Niche modeling reveals life history shifts in birds at La Brea over the last twenty millennia

Robert M. Zink
*University of Nebraska - Lincoln*, rzink2@unl.edu

Sebastian Botero-Canola
*University of Nebraska - Lincoln*, sebastian.botero@huskers.unl.edu

Helen Martinez
*University of Nebraska - Lincoln*

Katelyn M. Herzberg
*University of Nebraska - Lincoln*

Follow this and additional works at: https://digitalcommons.unl.edu/natrespapers

Part of the Natural Resources and Conservation Commons, Natural Resources Management and Policy Commons, and the Other Environmental Sciences Commons

Zink, Robert M.; Botero-Canola, Sebastian; Martinez, Helen; and Herzberg, Katelyn M., "Niche modeling reveals life history shifts in birds at La Brea over the last twenty millennia" (2020). *Papers in Natural Resources*. 1075.
https://digitalcommons.unl.edu/natrespapers/1075

This Article is brought to you for free and open access by the Natural Resources, School of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Natural Resources by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.
Niche modeling reveals life history shifts in birds at La Brea over the last twenty millennia

Robert M. Zink,1,2,3*, Sebastian Botero-Cañola2,4, Helen Martinez5, Katelyn M. Herzberg5

1 School of Natural Resources, University of Nebraska, Lincoln, Nebraska, United States of America, 2 School of Biological Sciences, University of Nebraska, Lincoln, Nebraska, United States of America, 3 Nebraska State Museum, University of Nebraska, Lincoln, Nebraska, United States of America, 4 Harold W. Manter Laboratory of Parasitology, University of Nebraska, Lincoln, Nebraska, United States of America, 5 College of Agriculture and Natural Resources, University of Nebraska, Lincoln, Nebraska, United States of America

* rzink2@unl.edu

Abstract

A species presence at a particular site can change over time, resulting in temporally dynamic species pools. Ecological niche models provide estimates of species presence at different time intervals. The avifauna of La Brea includes approximately 120 species dating to approximately 15,000 years ago. Niche models predicted presence at the Last Glacial Maximum for over 90% of 89 landbird species. This confirms that niche modeling produces sensible range estimates at the Last Glacial Maximum. For 97 currently local species that are as yet undocumented at La Brea over 90% were predicted to occur; absence is due to insufficient study, lack of the ecological niche, transient occurrence or a behavioral ability to avoid entrapment. Our 366 niche models provide a prospective checklist of the landbird fauna of La Brea. The models indicate fluidity in life history strategies and a higher proportion of resident birds at the LGM (88% to 60%). We evaluated a subset of 103 species in breeding and winter periods using two climate models (MIROC–ESM, CCSM4) with a variety of differing parameters, finding differences in 5% of the niche models. Niche breadths in bark-foraging birds changed little between the present and LGM, suggesting that greater species diversity at the LGM was due to greater niche availability rather than contractions of niche breadths (i.e., niche partitioning).

Introduction

Lists of species from specific localities form the basis for many ecological analyses such as characterizing geographic patterns in species diversity and identifying high-priority conservation areas. Species lists from modern and recent localities have also been used to estimate species turnover over time [1,2]. Niche modeling is a major research tool for predicting past and future species’ distributions [3,4], which aid in understanding how community species composition changes over time. In most niche-model studies, predicted species distributions in the past were not informed by actual locality information, but rather through identifying where
the current niche conditions existed at that earlier time. Some recent studies have attempted to integrate paleodata, such as historical localities obtained from microfossils, to improve model predictions in past environments [5–8]. However, paleo records are lacking for many species, and most studies rely on projected ranges without direct testing of their accuracy. To validate such approaches, a densely sampled archaeological or Holocene site with a verified list of species, which can be compared to projected distributions from niche modeling using current records across a large sample of species, is needed.

Identified skeletal remains of animals entombed in the sticky tar at La Brea provide an opportunity to test whether distributions predicted by ecological niche models at the Last Glacial Maximum (LGM) overlap the site. The fauna of La Brea is a heterogeneous assemblage and not likely a random sample of what was in the area at a given time. For example, mammals are over-represented by large predators, such as dire wolves (*Canus dirus*) and sabre-tooth cats (*Smilodon fatalis*), which came to prey on entrapped ungulates, including camels (*Camelops hesternus*) and mastodons (*Mammut americanum*). In fact, over 90% of identified entombed large mammals are carnivores, leading La Brea to be known as a “carnivore trap”. Whether this reflects the species community surrounding La Brea, or the allure of large carnivores to paleontologists, is unclear. Nonetheless, many vertebrates have been preserved during the period of 10 to 30 thousand years ago (ka).

