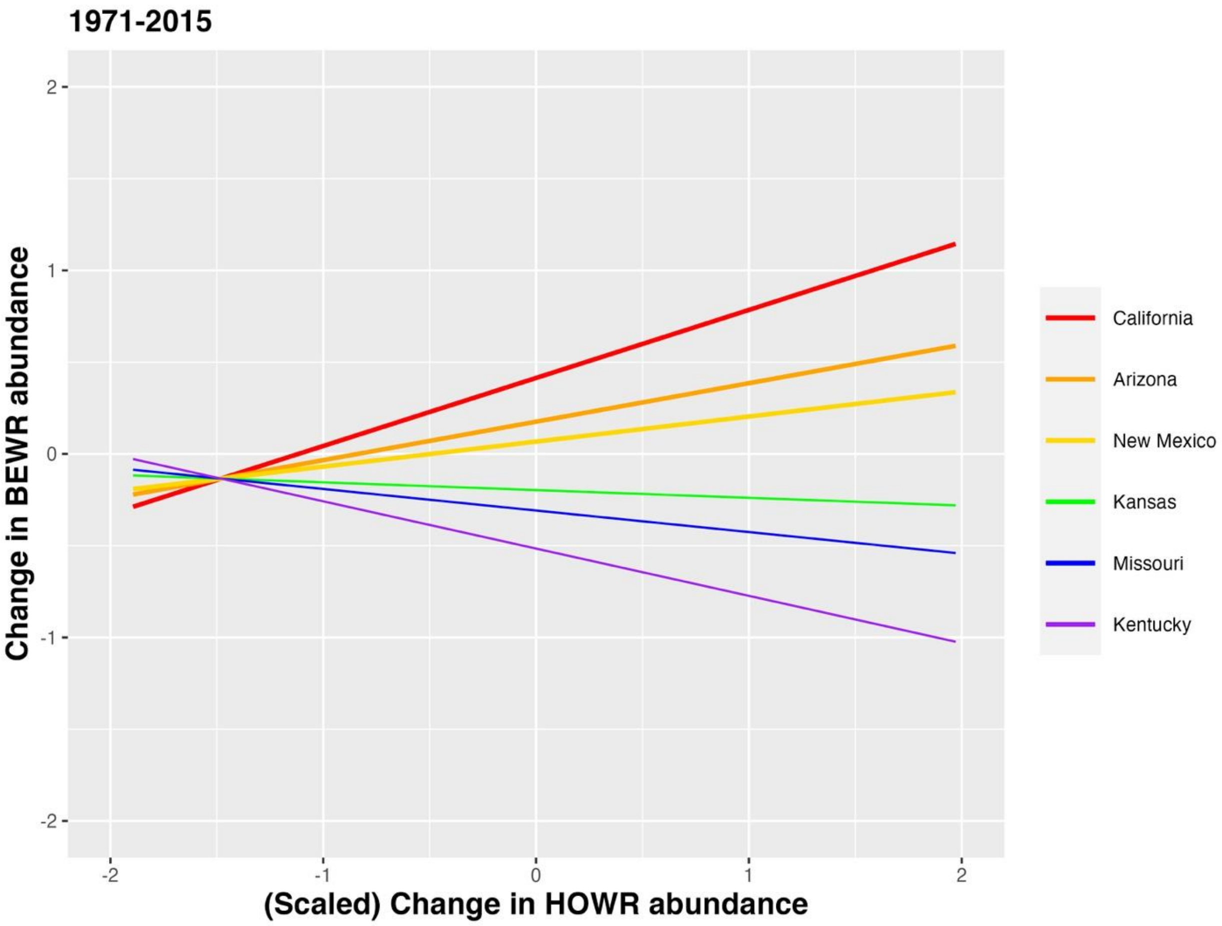
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Change in BEWR abundance
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2
(Scaled) Change in HOWR abundance
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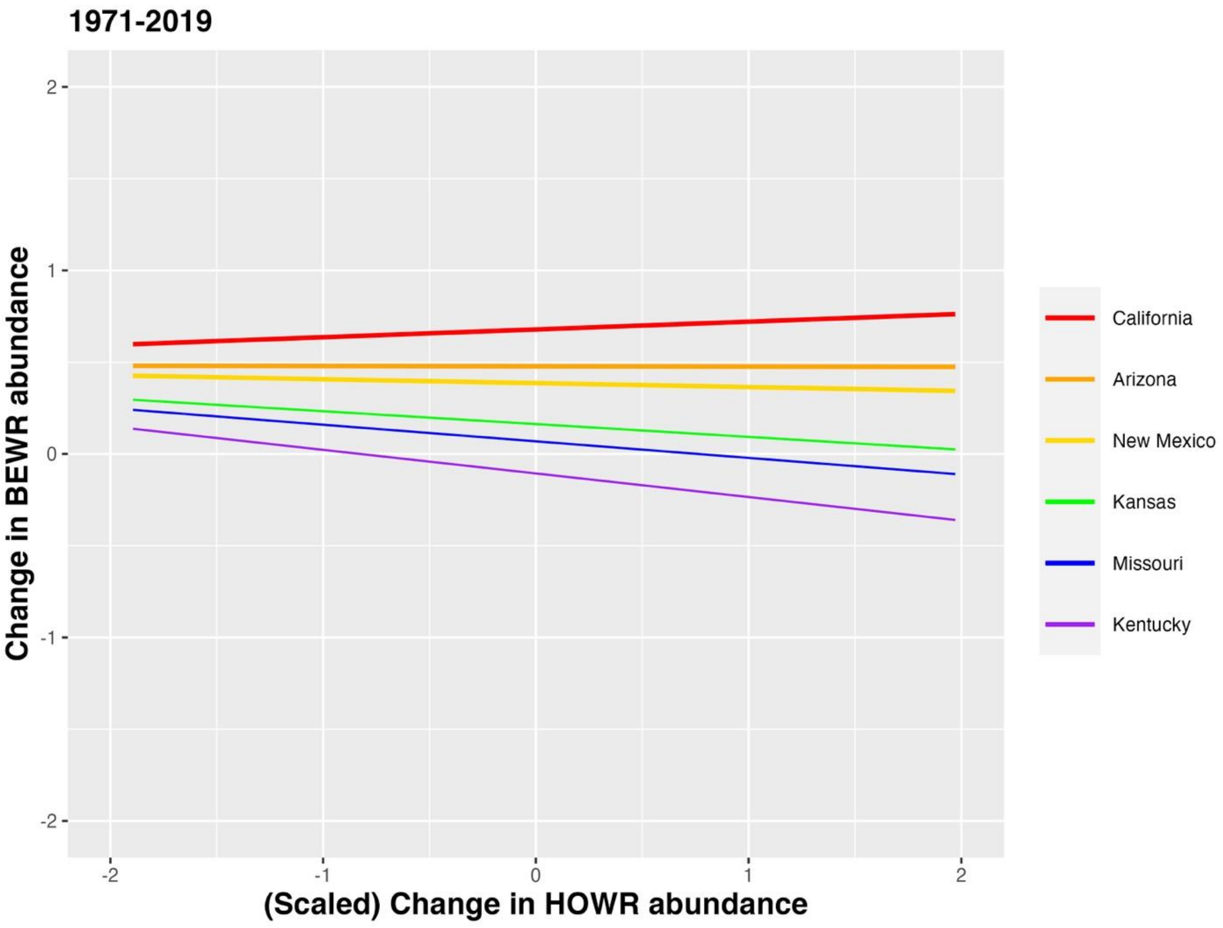
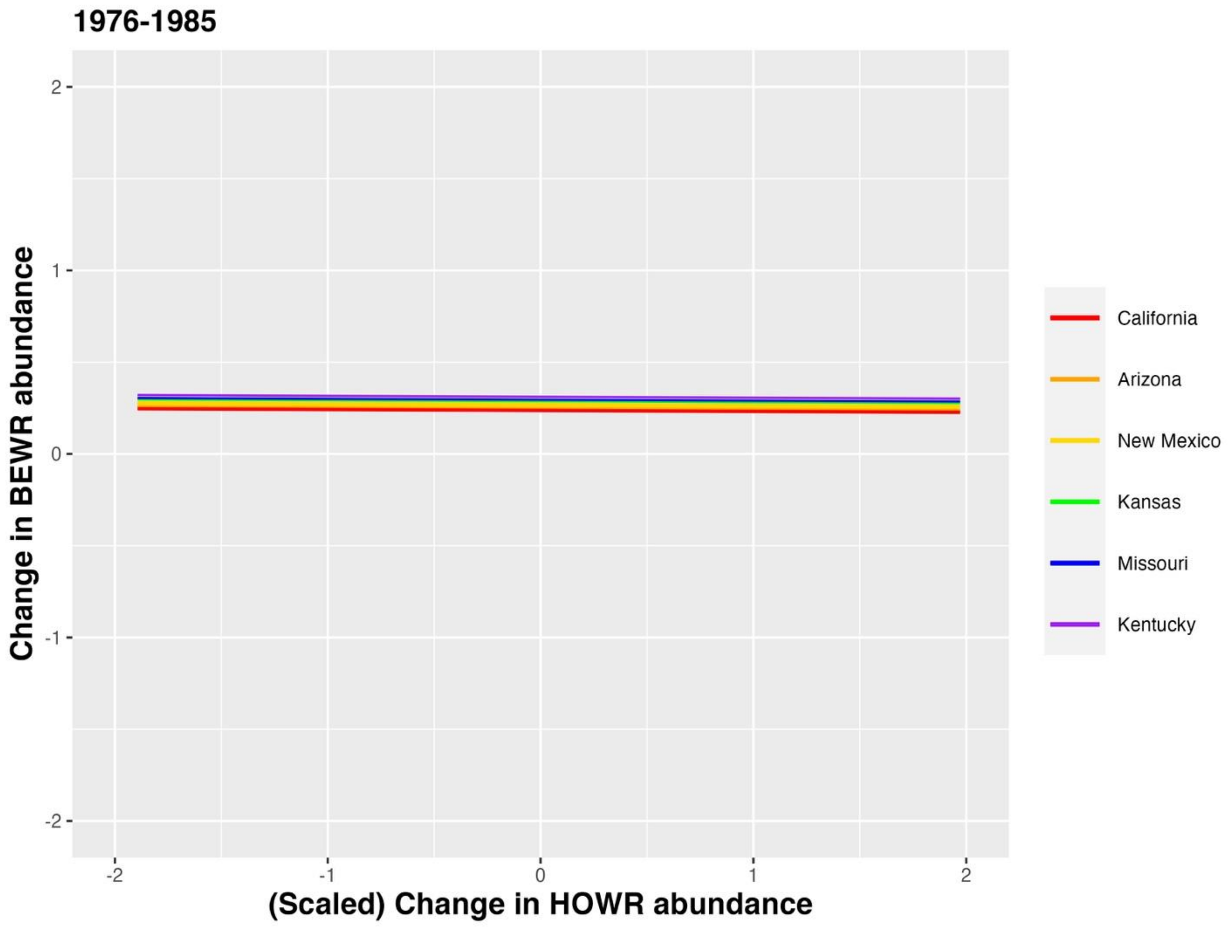


1971-2019

Change in BEWR abundance
2
1
0
-1
-2
(Scaled) Change in HOWR abundance
-2
-1
0
1
2
California
Arizona
New Mexico
Kansas
Missouri
Kentucky


1976-1985
2
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0
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Change in BEWR abundance
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-1
0
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2
(Scaled) Change in HOWR abundance
California
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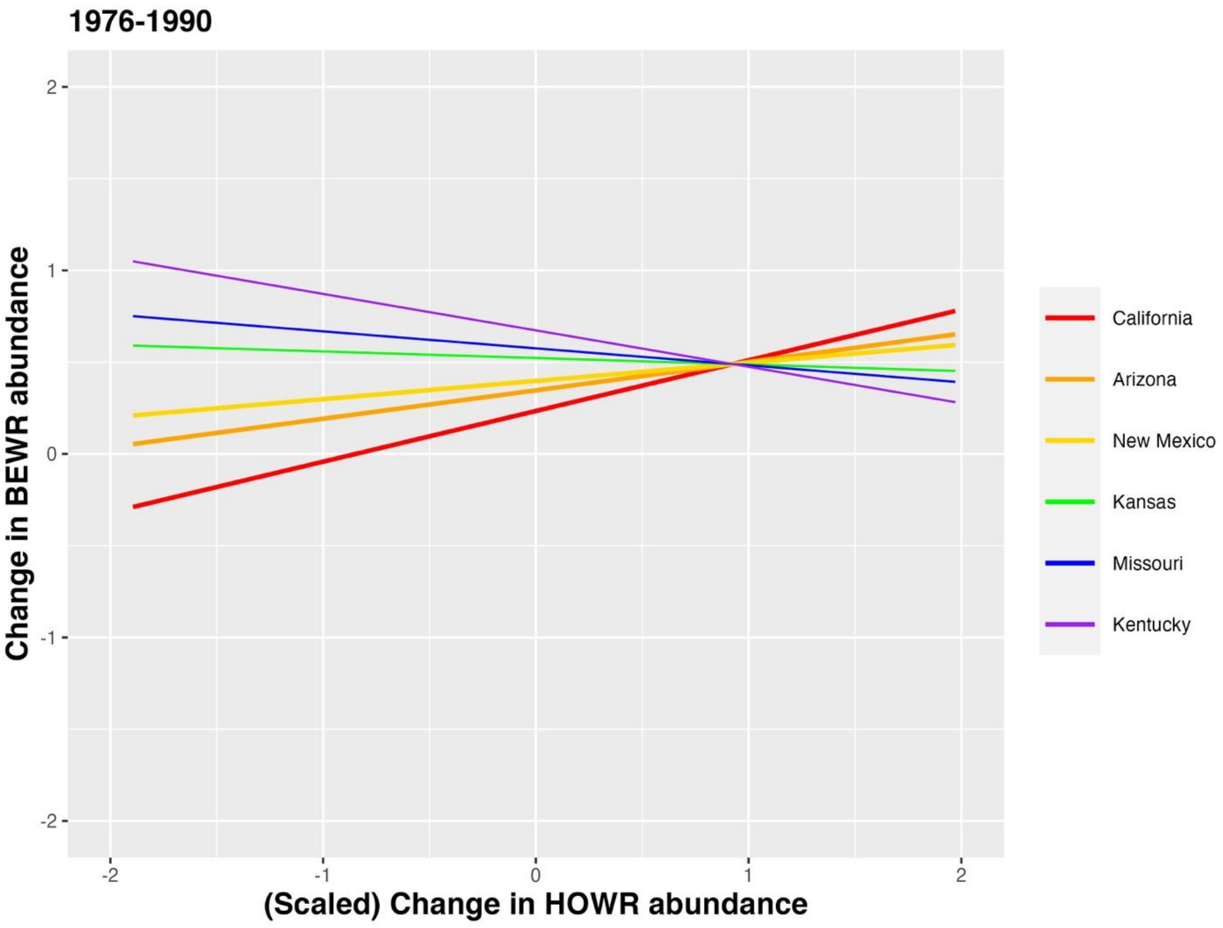
New Mexico
Kansas
Missouri
Kentucky


1976-1990
Change in BEWR abundance
(Scaled) Change in HOWR abundance
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-1
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-2
-1
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1
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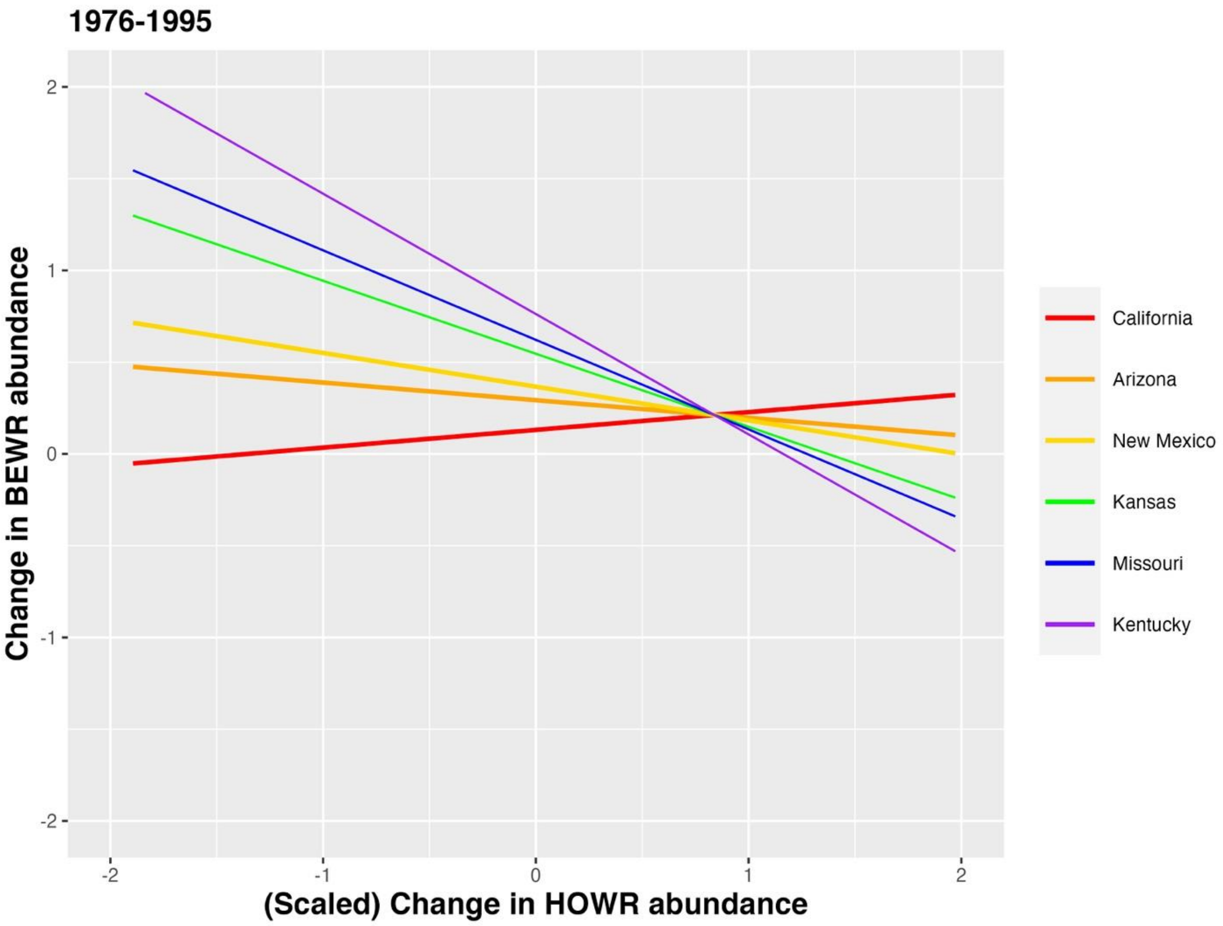
New Mexico
Kansas
Missouri
Kentucky