The avian assemblage of La Brea (Table 1) was documented by Howard [9–11]; see http://www.tarpits.org/research-collections/collections/bird-collections. The list is scheduled to be updated (K. Campbell, in litt. 22 Sept. 2017). Miller [12] noted that identified avian remains are biased towards large-bodied, mostly raptorial taxa. A total of 122 species (including 21 extinct) were identified; in five cases, tentative identifications were made to the species level owing to the difficulty in identifying many species, especially passerines, from skeletons alone. Several other specimens were identified to genus only. For example, no New World Wood Warblers were identified to species, instead warbler skeletons were referred to simply as “Indeterminate Parulinae”. The same generic identification was offered for orioles (“*Icterus spp.*”) and some sparrows (“Indeterminate Fringillidae”). In some cases, it appears that geography played a role. For example, the list includes the red-shafted flicker (*Colaptes auratus cafer*), which likely cannot be told apart from the yellow-shafted flicker (*Colaptes a. auratus*) by skeletal features alone (pers. obs.); however, only the former (sub)species occurs in that part of California, and therefore it is likely that the subspecies identification was based on current ranges. The list of species represents the pooling of individuals from different pits, which themselves differ in age and extent [11]; K. Campbell (in litt.) noted that the fossils from Rancho La Brea range from 10000 to 40000 yrs.

What is puzzling about the La Brea record is the absence of many passerine and other small-bodied birds that are today common in western North America, including hummingbirds, tanagers, nuthatches, titmice, vireos, wrens, thrushes, swallows, and flycatchers (identified remains include a single flycatcher species, *Tyrannus vociferans* (Cassin’s kingbird)). It is unclear whether they were not present near La Brea, they have simply not yet been identified among the currently unstudied remains, their remains have yet to be recovered, or they were present at the site but behaviorally unlikely to become entrapped. For example, perhaps aerial insectivores such as swifts or swallows avoided the tar. In addition, the list of passerines seems to include fewer migrant species than sedentary ones, and it is possible that migrants were in the area of La Brea too briefly during migration to become entrapped, at least in high enough frequency to have been detected to date. Changes in species diversity between the LGM and the present could be a result of changes in niche breadths or the number of niches for which the site presents suitable conditions at a given time, and testing these factors is possible through (climatic) niche modeling.
Table 1. List of species analyzed, presence in La Brea deposits, number of specimens and tar pit layers for each species, distance in km from La Brea to nearest predicted breeding occurrence at Last Glacial Maximum, distance in km from La Brea to nearest predicted wintering occurrence at Last Glacial Maximum, residency status at La Brea at the Last Glacial Maximum, and present status at La Brea (within 100 km). An asterisk indicates that the condition shown is most probable given the data.