1976-1995
Change in BEWR abundance
2
1
0
-1
-2
(Scaled) Change in HOWR abundance
-2
-1
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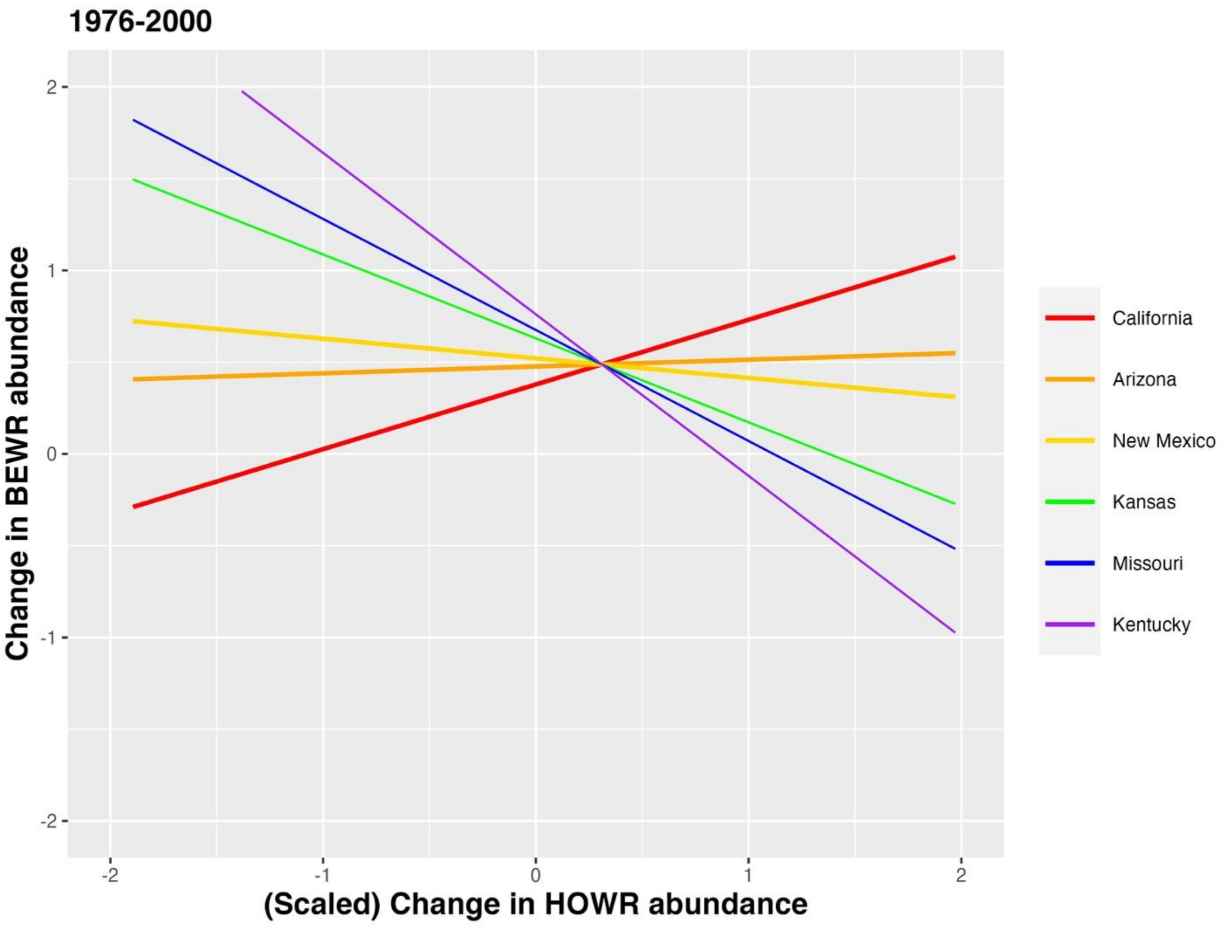
Kansas
Missouri
Kentucky


1976-2000
Change in BEWR abundance
2
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(Scaled) Change in HOWR abundance
California
Arizona
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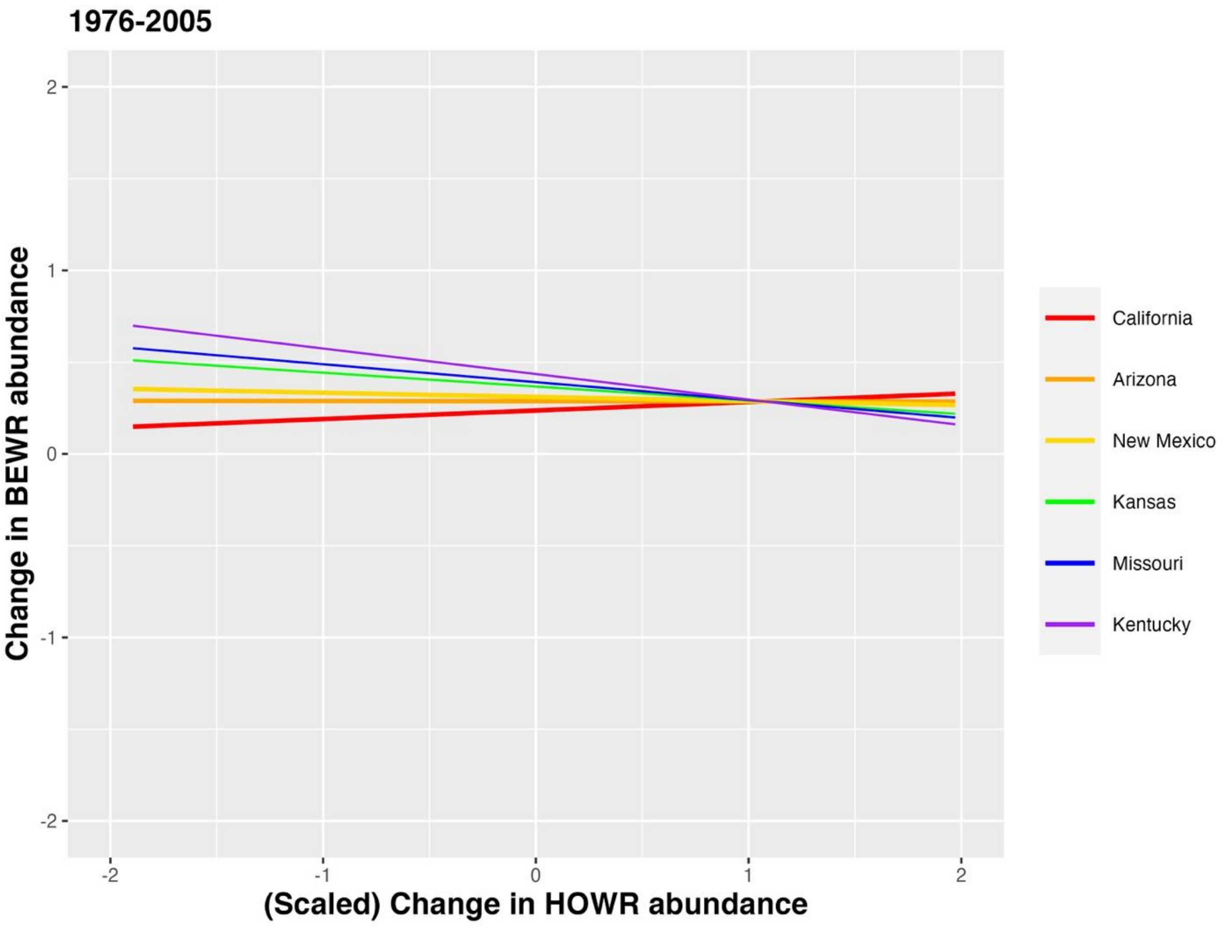
Kansas
Missouri
Kentucky


1976-2005
Change in BEWR abundance
2
1
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-2
(Scaled) Change in HOWR abundance
-2
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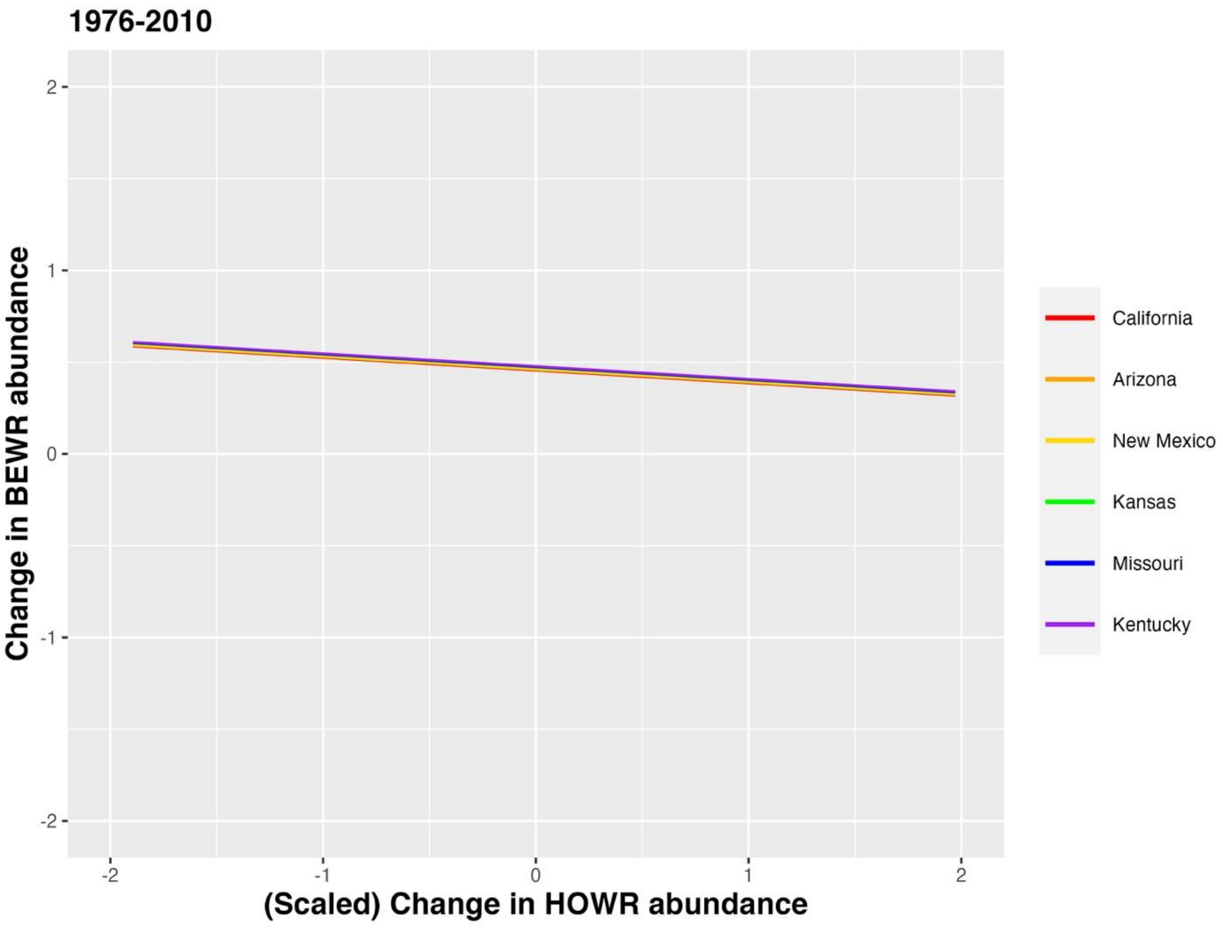

1976-2010
Change in BEWR abundance
2
1
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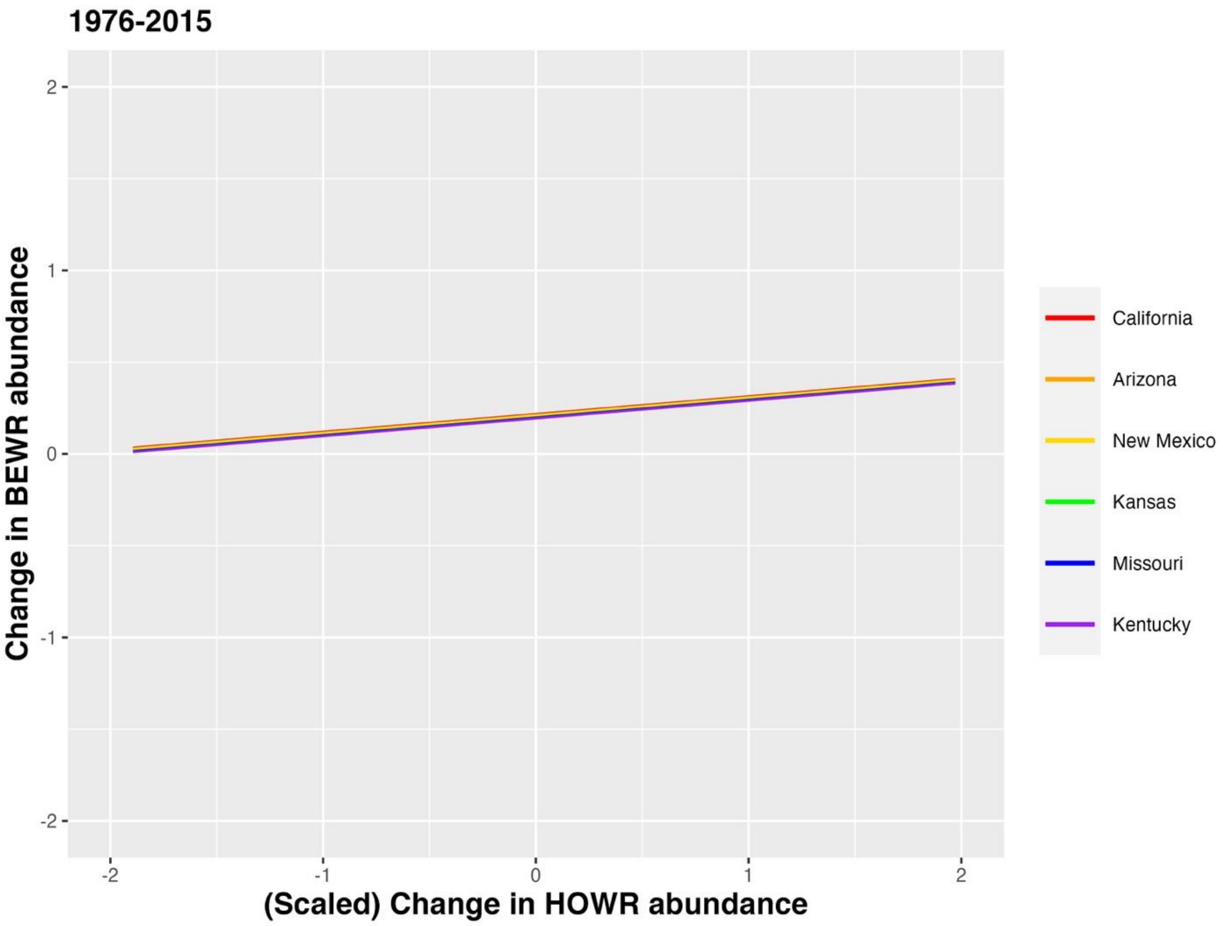
-1
-2
-2
-1
0
1
2
(Scaled) Change in HOWR abundance
California
Arizona
New Mexico
Kansas
Missouri
Kentucky


1976-2015
Change in BEWR abundance
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1
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-1
-2
(Scaled) Change in HOWR abundance
-2
-1
0
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California
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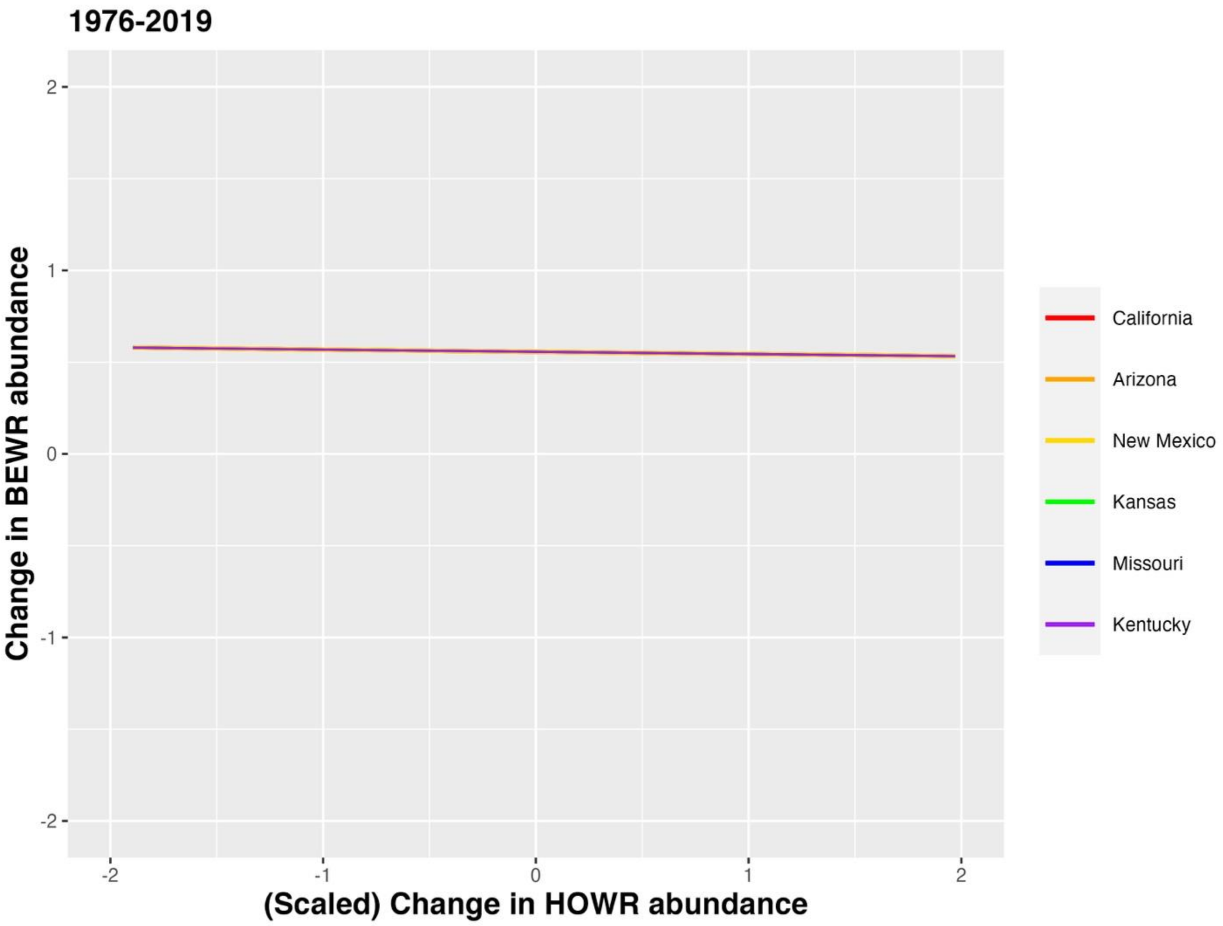
Kansas
Missouri
Kentucky


1976-2019
Change in BEWR abundance
2
1
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-2
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-1
0
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2
(Scaled) Change in HOWR abundance
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Arizona
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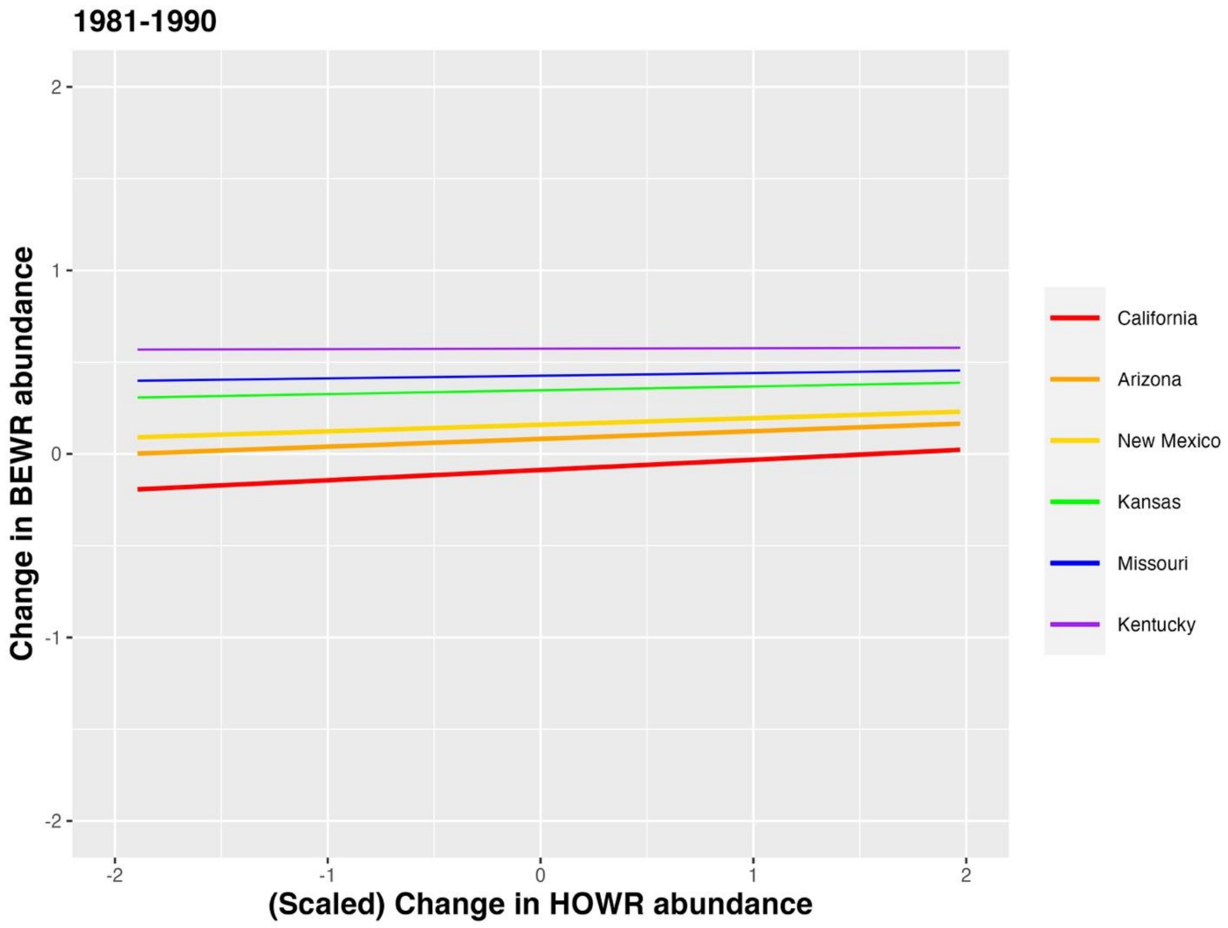
Kansas
Missouri
Kentucky


1981-1990
Change in BEWR abundance
(Scaled) Change in HOWR abundance
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-2
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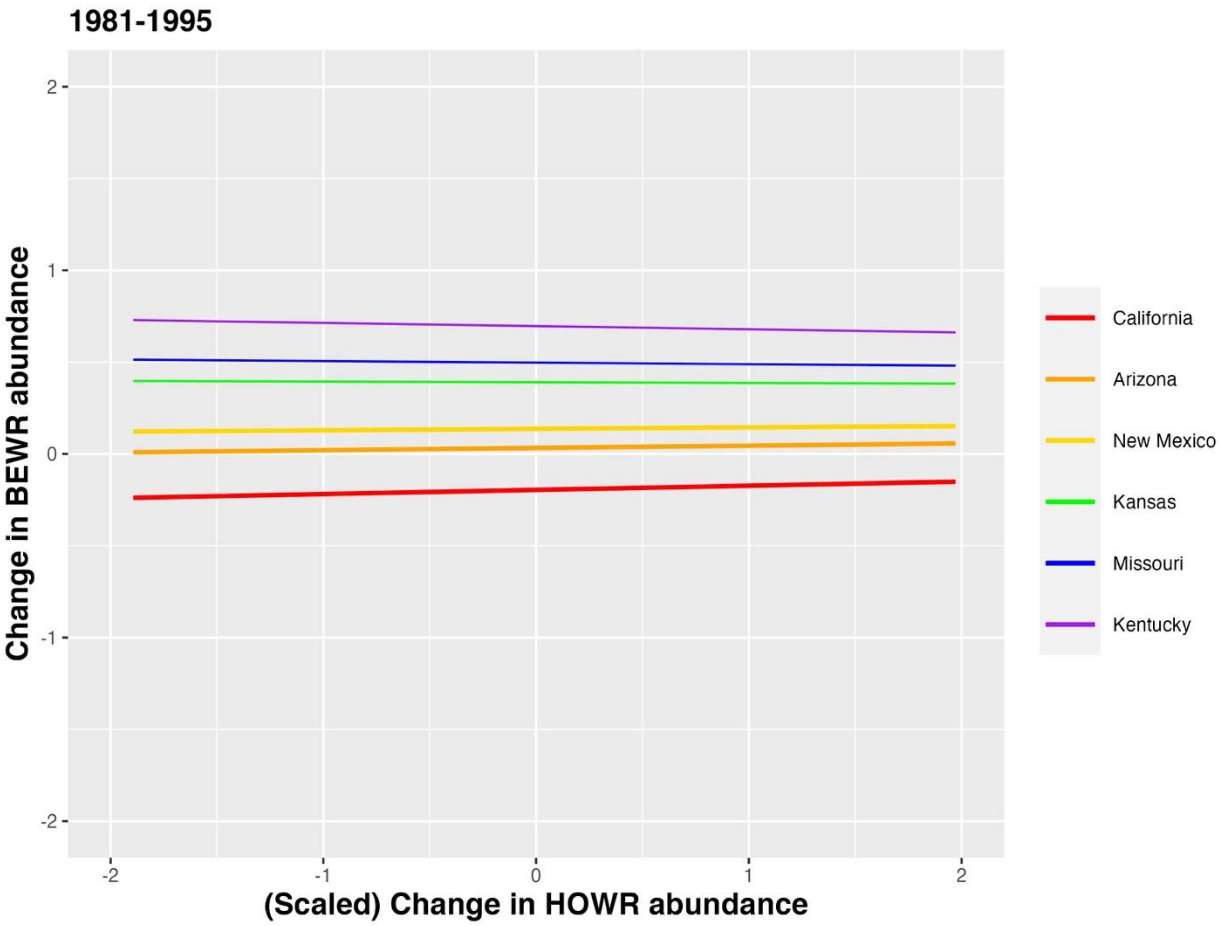
New Mexico
Kansas
Missouri
Kentucky


1981-1995
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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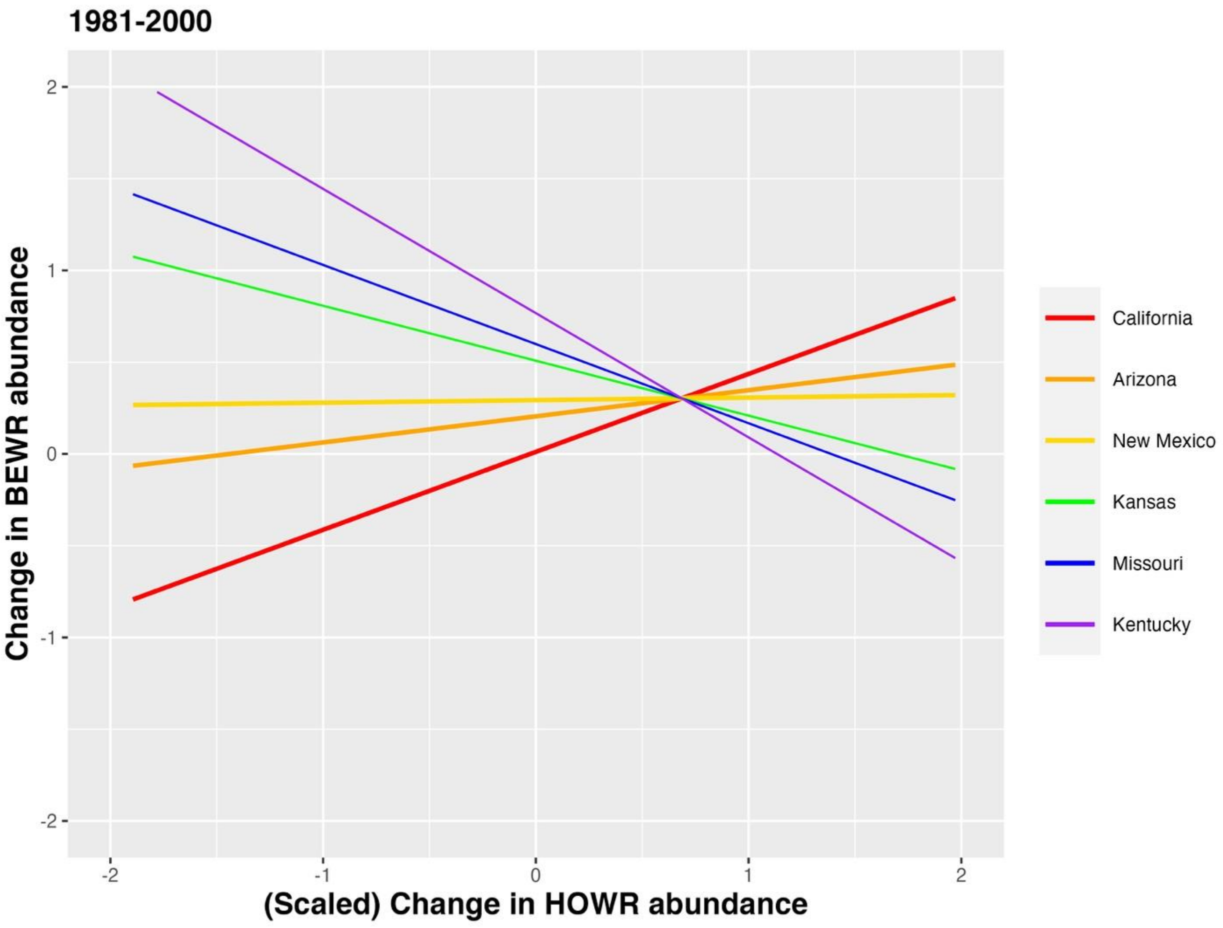
New Mexico
Kansas
Missouri
Kentucky


1981-2000
Change in BEWR abundance
(Scaled) Change in HOWR abundance
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-2
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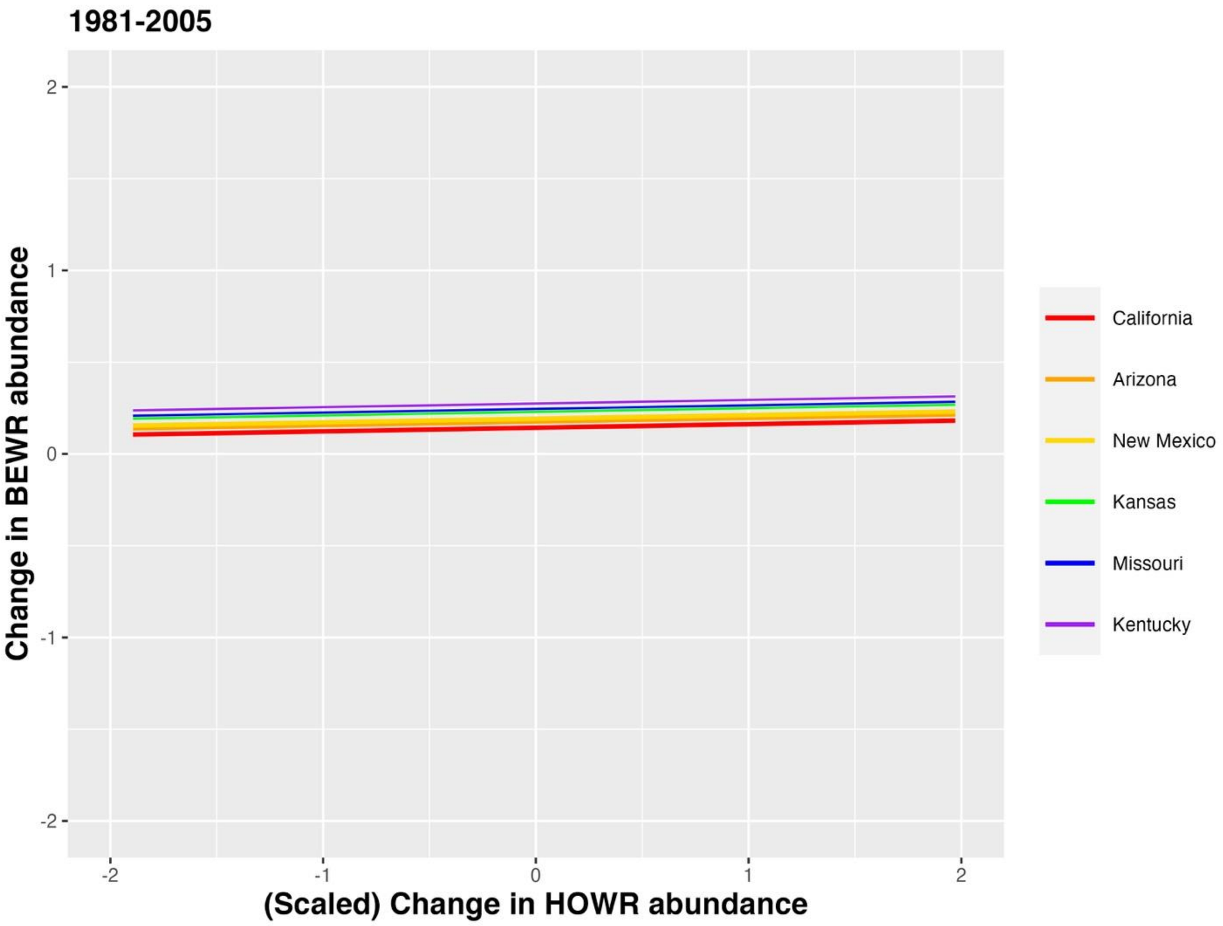
Kansas
Missouri
Kentucky