| Common name             | Scientific name            | Present at La Brea | Number of specimens, number of pits | LGM: Distance (km) to predicted breeding | LGM: Distance (km) to winter prediction | LGM status | Present status |
|-------------------------|----------------------------|--------------------|-------------------------------------|------------------------------------------|----------------------------------------|------------|----------------|
| Acorn Woodpecker        | Melanerpes formicivorus    | N                  | NA                                  | 0                                       | 0                                      | resident   | resident       |
| Allen’s Hummingbird     | Selasphorus sasin          | N                  | NA                                  | 0                                       | 0                                      | resident   | resident       |
| American Crow           | Corvus brachyrhynchos      | Y                  | 22,7                                | 5                                       | 0                                      | resident   | resident       |
| American dipper         | Cinclus mexicanus          | N                  | NA                                  | 5                                       | 0                                      | resident   | resident       |
| American Goldfinch      | Spinus tristis             | Y                  | 3,1                                 | 0                                       | 0                                      | resident   | winter         |
| American Kestrel        | Falco sparverius           | Y                  | 79,11                               | 0                                       | 0                                      | resident   | resident       |
| American Pipit          | Anthus rubescens           | N                  | NA                                  | 0                                       | 0                                      | resident   | winter         |
| American Robin          | Turdus migratorius         | Y                  | 18,3                                | 0                                       | 0                                      | resident   | resident       |
| Anna’s Hummingbird      | Calypte anna               | N                  | NA                                  | 0                                       | 0                                      | resident   | resident       |
| Ash-throated flycatcher | Tyrannus vociferans        | Y                  | 4,1                                 | 0                                       | 0                                      | resident   | breeding       |
| Bald Eagle              | Haliaeetus leucocephalus   | Y                  | 175,10                               | 5                                       | 0                                      | resident   | winter         |
| Band-tailed Pigeon      | Patagioenas fasciata       | Y                  | 3,3                                 | 0                                       | 0                                      | resident   | resident       |
| Barn Owl                | Tyto alba                  | Y                  | 205,10                               | 0                                       | 0                                      | resident   | resident       |
| Barn Swallow            | Hirundo rustica            | N                  | NA                                  | 0                                       | 0                                      | resident   | breeding       |
| Bell’s Sparrow          | Artemisiospiza belli       | Y                  | 6                                    | 0                                       | 0                                      | resident   | resident       |
| Bell’s Vireo            | Vireo bellii               | N                  | NA                                  | 0                                       | 0                                      | resident   | breeding       |
| Belted Kingfisher       | Megaceryle alcyon          | N                  | NA                                  | 0                                       | 0                                      | resident   | winter         |
| Bendire’s thrasher      | Toxostoma bendirei         | N                  | NA                                  | 80                                      | 200                                    | breeding   | not present    |
| Bewick’s Wren           | Thryomanes bewickii        | N                  | NA                                  | 0                                       | 0                                      | resident   | resident       |
| Black Phoebe            | Sayornis nigricans         | N                  | NA                                  | 0                                       | 0                                      | resident   | resident       |
| Black Swift             | Cypseloides niger          | N                  | NA                                  | 0                                       | 15                                     | resident   | breeding       |
| Black-backed woodpecker | Picoideas arcticus         | N                  | NA                                  | 25                                      | 50                                     | resident   | not present    |
| Black-chinned Hummingbird | Archilochus alexandri    | N                  | NA                                  | 0                                       | 0                                      | resident   | breeding       |
| Black-chinned Sparrow   | Spizella atrogularis       | N                  | NA                                  | 0                                       | 150                                    | breeding   | breeding       |
| Black-headed Grosbeak   | Pheucticus melanoccephalus | Y                  | 1,1                                 | 0                                       | 0                                      | resident   | breeding       |
| Black-throated Gray Warbler | Setophaga nigrescens    | ?                   | ?                                   | >500                                    | 700                                    | not present| breeding       |
| Black-throated Sparrow  | Amphispiza bilineata       | Y                  | 4,1                                 | 45                                      | 80                                     | resident   | breeding’      |
| Blue Grosbeak           | Passerina caerulea         | N                  | NA                                  | 70                                      | 0                                      | resident   | breeding       |
| Blue-gray Gnatcatcher   | Poliostia caerulea         | N                  | NA                                  | 0                                       | 0                                      | resident   | resident       |
| Bohemian Waxwing        | Bombycilla garrulus        | N                  | NA                                  | 100                                     | 50                                     | winter     | winter         |
| Brea owl                | Oraristrix brea            | Y                  | 23,1                                |                                          |                                        | resident?  | not present    |
| Brewer’s Blackbird      | Euphagus cyanoccephalus    | ?                   | ?                                   | 0                                       | 0                                      | resident   | resident       |
| Brown Creeper           | Certhia americana          | N                  | NA                                  | 0                                       | 0                                      | resident   | resident’      |
| Brown-headed cowbird    | Molothrus ater             | Y                  | 1,1                                 | 0                                       | 0                                      | resident   | resident       |