1981-2005
Change in BEWR abundance
2
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-2
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(Scaled) Change in HOWR abundance
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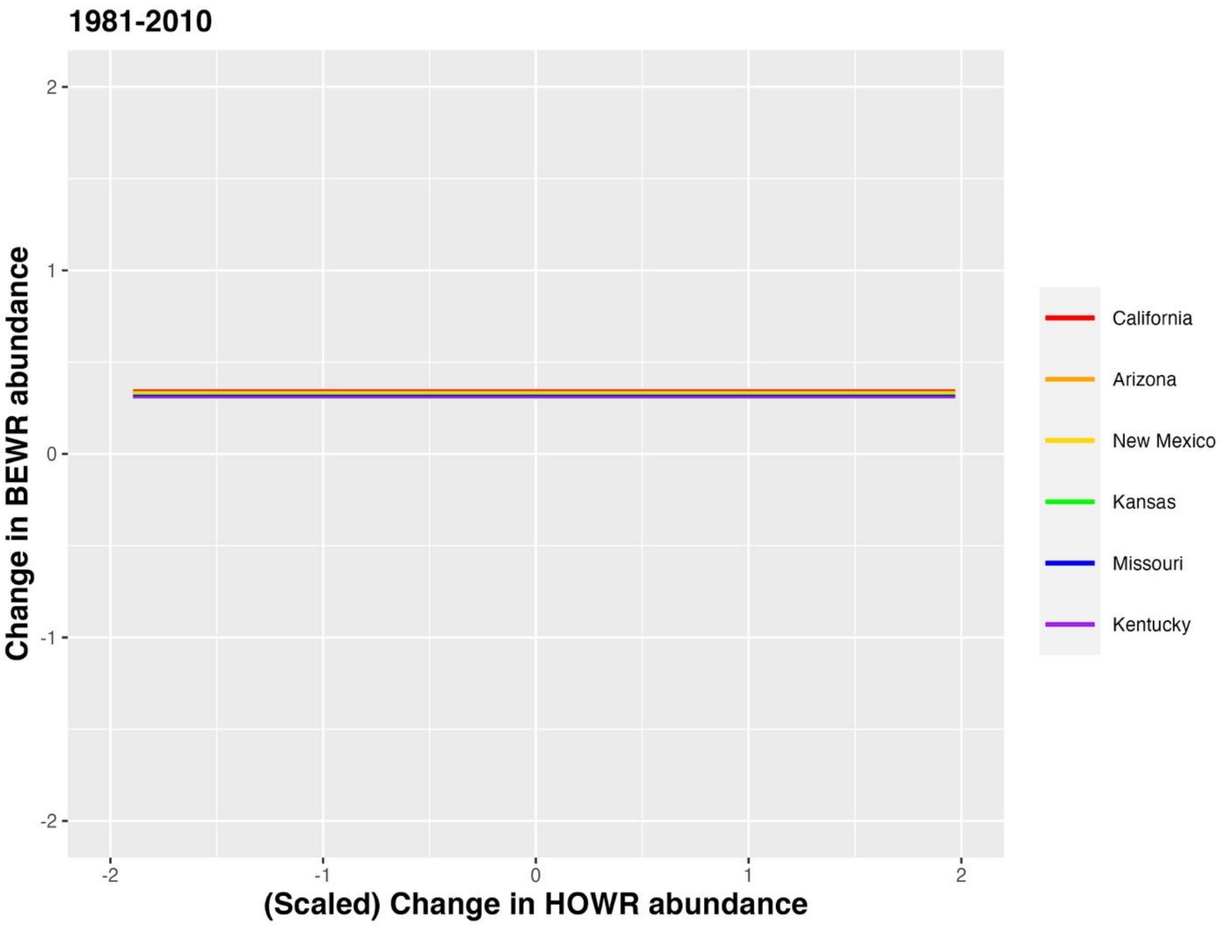
Arizona
New Mexico
Kansas
Missouri
Kentucky


1981-2010
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-1
-2
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
California
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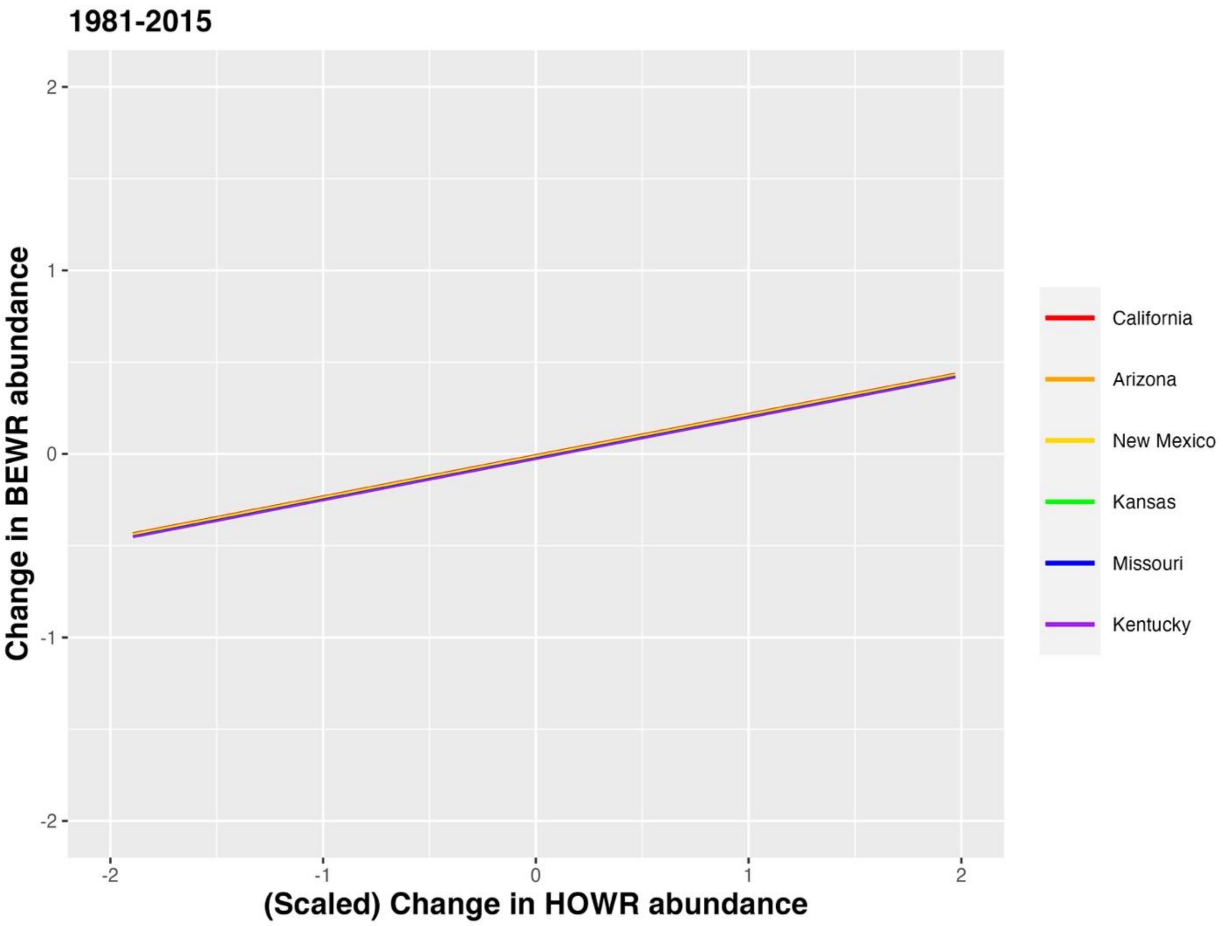
Kentucky


1981-2015
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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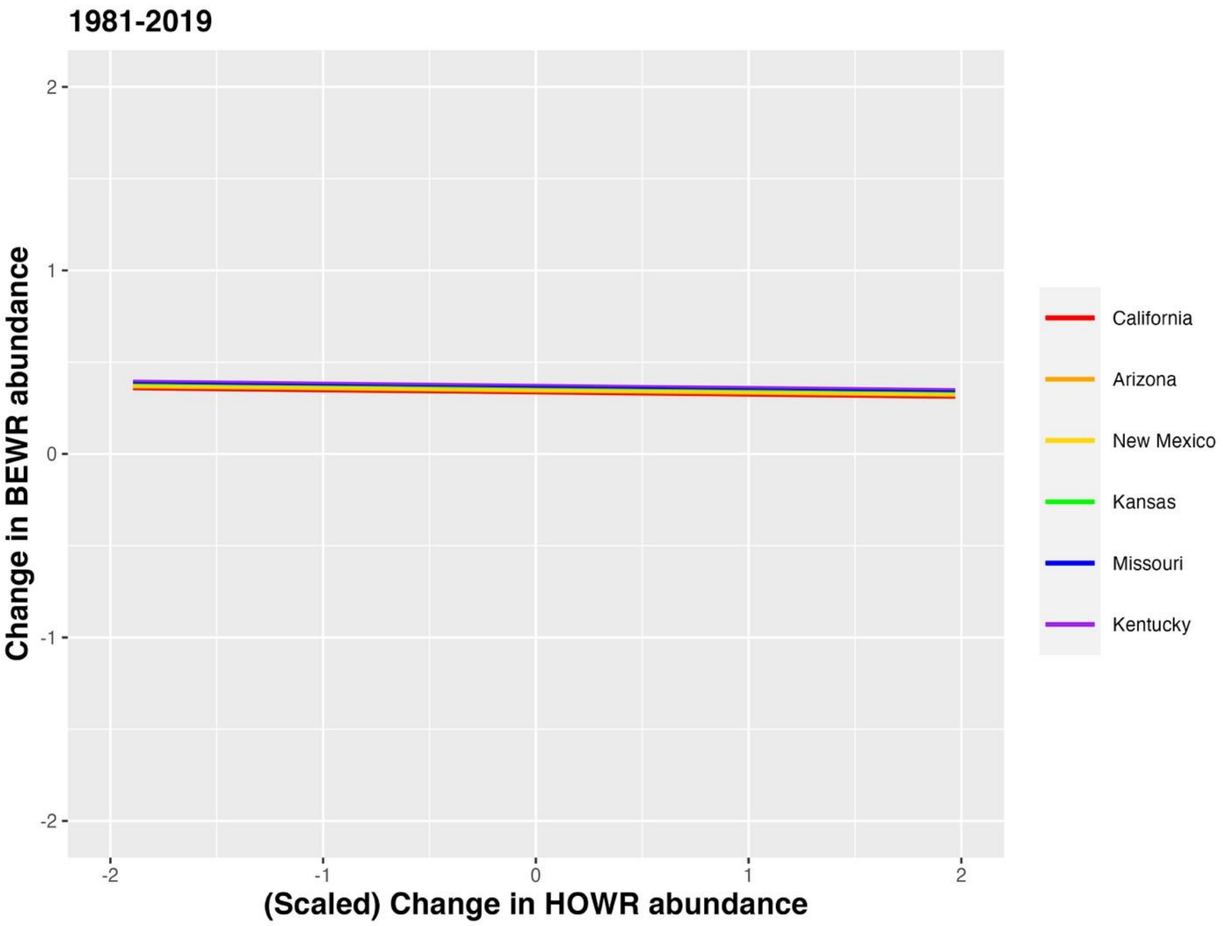
Kentucky


1981-2019
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-1
-2
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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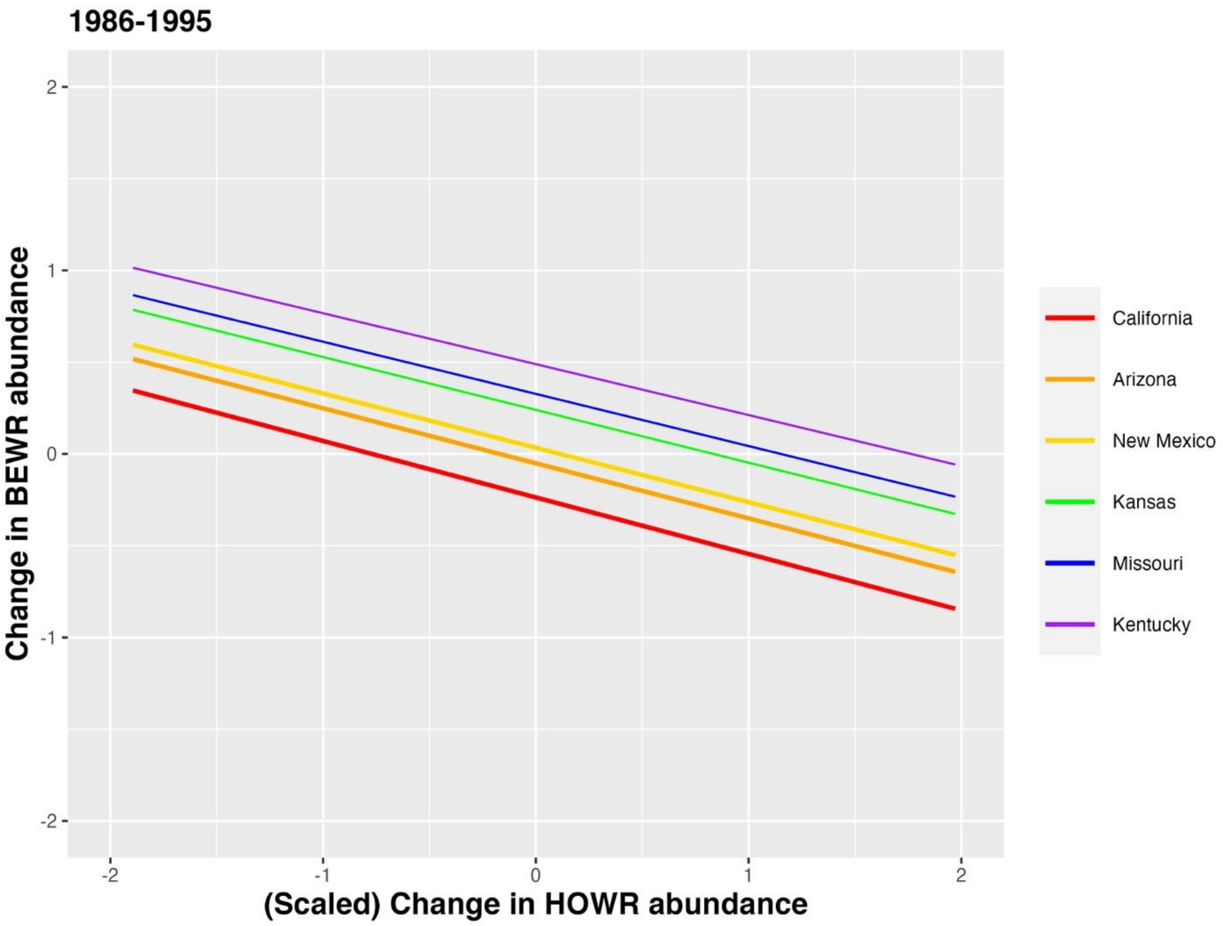
Missouri
Kentucky


1986-1995
Change in BEWR abundance
(Scaled) Change in HOWR abundance
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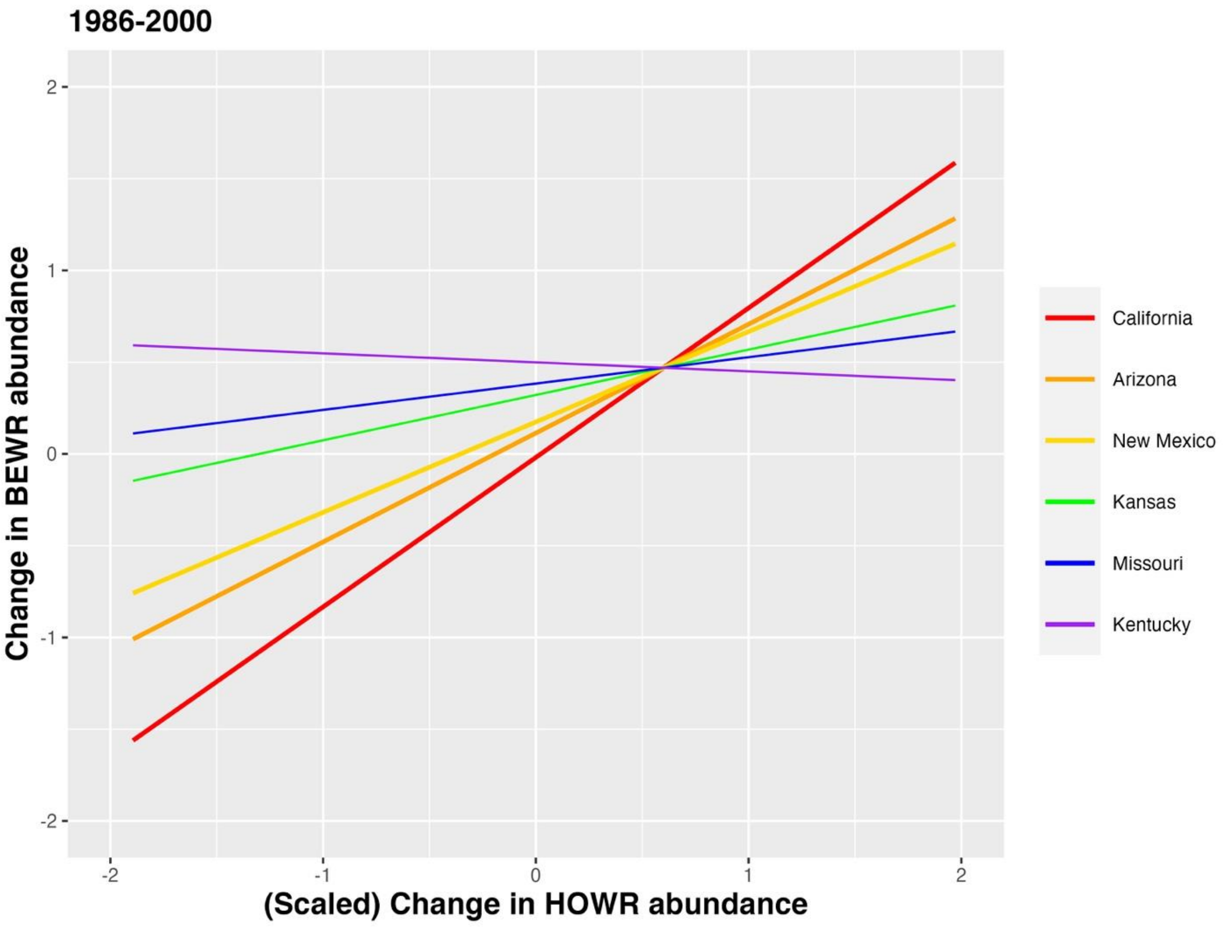
Kentucky


1986-2000
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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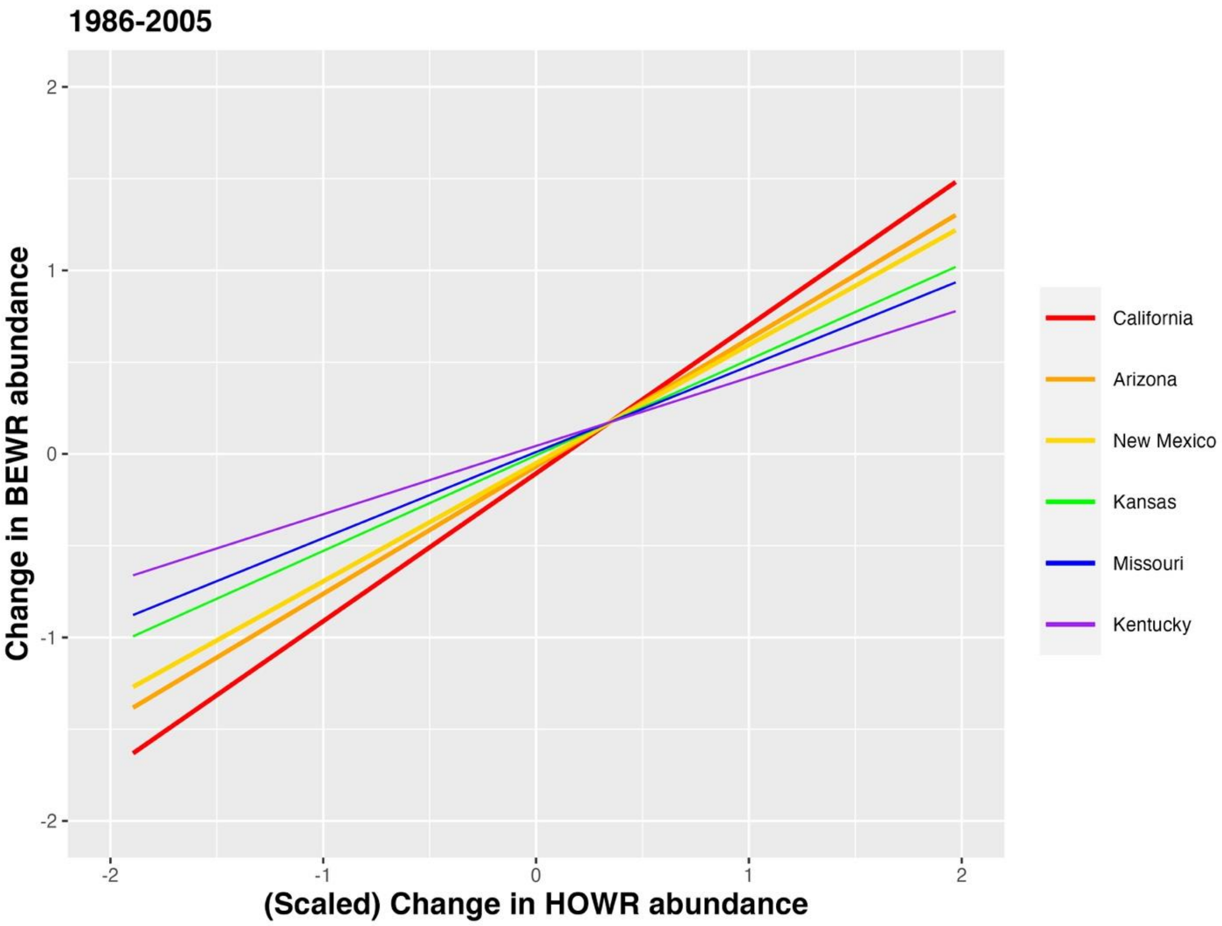
1986-2005
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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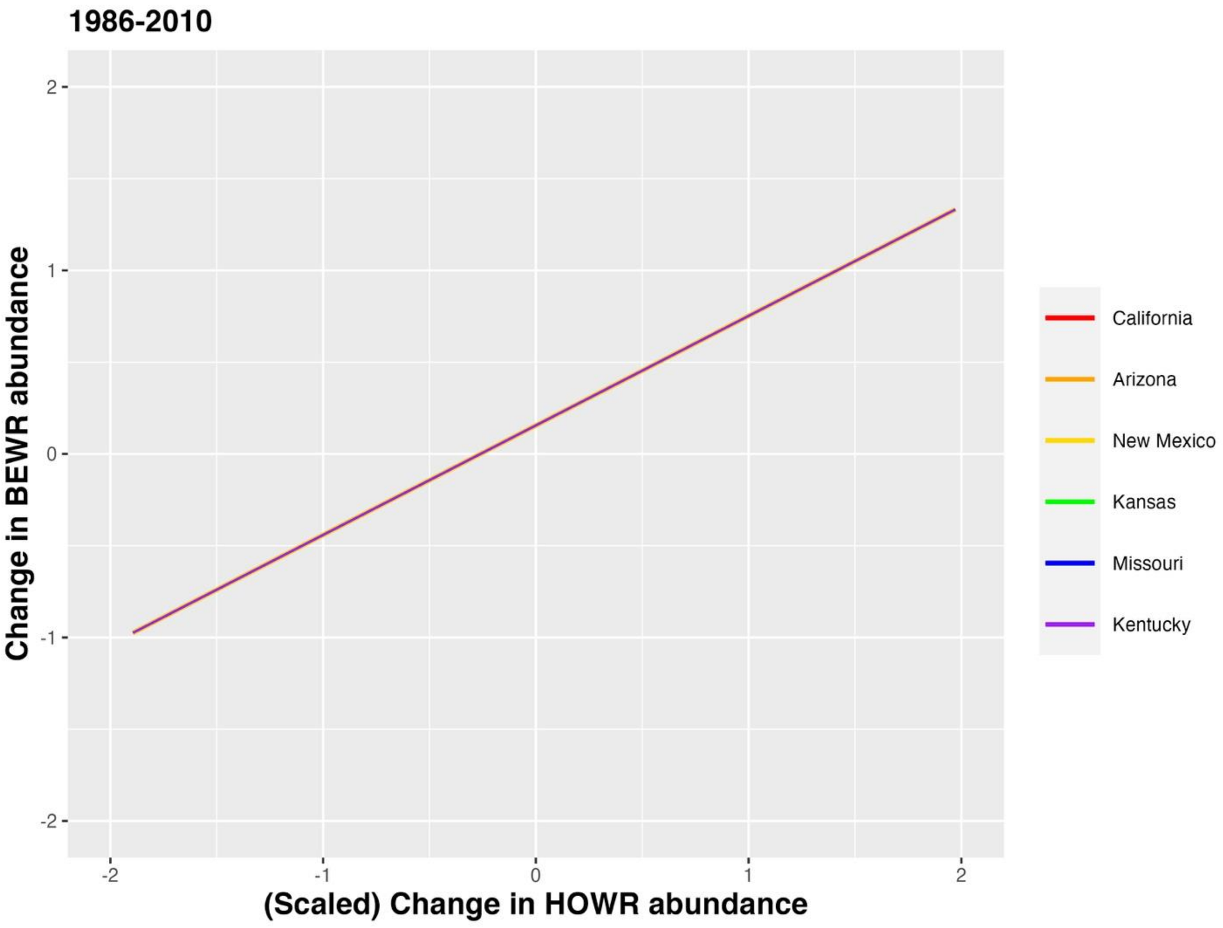
1986-2010
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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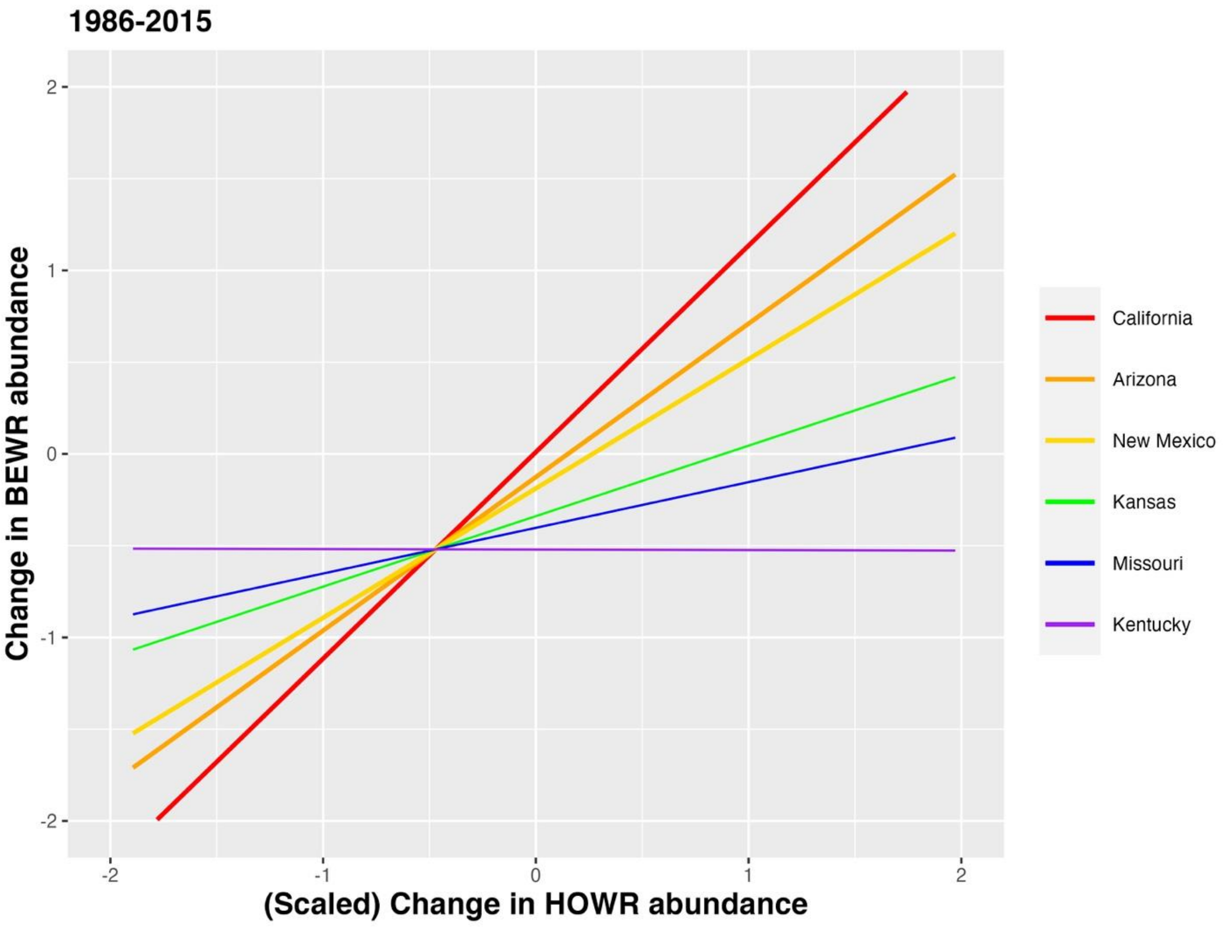
Kentucky


1986-2015
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Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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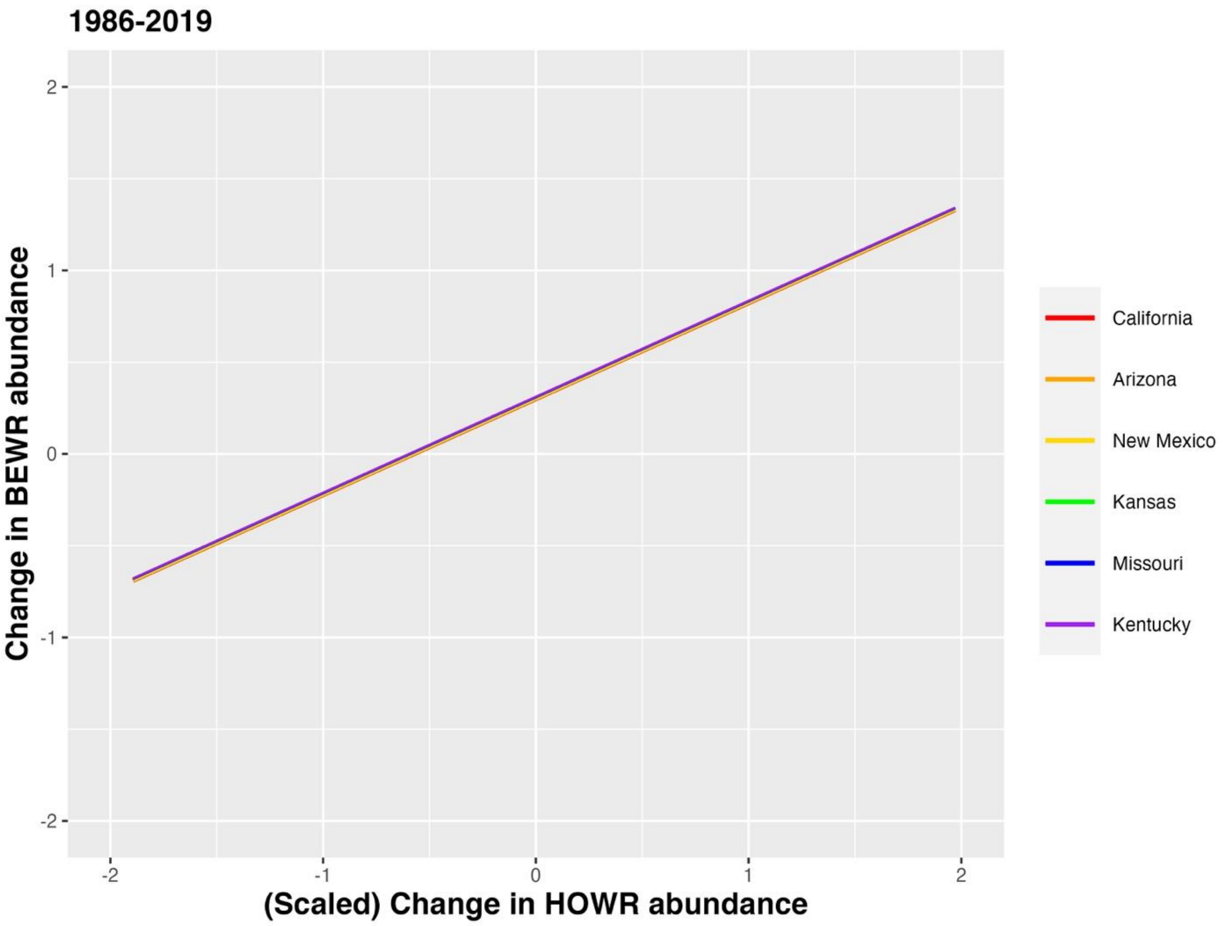
1986-2019
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-1
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Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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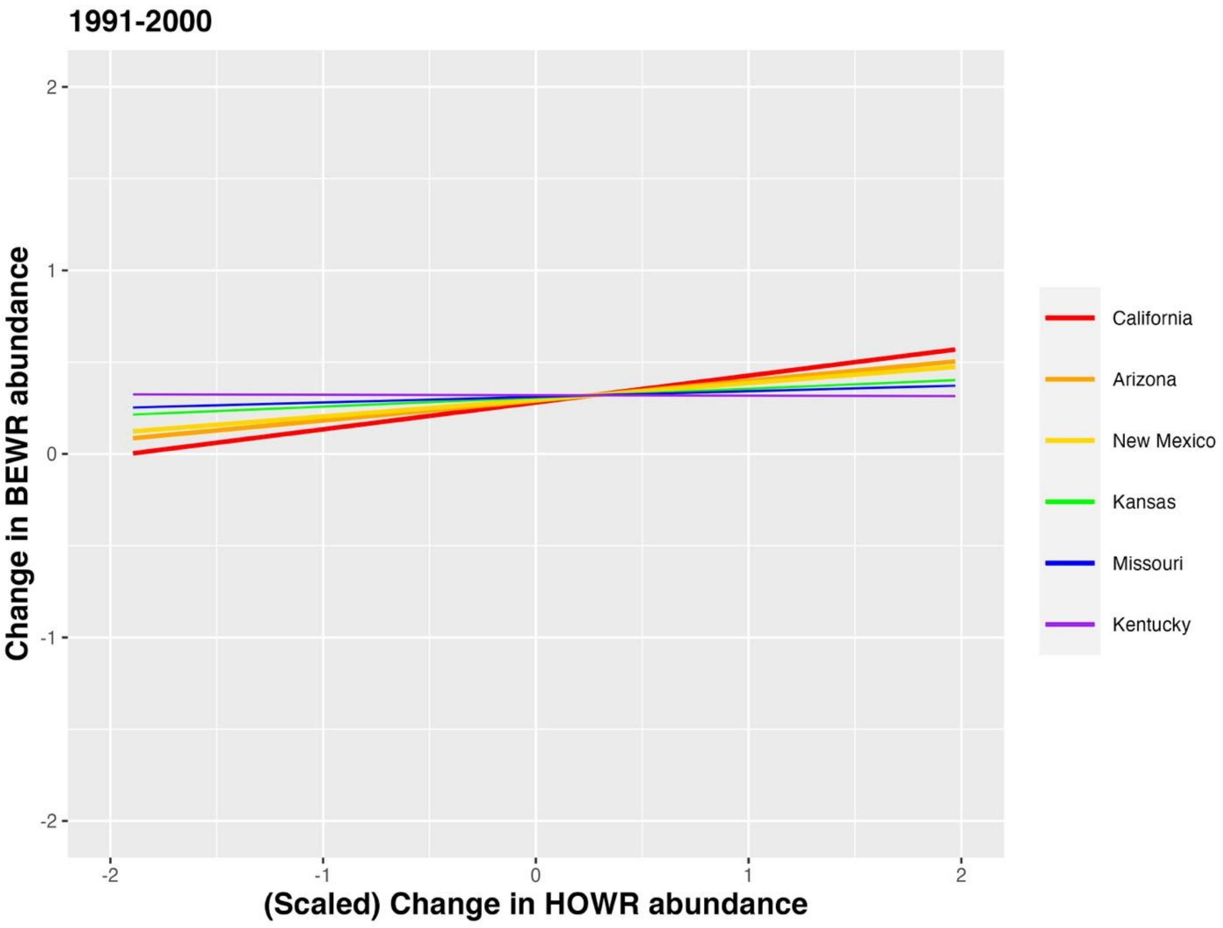
1991-2000
Change in BEWR abundance
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2
(Scaled) Change in HOWR abundance
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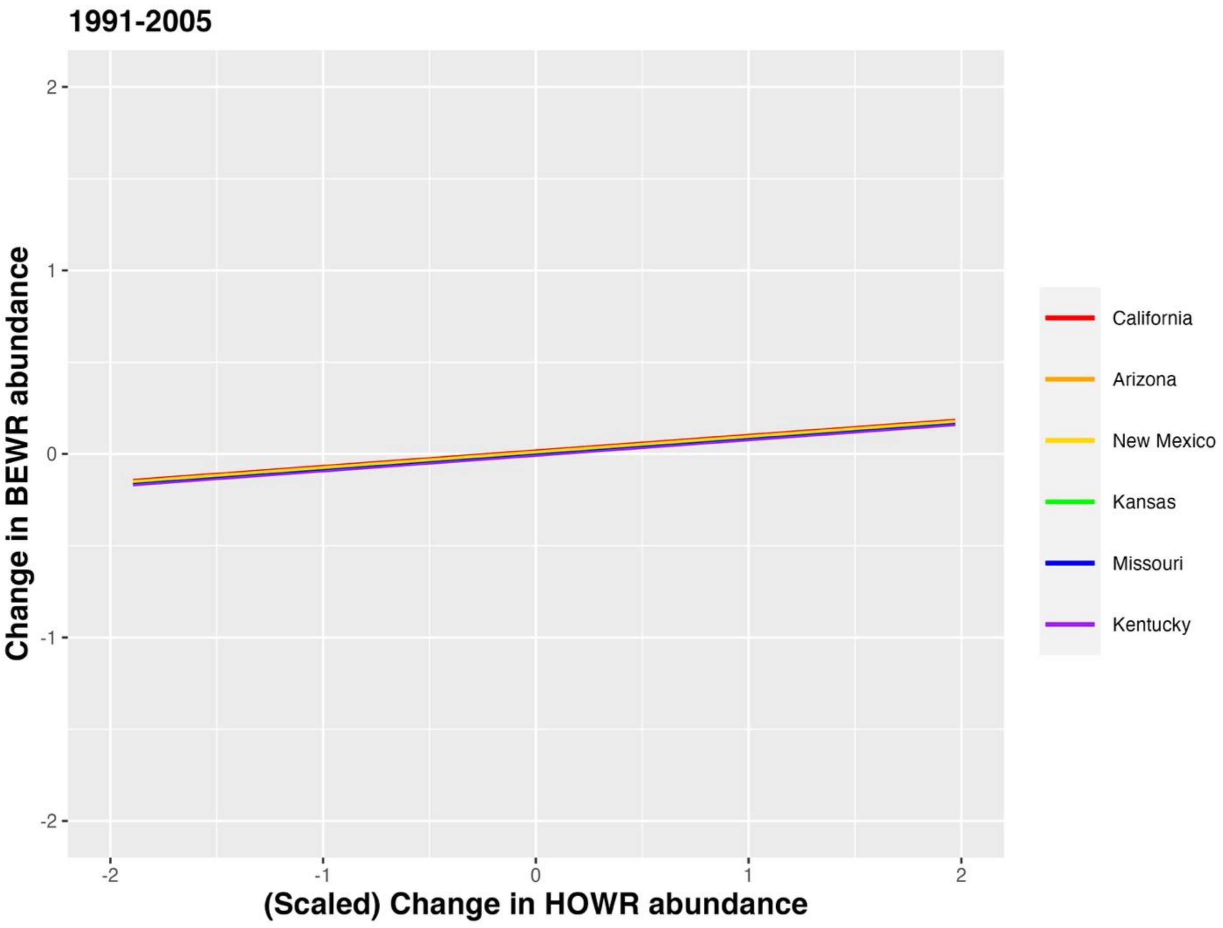
Kentucky