(Continued)
| Common name          | Scientific name              | Present at La Brea | Number of specimens, number of pits | LGM: Distance (km) to predicted breeding | LGM: Distance (km) to winter prediction | LGM status | Present status |
|----------------------|------------------------------|--------------------|-------------------------------------|------------------------------------------|------------------------------------------|------------|----------------|
| Bullock’s Oriole     | Icterus bullockii            | ?                  | ?                                   | 0                                        | 0                                        | resident   | breeding       |
| Burrowing Owl        | Athene cunicularia           | Y                  | 228,9                               | 50                                       | 0                                        | resident   | resident       |
| Bush tit             | Psaltriparus minimus         | N                  | NA                                  | 0                                        | 0                                        | resident   | resident       |
| Cactus Wren          | Campylorhynchus brunneicapillus | N               | NA                                  | 500                                      | 20                                       | winter     | resident       |
| California Condor    | Gymnogyps californianus      | N                  | NA                                  | 0                                        | 0                                        | resident   | breeding       |
| California Gnatcatcher | Polioptila californica     | N                  | NA                                  | 0                                        | 0                                        | resident   | resident       |
| California Quail     | Callipepla californica       | Y                  | 138,7                               | 0                                        | 0                                        | resident   | resident       |
| California Scrub-jay | Apelocoma californica        | Y                  | 8,3                                 | 0                                        | 0                                        | resident   | resident       |
| California Thrasher  | Toxostoma redivivum          | Y                  | 6,3                                 | 0                                        | 0                                        | resident   | resident       |
| California Towhee    | Melozone crissalis           | Y                  | 2,1                                 | 0                                        | 0                                        | resident   | resident       |
| Calliope Hummingbird | Selasphorus calliope         | N                  | NA                                  | 25                                       | 0                                        | resident   | breeding       |
| Canyon Wren          | Catherpes mexicanus          | N                  | NA                                  | 0                                        | 0                                        | resident   | resident       |
| Cassin’s Finch       | Haemorhous cassinii          | N                  | NA                                  | 15                                       | 20                                       | resident   | resident       |
| Cassin’s kingbird    | Tyrannus vociferans          | N                  | NA                                  | 0                                        | 20                                       | resident   | breeding       |
| Cassin’s Vireo       | Vireo cassinii               | N                  | NA                                  | 0                                        | 5                                        | resident   | breeding       |
| Cedar Waxwing        | Bombycilla cedrorum          | Y                  | ?                                   | 5                                        | 0                                        | resident   | winter          |
| Chestnut-backed Chickadee | Poecile rufescens      | ?                  | ?                                   | 0                                        | 0                                        | resident   | not present    |
| Chihuahuan Raven     | Corvus cryptoleucus          | Y                  | 1,1                                 | 200                                      | 500                                      | not present| not present    |
| Chipping Sparrow     | Spizella passerina           | Y                  | 6,6                                 | 0                                        | 0                                        | resident   | resident       |
| Clark’s nutcracker   | Nucifraga columbiana         | Y                  | 2,1                                 | 35                                       | 20                                       | resident   | resident*       |
| Cliff Swallow        | Petrochelidon pyrrhonota    | N                  | NA                                  | 0                                        | 0                                        | resident   | breeding       |
| Common Poorwill      | Phalaenoptilus nuttallii     | Y                  | 7,1                                 | 0                                        | 0                                        | resident   | resident       |
| Common Raven         | Corvus corax                 | Y                  | 114,13                              | 0                                        | 0                                        | resident   | resident       |
| Common Yellowthroat  | Geothlypis trichas           | ?                   | ?                                   | 30                                       | 0                                        | resident   | resident       |
| Cooper’s Hawk        | Accipiter cooperi            | Y                  | 52,8                                | 0                                        | 0                                        | resident   | resident       |
| Costa’s Hummingbird  | Calypte costae               | N                  | NA                                  | 0                                        | 0                                        | resident   | resident       |
| Crissal Thrasher     | Toxostoma crissale           | N                  | NA                                  | 150                                      | 100                                      | not present| not present    |
| Dark-eyed Junco (Oregon) | Junco hyemalis              | N                  | NA                                  | 0                                        | 0                                        | resident   | resident       |
| Downy Woodpecker     | Picoides pubescens           | N                  | NA                                  | 0                                        | 0                                        | resident   | resident       |
| Dusky Flycatcher     | Empidonax oberholseri        | N                  | NA                                  | 20                                       | NC                                       | breeding   | breeding       |
| Evening Grosbeak     | Coccothraustes vespertinus   | Y                  | 1,1                                 | 5                                        | 0                                        | resident   | winter          |
| Extinct blackbird    | Euphagus magnostris          | Y                  | 1,1                                 | 0                                        | 0?                                       | resident?  | not present*    |
| Extinct Icterid      | Pandanaris convexa           | Y                  | 1,1                                 | 0                                        | 0?                                       | resident?  | not present*    |
| Extinct towhee       | Melozone angelensis          | Y                  | 11,1                                | 0                                        | 0?                                       | resident?  | not present*    |
| Ferruginous Hawk     | Bateo regalis                | Y                  | 127,13                              | 100                                      | 0                                        | resident   | winter          |
| Flammulated Owl      | Psiloscops flammeolus        | N                  | NA                                  | 15                                       | 0                                        | resident   | breeding       |