1991-2005
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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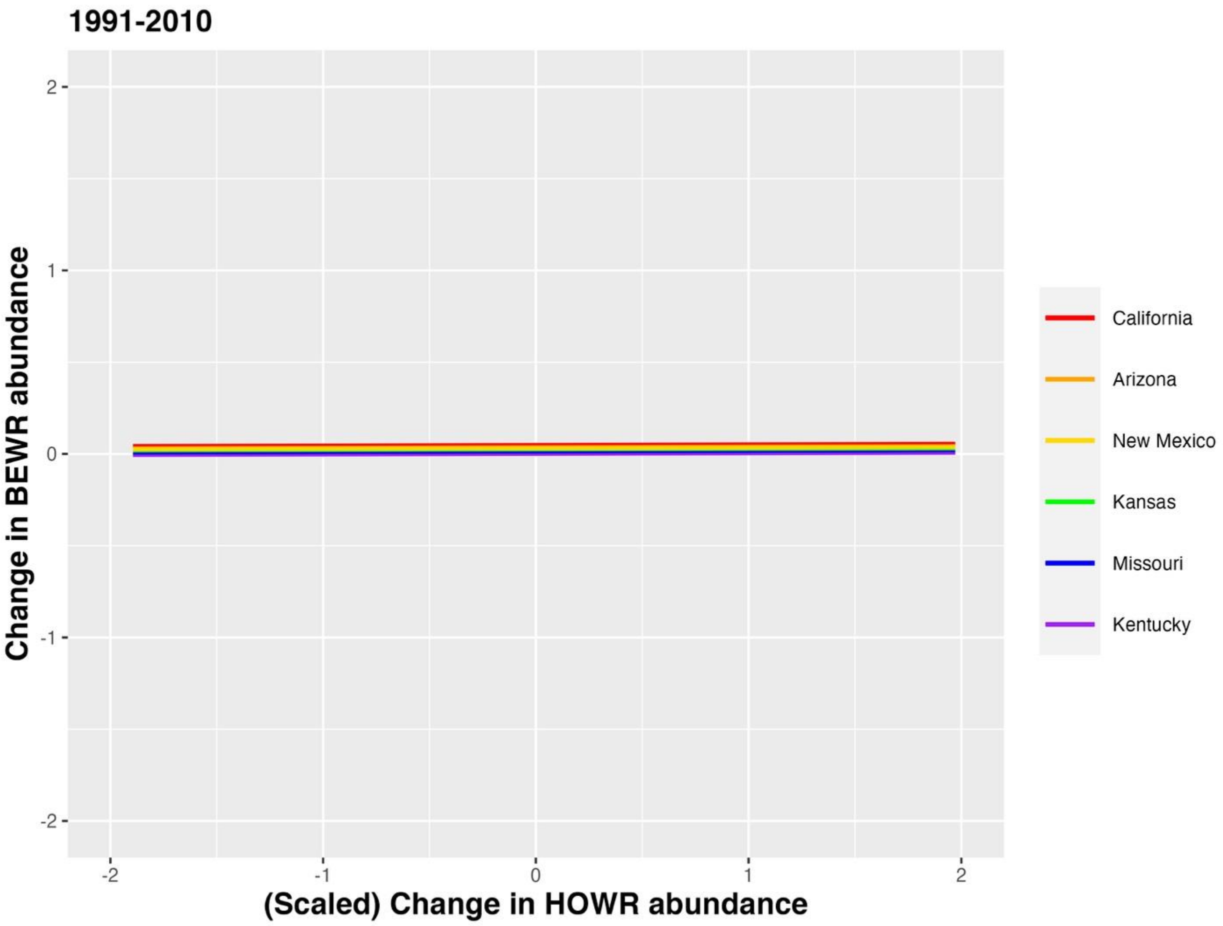
1991-2010
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Change in BEWR abundance
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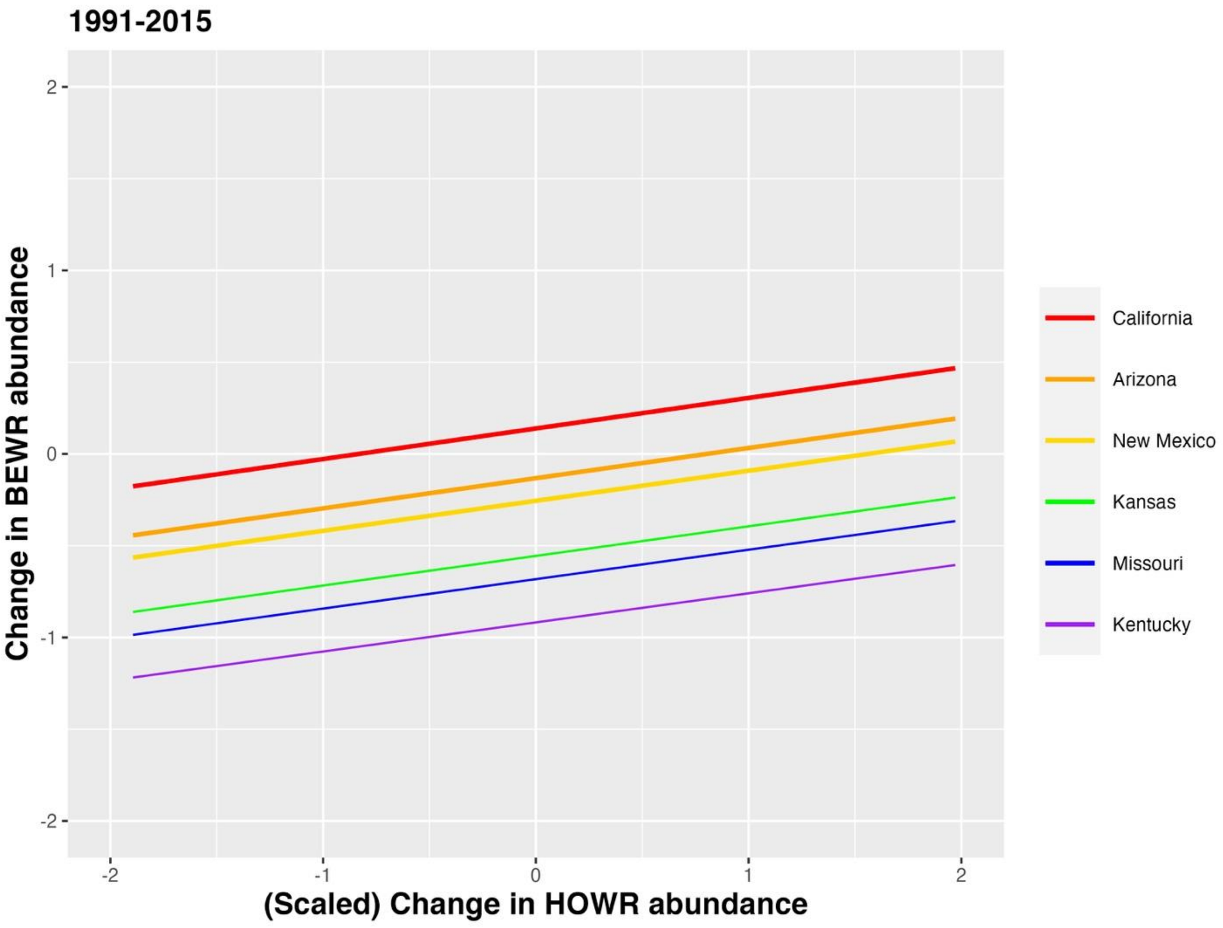
1991-2015
Change in BEWR abundance
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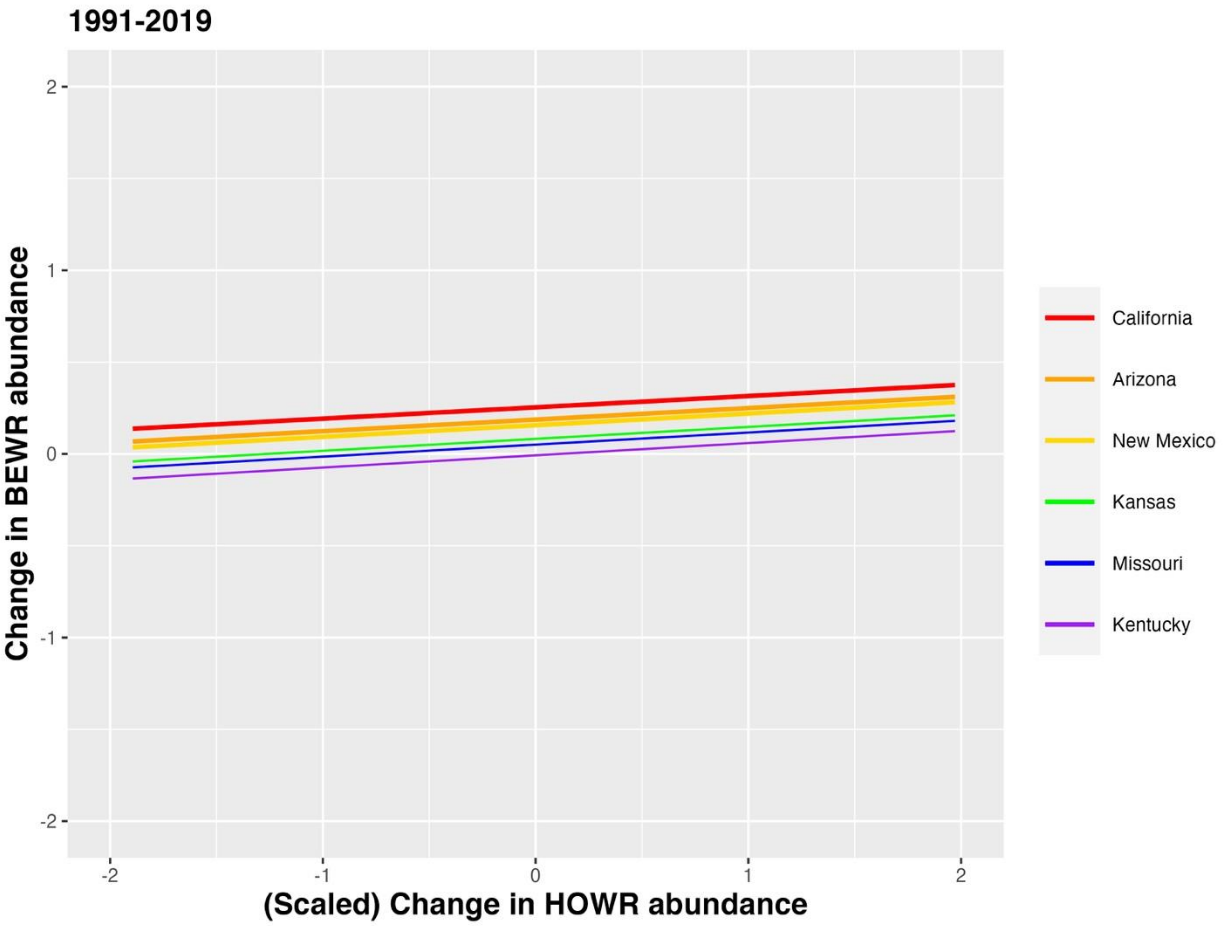
1991-2019
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Change in BEWR abundance
(Scaled) Change in HOWR abundance
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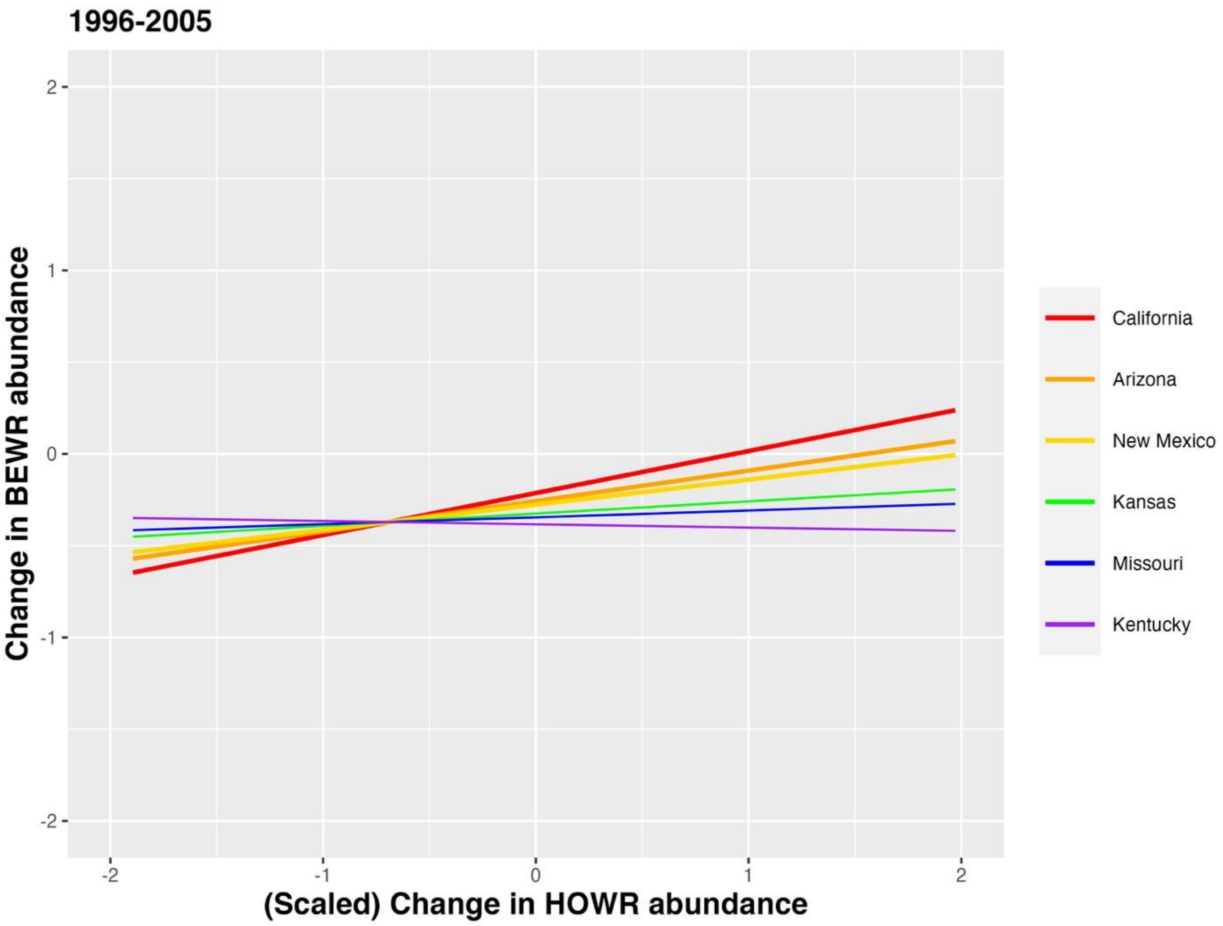
1996-2005
Change in BEWR abundance
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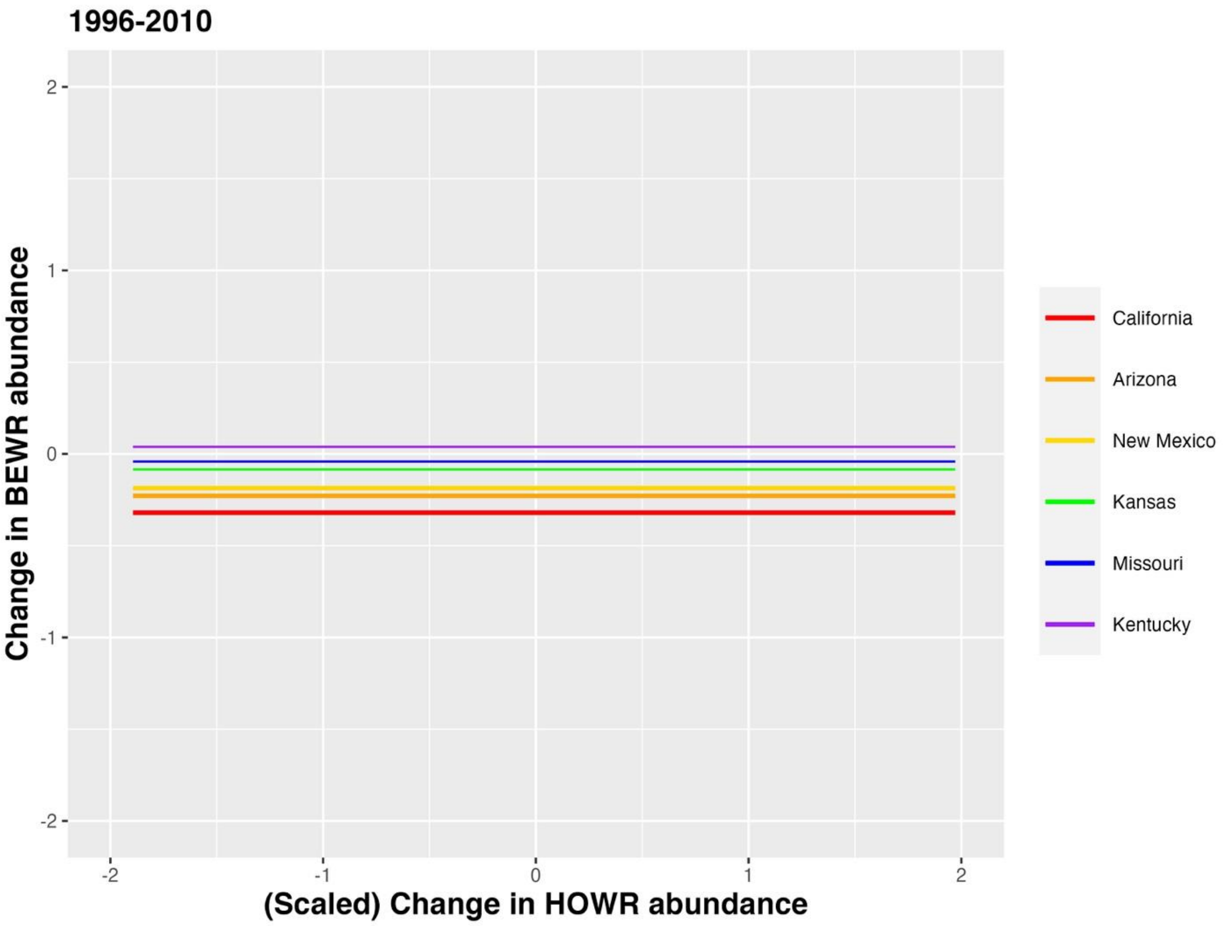
1996-2010
Change in BEWR abundance
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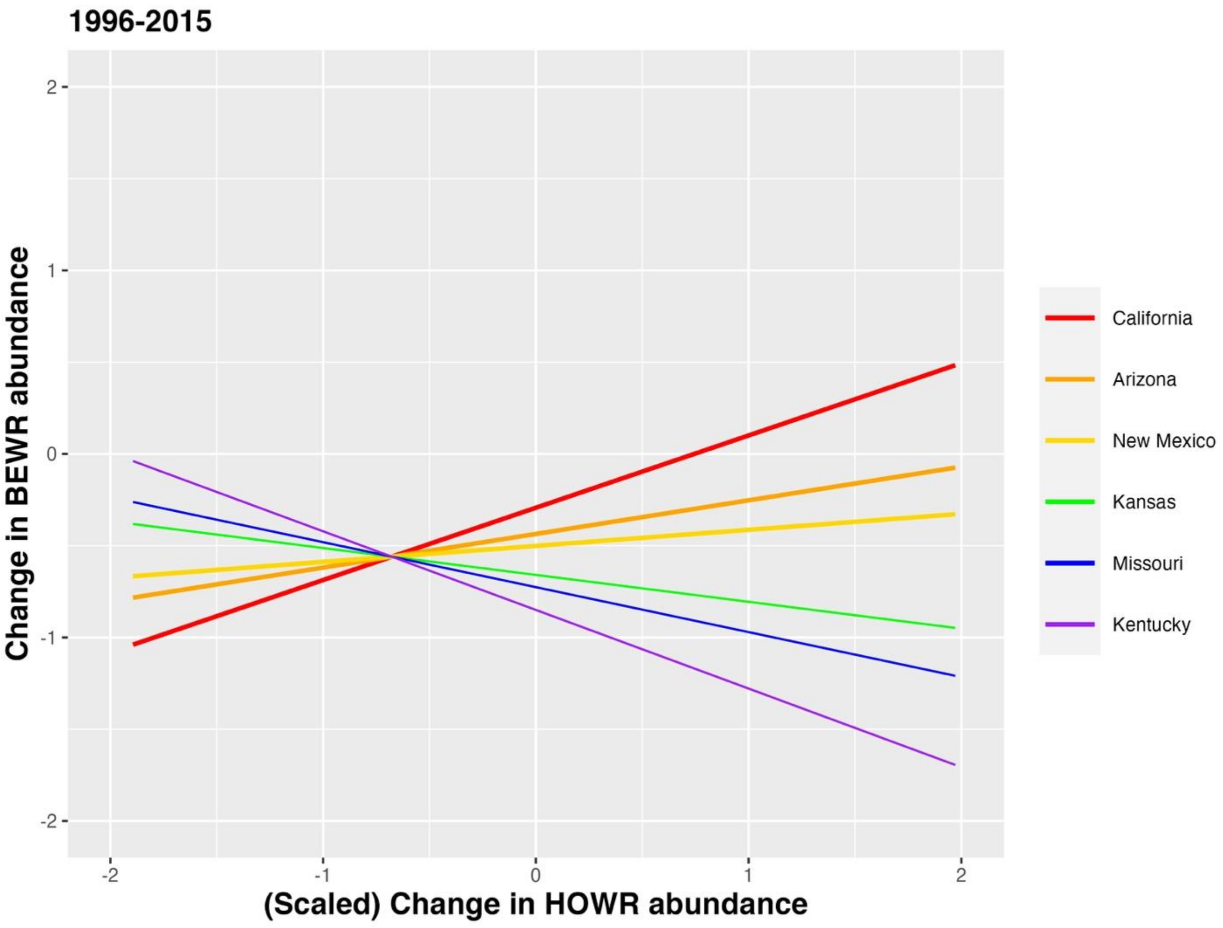
1996-2015
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Change in BEWR abundance
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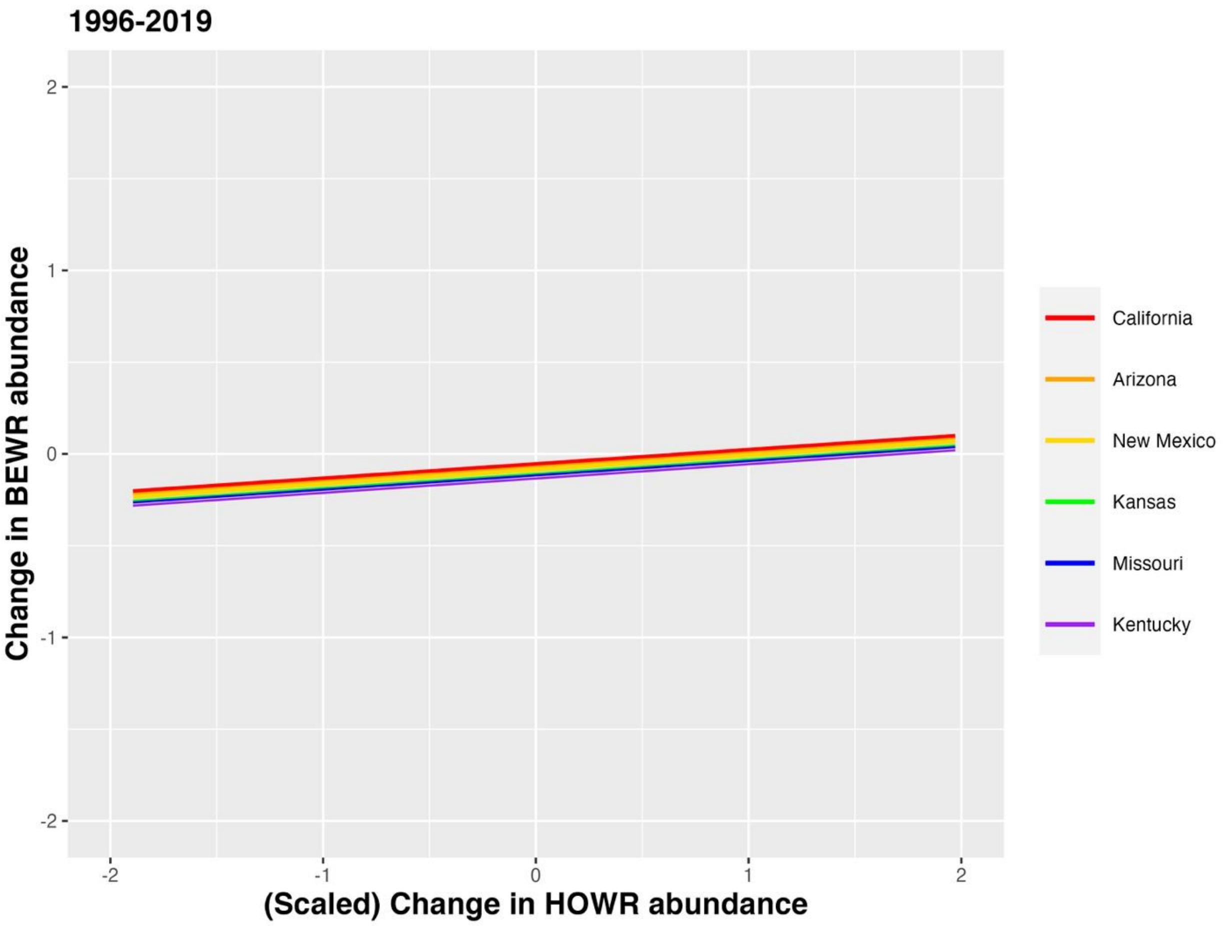
1996-2019
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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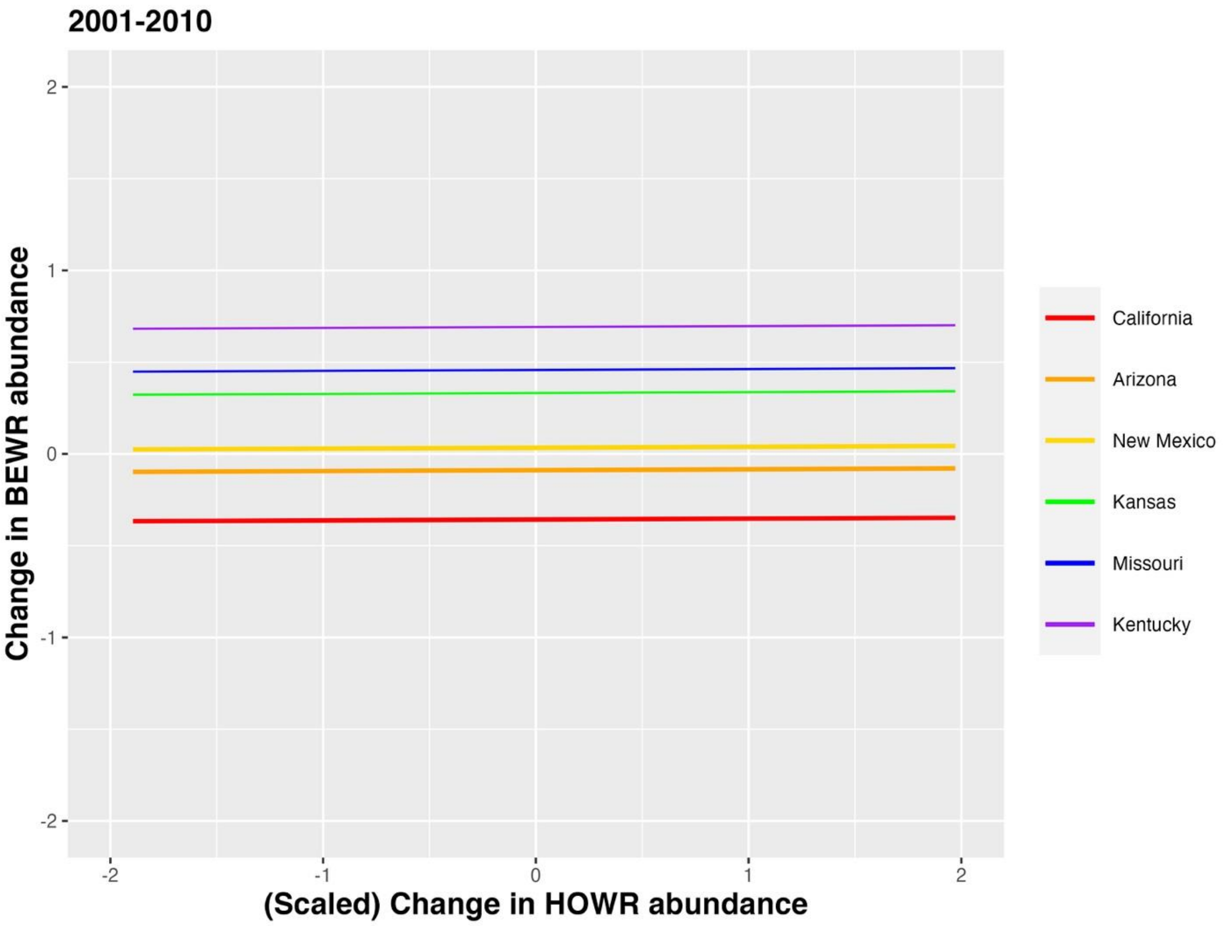
Kentucky


2001-2010
Change in BEWR abundance
2
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(Scaled) Change in HOWR abundance
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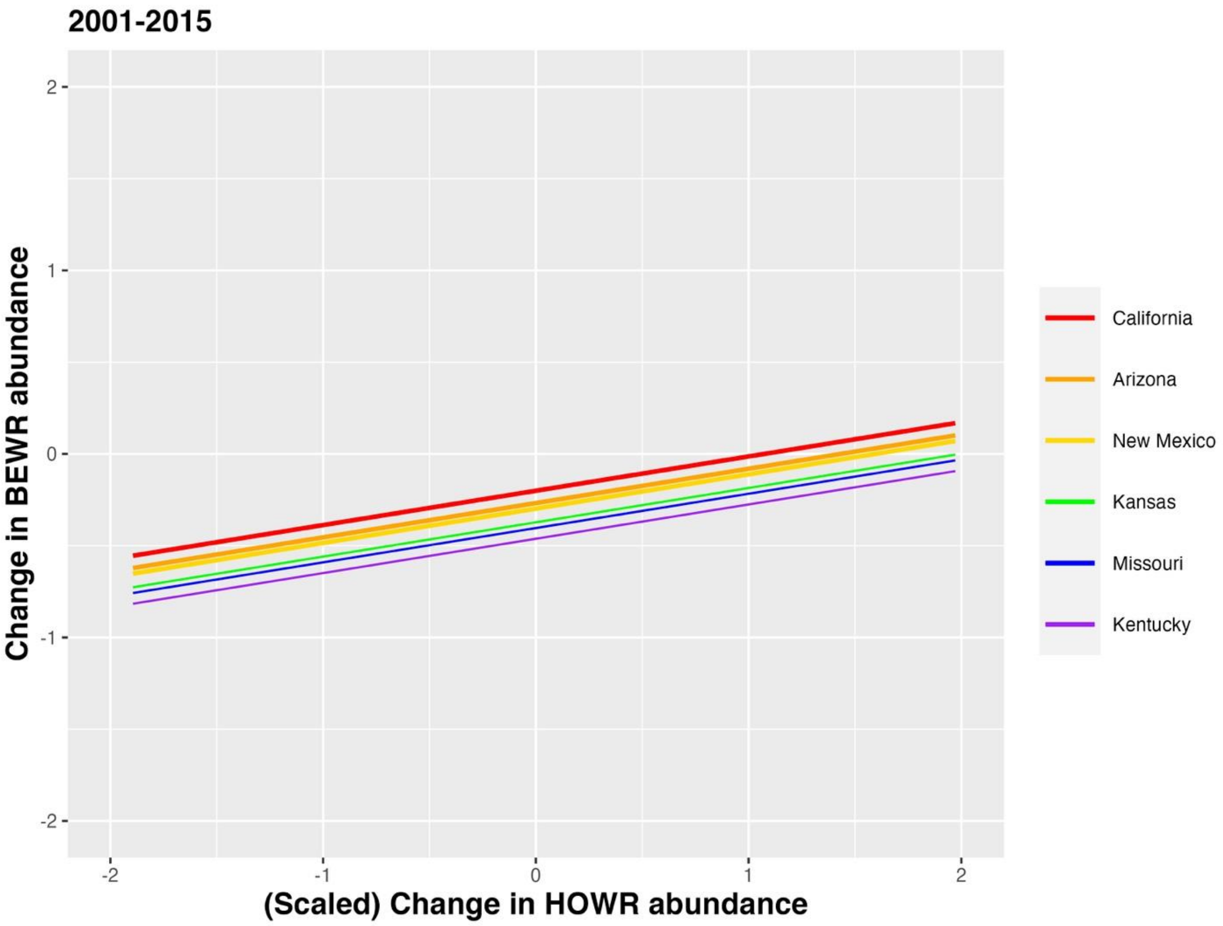
Missouri
Kentucky