(Continued)
| Common name          | Scientific name                  | Present at La Brea | Number of specimens, number of pits | LGM: Distance (km) to predicted breeding | LGM: Distance (km) to winter prediction | LGM status | Present status |
|----------------------|----------------------------------|--------------------|-------------------------------------|------------------------------------------|----------------------------------------|------------|----------------| 
| Fox Sparrow          | Passerella iliaca               | Y                  | 2,1                                 | 0                                        | 0                                      | resident   | resident       |
| Gambel’s Quail       | Callipepla gambelii             | N                  | NA                                  | 50                                       | 100                                    | breeding   | resident       |
| Golden Eagle         | Aquila chrysaetos               | Y                  | 960,12                              | 0                                        | 0                                      | resident   | resident       |
| Golden-crowned Kinglet | Regulus satrapa              | N                  | NA                                  | 0                                        | 0                                      | resident   | resident, winter |
| Golden-crowned Sparrow | Zonotrichia atricapilla     | N                  | NA                                  | 0                                        | 0                                      | resident   | winter          |
| Grasshopper Sparrow  | Ammodramus savannarum           | N                  | NA                                  | 10                                       | 0                                      | resident   | breeding       |
| Gray Flycatcher      | Empidonax wrightii              | N                  | NA                                  | 20                                       | NC                                     | breeding   | breeding       |
| Great Horned Owl     | Bubo virginianus                | Y                  | 128,12                              | 2                                        | 0                                      | resident   | resident       |
| Greater Roadrunner   | Geococcyx californianus         | Y                  | 25,6                                | 10                                       | 0                                      | resident   | resident       |
| greater sage grouse | Centrocercus urophasianus       | N                  | NA                                  | 55                                       | 80                                     | breeding   | not present    |
| Green-tailed Towhee  | Pipilo chlorurus                | N                  | NA                                  | 15                                       | 0                                      | resident   | resident       |
| Hairy Woodpecker     | Leuconotopicus villosus         | N                  | NA                                  | 0                                        | 0                                      | resident   | resident       |
| Hammond’s Flycatcher | Empidonax hammondii            | N                  | NA                                  | 0                                        | NC                                     | breeding   | breeding       |
| Hermit Thrush        | Catharus guttatus              | N                  | NA                                  | 15                                       | 0                                      | resident   | winter          |
| Hermit Warbler       | Setophaga occidentalis          | ?                  | ?                                   | 0                                        | 10                                     | resident   | breeding’       |
| Hooded Oriole        | Icterus cucullatus             | ?                  | ?                                   | 0                                        | >500                                   | breeding   | breeding        |
| Horned Lark          | Eremophila alpestris            | Y                  | 1,1                                 | 10                                       | 0                                      | resident   | resident       |
| House Finch          | Haemorhous mexicanus           | N                  | NA                                  | 0                                        | 150                                    | resident   | resident       |
| House Wren           | Troglydotes aedon               | N                  | NA                                  | 0                                        | 0                                      | resident   | resident       |
| Hutton’s Vireo       | Vireo hattoni                   | N                  | NA                                  | 0                                        | 0                                      | resident   | resident       |
| Lark Sparrow         | Chondestes grammacus           | Y                  | 3,1                                 | 0                                        | 0                                      | resident   | resident       |
| Lawrence’s Goldfinch | Spinus lawrencei               | N                  | NA                                  | 0                                        | 0                                      | resident   | resident       |
| Lazuli Bunting       | Passerina amoena               | N                  | NA                                  | 0                                        | 5                                      | resident   | breeding       |
| LeConte’s Thrasher   | Toxostoma lecontei             | N                  | NA                                  | 100                                      | 100                                    | not present| resident      |
| Lesser Goldfinch     | Spinus psaltria                 | N                  | NA                                  | 0                                        | 0                                      | resident   | resident       |
| Lesser Nighthawk     | Chordeiles acutipennis         | N                  | NA                                  | 60                                       | 700                                    | breeding   | breeding       |
| Lewis’s Woodpecker   | Melanerpes lewis                | Y                  | 7,3                                 | 3                                        | 0                                      | resident   | winter          |
| Lincoln’s Sparrow    | Melospiza lincolni              | N                  | NA                                  | 20                                       | 0                                      | resident   | winter          |
| Loggerhead Shrike    | Lanius ludovicianus            | Y                  | 3,2                                 | 0                                        | 0                                      | resident   | resident       |
| Long-eared owl       | Asio otus                       | N                  | NA                                  | 0                                        | 0                                      | resident   | resident       |
| MacGillivray’s Warbler | Geothlypis tolmidie        | ?                  | ?                                   | 5                                        | 500                                    | breeding   | breeding       |
| Marsh Wren           | Cistothorus palustris           | N                  | NA                                  | 0                                        | 0                                      | resident   | winter          |
| Merlin               | Falco columbarius               | Y                  | 16,8                                | 25                                       | 0                                      | resident   | winter          |
| Mountain Bluebird    | Sialia currucoides             | ?                  | ?                                   | 30                                       | 0                                      | resident   | resident’       |
| Mountain Chickadee   | Poecile gambeli                 | ?                  | ?                                   | 10                                       | 0                                      | resident   | resident       |
| Mountain Quail       | Oreortyx pictus                | N                  | NA                                  | 0                                        | 0                                      | resident   | resident       |
| Mourning Dove        | Zenaida macroura                | Y                  | 30,6                                | 0                                        | 0                                      | resident   | resident       |
| Nashville Warbler    | Oreothlypis ruficapilla         | ?                  | ?                                   | 20                                       | 0                                      | resident   | breeding’       |
| Northern Goshawk     | Accipiter gentilis             | Y                  | 2,1                                 | 10                                       | 5                                      | resident   | winter          |
| Northern Harrier     | Circus hudsonius               | Y                  | 164,11                              | 0                                        | 0                                      | resident   | resident       |
Table 1. (Continued)

| Common name                  | Scientific name            | Present at La Brea | Number of specimens, number of pits (LGM) to predicted breeding | LGM: Distance (km) to winter prediction | LGM status | Present status |
|------------------------------|-----------------------------|--------------------|------------------------------------------------------------------|----------------------------------------|------------|----------------|
| Northern Mockingbird         | Mimus polyglottos           | N                  | NA                                                               | 35                                     | 0          | resident       |
| Northern Pygmy-Owl           | Glaucidium gnoma            | Y                  | 5,1                                                             | 0                                      | 0          | resident       |
| Northern Rough-winged Swallow| Stelgidopteryx serripennis  | N                  | NA                                                               | 0                                      | 0          | resident       |
| Northern Saw-whet Owl        | Asio flammeus               | N                  | NA                                                               | 0                                      | 0          | resident       |
| Nuttall's Woodpecker         | Picoides nuttallii          | N                  | NA                                                               | 0                                      | 0          | resident       |
| Oak Titmouse                 | Baeolophus inornatus        | N                  | NA                                                               | 0                                      | 0          | resident       |
| Olive-sided Flycatcher       | Empidonax difficilis        | N                  | NA                                                               | 0                                      | 0          | resident       |
| Pacific Wren                 | Troglodytes pacificus       | N                  | NA                                                               | 0                                      | 0          | resident       |
| Pacific-slope Flycatcher     | Empidonax difficilis        | N                  | NA                                                               | 0                                      | NC         | breeding       |
| Passenger Pigeon             | Ectopistes migratorius      | Y                  | 3,3                                                             | 125                                    | NC         | resident       |
| Peregrine Falcon             | Falco peregrinus            | Y                  | 29,9                                                            | 0                                      | 0          | resident       |
| Phainopepla                  | Phainopepla nitens          | N                  | NA                                                               | 0                                      | 0          | resident       |
| Pileated Woodpecker          | Dryocopus pileatus          | Y                  | 1,1                                                             | 0                                      | 0          | resident       |
| Pine Siskin                  | Spinus pinus                | Y                  | ?                                                               | 0                                      | 0          | resident       |
| Prairie Falcon               | Falco mexicanus             | Y                  | 24,10                                                           | 0                                      | 0          | resident       |
| Purple Finch                 | Haemorhous purpureus        | N                  | NA                                                               | 1200                                   | 0          | resident       |
| Pygmy Nuthatch               | Sitta pygmaea               | N                  | NA                                                               | 0                                      | 0          | resident       |
| Red crossbill                | Loxia curvirostra           | N                  | NA                                                               | 0                                      | 0          | resident       |
| Red-breasted Nuthatch        | Sitta canadensis            | N                  | NA                                                               | 0                                      | 0          | resident       |
| Red-breasted Sapsucker       | Sphyrapicus ruber           | Y                  | 1,1                                                             | 0                                      | 0          | resident       |
| Red-shouldered Hawk          | Bateo lineatus              | ?                  | ?                                                               | 0                                      | 0          | resident       |
| Red-tailed Hawk              | Bateo jamaicensis           | Y                  | 108,13                                                          | 0                                      | 0          | resident       |
| Red-winged Blackbird         | Agelaius phoeniceus         | ?                  | ?                                                               | 0                                      | 0          | resident       |
| Rock Wren                    | Salpinx obsoletus           | N                  | NA                                                               | 20                                     | 0          | resident       |
| Rough-legged Hawk            | Buteo lagopus               | Y                  | 7,4                                                             | 200                                    | 10         | winter not present |
| Ruby-crowned Kinglet         | Regulus calendula           | N                  | NA                                                               | 0                                      | 0          | resident       |
| Rufous hummingbird           | Selasphorus rufus           | N                  | NA                                                               | 0                                      | 0          | resident       |
| Rufous-crowned Sparrow       | Aimophila ruficeps          | N                  | NA                                                               | 0                                      | 0          | resident       |
| Sage Thrasher                | Oreoscoptes montanus        | Y                  | 1,1                                                             | 70                                     | 0          | resident       |
| Savannah Sparrow             | Passer domesticus montanus  | N                  | NA                                                               | 0                                      | 0          | resident       |
| Say's Phoebe                 | Sayornis saya               | N                  | NA                                                               | 45                                     | 0          | resident       |
| Scott's Oriole               | Icterus parisorum           | N                  | NA                                                               | 50                                     | 0          | resident       |
| Sharp-shinned Hawk           | Accipiter striatus velox    | Y                  | 5,4                                                             | 5                                      | 0          | resident       |
| Short-eared Owl              | Asio flammeus               | Y                  | 157,12                                                          | 40                                     | 0          | resident       |
| Song Sparrow                 | Melospiza melodia           | Y                  | 10,1                                                            | 0                                      | 0          | resident       |
| Sooty Grouse                 | Dendragapus fuliginosus     | N                  | NA                                                               | 5                                      | 0          | resident       |
| Spotted Owl                  | Strix occidentalis          | N                  | NA                                                               | 0                                      | 0          | resident       |