2001-2015
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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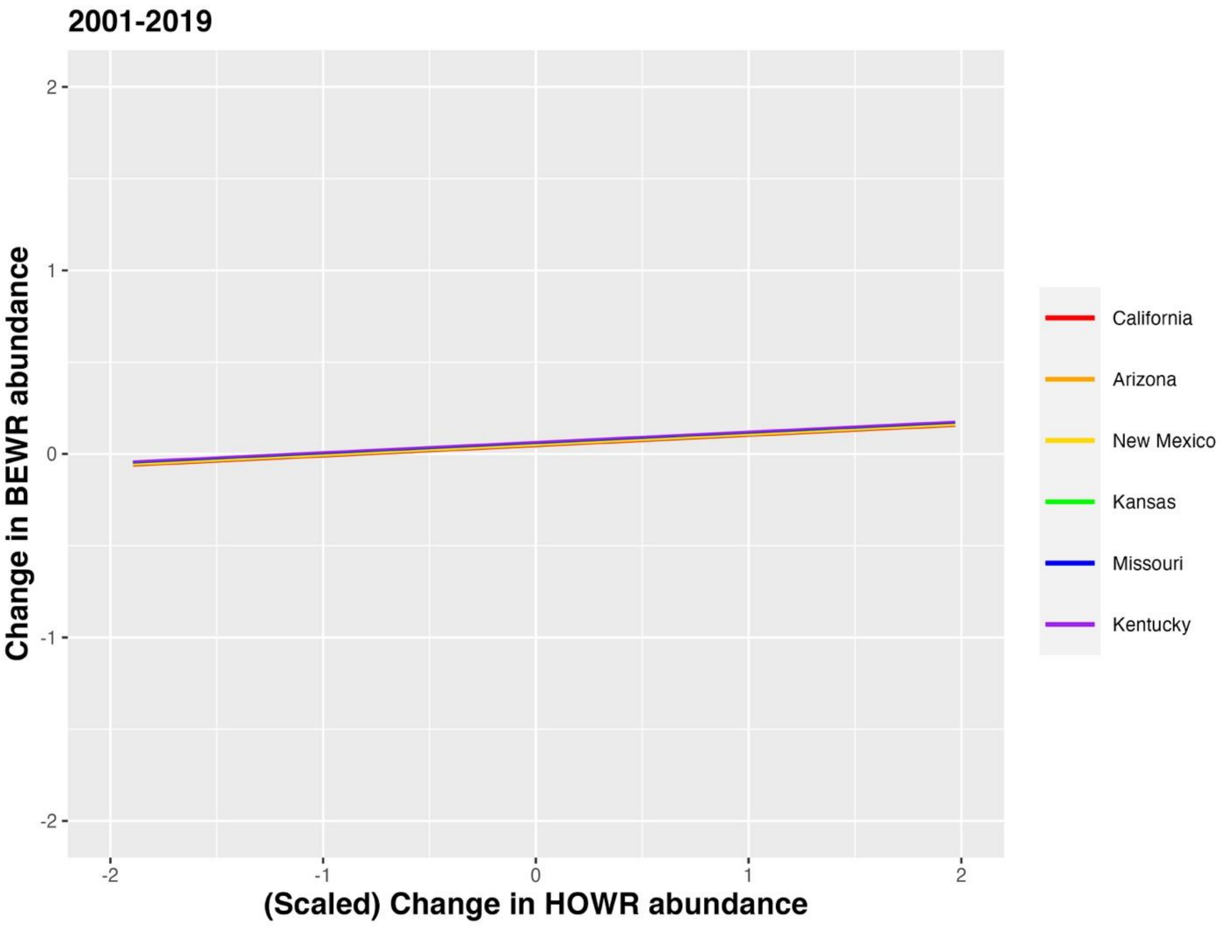
2001-2019
Change in BEWR abundance
2
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(Scaled) Change in HOWR abundance
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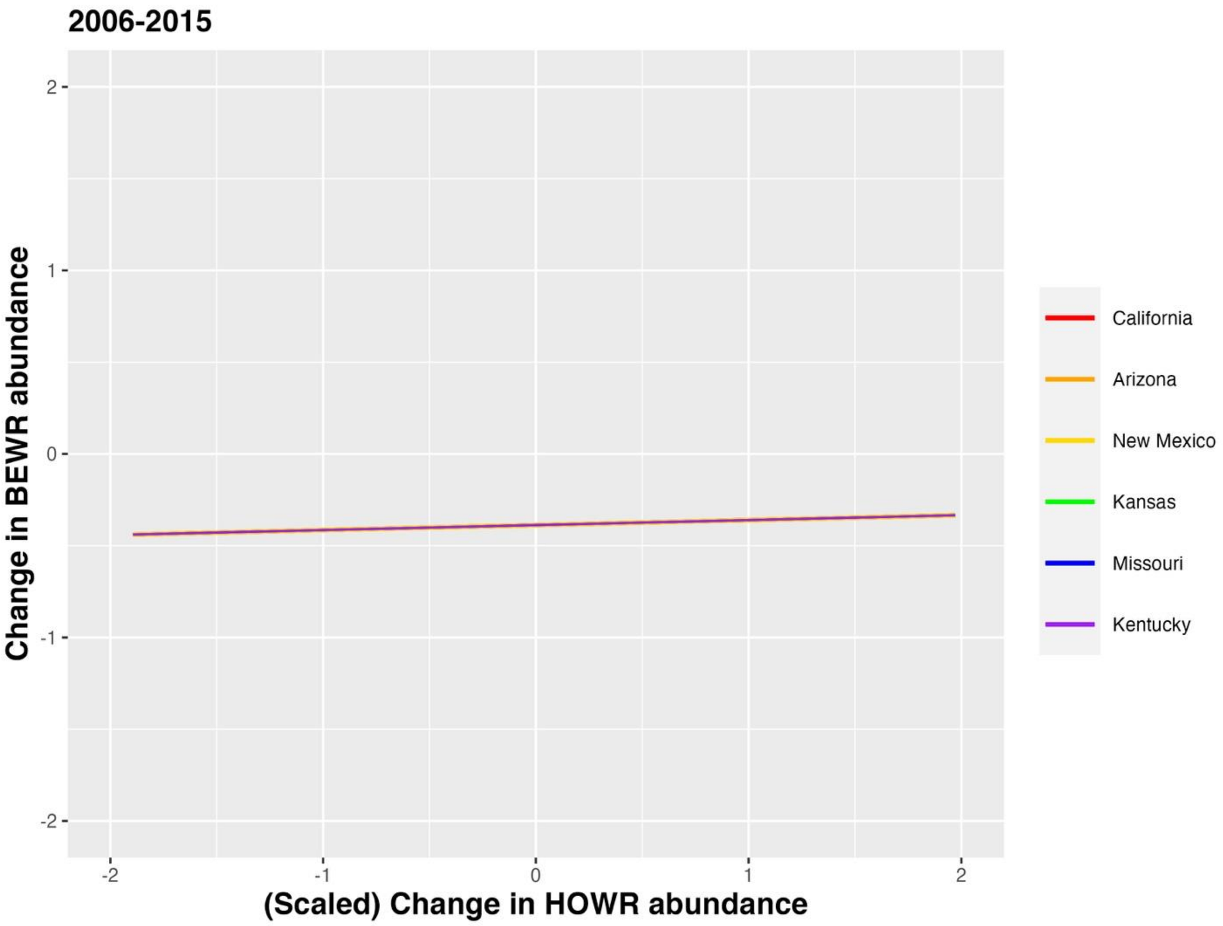
Kansas
Missouri
Kentucky


2006-2015
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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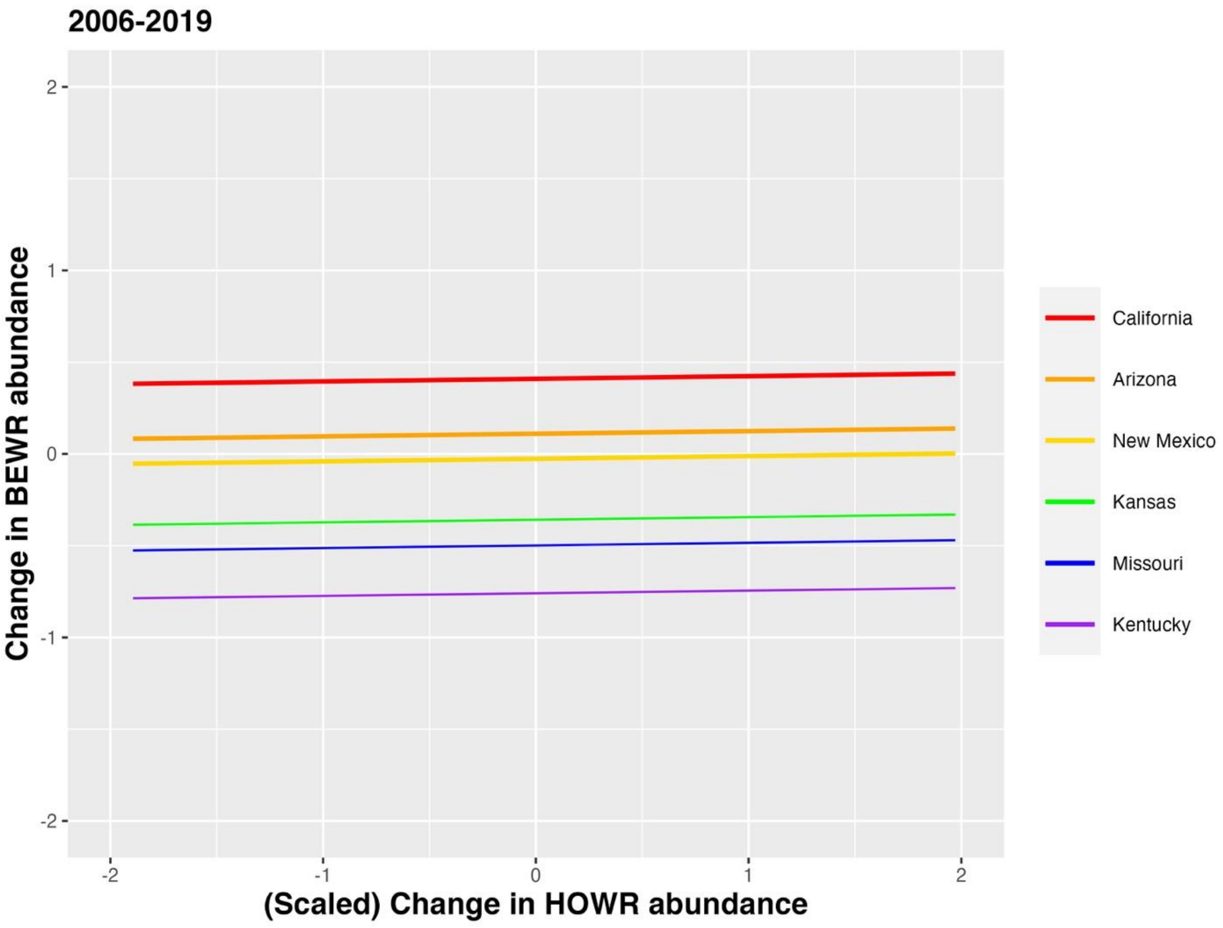
Kentucky


2006-2019
Change in BEWR abundance
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(Scaled) Change in HOWR abundance
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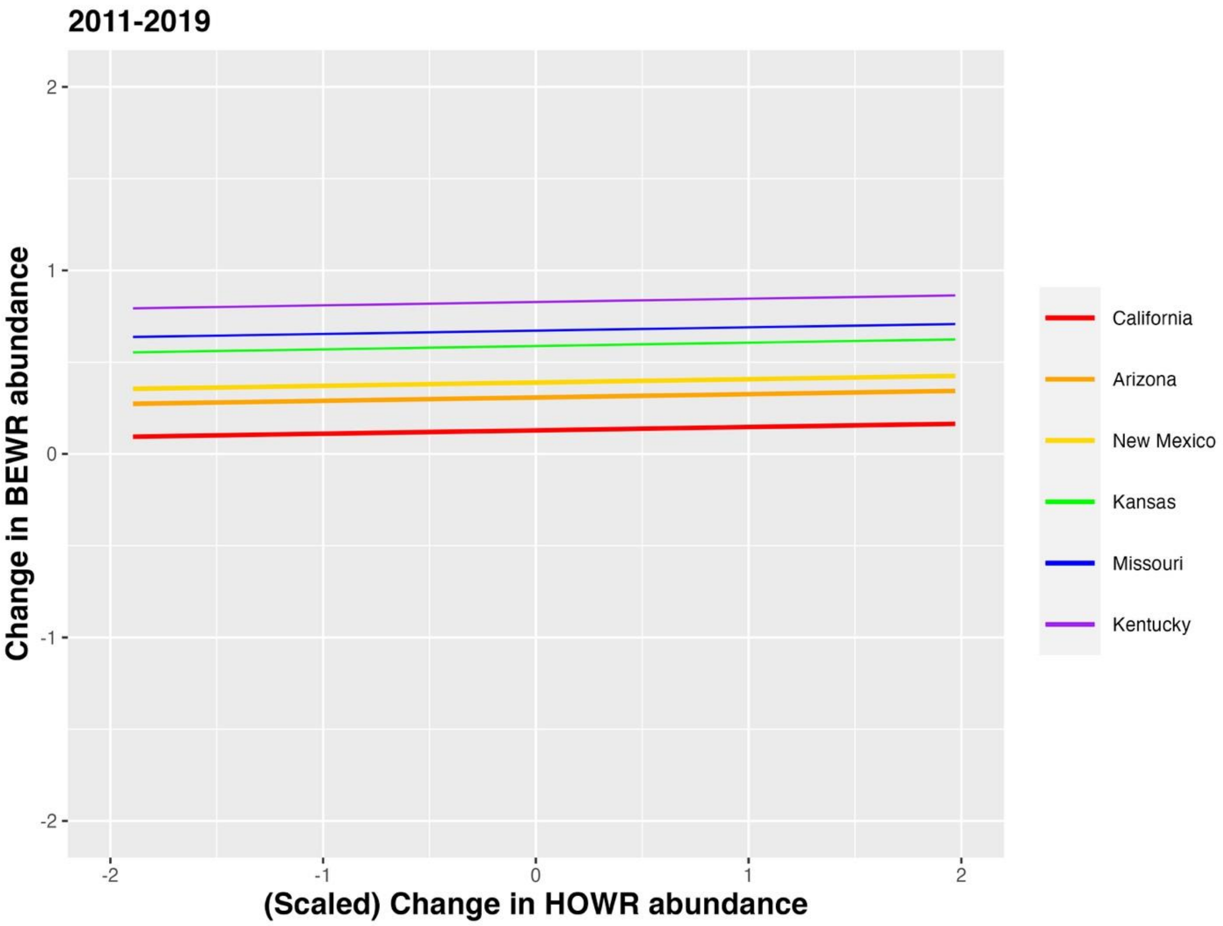
2011-2019
Change in BEWR abundance
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-2
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2
(Scaled) Change in HOWR abundance
California
Arizona
New Mexico
Kansas
Missouri
Kentucky