(Continued)
| Common name      | Scientific name     | Present at La Brea | Number of specimens, number of pits | LGM: Distance (km) to predicted breeding | LGM: Distance (km) to winter prediction | LGM status | Present status |
|------------------|---------------------|--------------------|--------------------------------------|------------------------------------------|------------------------------------------|------------|----------------|
| Spotted Towhee   | Pipilo maculatus    | Y                  | 4,1                                  | 0                                        | 0                                        | resident   | resident       |
| Steller’s Jay    | Cyanocitta stelleri | Y                  | 4,3                                  | 0                                        | 0                                        | resident   | resident       |
| Summer Tanager   | Piranga rubra       | ?                  | ?                                    | 65                                       | 0                                        | resident   | not present    |
| Swainson’s Hawk  | Buteo swainsoni     | Y                  | 130,11                               | 25                                       | 700                                      | breeding   | not present    |
| Swainson’s Thrush| Catharus ustulatus  | N                  | NA                                   | 0                                        | 1000                                     | breeding   | breeding       |
| Townsend’s Solitaire | Myadestes townsendi | N  | NA                                   | 15                                       | 0                                        | resident   | resident       |
| Townsend’s Warbler | Setophaga townsendi | ?  | ?                                    | 20                                       | 0                                        | resident   | winter         |
| tree swallow     | Tachycineta bicolor | N                 | NA                                   | 5                                        | 0                                        | resident   | resident       |
| Tricolored Blackbird | Agelaius townsendi | ?  | ?                                    | 0                                        | 0                                        | resident?  | resident       |
| Turkey Vulture   | Cathartes aura      | Y                  | 34,13                                | 10                                       | 0                                        | resident   | resident       |
| Varied Thrush    | Ixoreus naevius     | N                  | NA                                   | 0                                        | 0                                        | resident   | winter         |
| Turkey Vulture   | Cathartes aura      | Y                  | 34,13                                | 10                                       | 0                                        | resident   | resident       |
| Vaux Swift       | Chaetura vauxi      | N                  | NA                                   | 0                                        | 0                                        | resident   | migrant        |
| Verdin           | Auirarius flaviceps | N                 | NA                                   | 60                                       | 150                                      | breeding   | resident       |
| Vesper Sparrow   | Poecetes gramineus  | Y                  | 1,1                                  | 75                                       | 0                                        | resident   | winter         |
| Violet-green Swallow | Tachycineta thalassina | N | NA                                   | 0                                        | 0                                        | resident   | breeding       |
| Warbling Vireo   | Vireo gilvus        | N                  | NA                                   | 250                                      | 0                                        | winter     | breeding       |
| Western Bluebird | Sialia mexicana     | ?                  | 7,2?                                 | 0                                        | 0                                        | resident   | resident       |
| Western Kingbird | Tyrannus verticalis | N                  | NA                                   | 0                                        | 0                                        | resident   | breeding       |
| Western Meadowlark | Sturnella neglecta | Y                 | 125,11                               | 10                                       | 0                                        | resident   | resident       |
| Western Screech-Owl | Megascops kennicottii | Y           | 16,7                                 | 0                                        | 0                                        | resident   | resident       |
| Western Tanager  | Piranga ludoviciana | N                 | NA                                   | 0                                        | 0                                        | resident   | breeding       |
| Western Wood-Pewee | Contopus sordidulus | N                | NA                                   | 0                                        | 0                                        | resident   | breeding       |
| White-breasted Nuthatch | Sitta carolinensis | N           | 5                                     | 0                                        | 0                                        | resident   | resident       |
| White-crowned Sparrow | Zonotrichia leucophrys | Y        | 6,1                                  | 0                                        | 0                                        | resident   | resident       |
| White-headed woodpecker | Picoides albolarvatus | N | NA                                   | 20                                       | 0                                        | resident   | resident       |
| White-tailed Kite | Elanus leucurus    | Y                  | 3,3                                  | 0                                        | 0                                        | resident   | resident       |
| White-throated Sparrow | Zonotrichia albicollis | N          | NA                                   | 500                                      | 0                                        | winter     | winter         |
| White-throated Swift | Aeronautes saxatalis | N        | NA                                   | 0                                        | 0                                        | resident   | resident       |
| Wild Turkey      | Meleagris gallopavo | Y                 | 599,12                               | 30                                       | 0                                        | resident   | not present    |
| Williamson’s Sapsucker | Sphyrapicus thyroides | ? | ?                                    | 20                                       | 0                                        | resident   | resident       |
| Willow Flycatcher | Empidonax tralili  | N                  | NA                                   | 0                                        | NC                                       | breeding   | breeding       |
| Wilson’s Warbler | Cardellina pusilla  | ?                  | ?                                    | 30                                       | 1000                                     | breeding   | breeding       |
| Wrentit          | Chamaea fasciata    | N                  | NA                                   | 0                                        | 0                                        | resident   | resident       |
| Yellow-billed Cuckoo | Coccyzus americanus | N               | NA                                   | 60                                       | 0                                        | resident   | not present    |
| Yellow-billed Magpie | Pica nutalli       | Y                 | 174,9                                | 0                                        | 0                                        | resident   | not present    |
| Yellow-breasted Chat | Icteria virens     | N                  | NA                                   | 5                                        | 0                                        | resident   | breeding       |
| Yellow-headed Blackbird | Xanthocephalus?     | ?                 | ?                                    | 60                                       | 0                                        | resident   | resident       |
| Yellow-rumped Warbler | Setophaga coronata | ?                 | ?                                    | 3                                        | 0                                        | resident   | resident*      |

https://doi.org/10.1371/journal.pone.0227361.t001
Here, we use the bird record of La Brea and ecological niche modeling to meet four objectives. First, we compare predicted LGM breeding and wintering distributions for landbird species (n = 86) identified (to species or genus) from La Brea to determine if niche models successfully predict species' presence. This provides a check on the validity of niche models for predicting LGM distributions. We also estimate the degree of species turnover. Secondly, for 97 species not yet identified from La Brea but found within or near the region today, we create breeding and wintering season niche models to predict which species might have been at La Brea, thereby creating a prospective checklist of birds. Third, we tally changes in seasonal status (resident, breeder, migrant) to evaluate the stability of life histories over the 21 millennia represented by the avifauna at La Brea. Lastly, we determine whether a guild of bark-foraging birds showed quantitative shifts in Eltonian niche breadths between the present and the LGM.

Methods

We constructed breeding season and wintering season ecological niche models for 63 landbird species documented from La Brea, representing considerable taxonomic diversity (Table 1) including 41 residents, 3 breeders, 11 winter visitors, 1 extinct, 1 introduced, and 6 that are not today found within 100 km of La Brea. In addition, we considered 23 species that are congeneric with taxa identified only to genus in the La Brea list. To determine whether other species could have been present, we selected 97 additional species that are today found within or near the La Brea region but not among the identified remains (to species or genus), and determined whether niche models predicted their occurrence at the site at the LGM; these included 30 breeding, 2 migrants, 44 residents, 14 winter visitors, and 7 species nearby but not present within 100 km of the tar pits. We excluded species associated with water (waterfowl, shorebirds), which are not easily amenable to niche modeling. We consider the wild turkey as not present today owing to well-documented recent introductions. We count the existence of three extinct species of landbirds [12–14], one extinct owl (Strix brea; [15]), and the passenger pigeon (Ectopistes migratorius), which we include in the overall tally of species but exclude from niche modeling. We also excluded the northwestern crow (Corvus caurinus) because Johnston [16] has shown that it is not distinguishable phenotypically from the American crow (C. brachyrhynchos). Howard [11] listed the number of specimens and number of pits (out of 13) for each species; we note that at least nine species are represented by a single specimen, and 25 species by five or fewer specimens (Table 1). Howard (11) did not list the number of specimens of pine siskin (Spinus pinus) or cedar waxwing (Bombycilla cedrorum) but these species are in the online list. We used maps of bird distributions (https://www.birds.cornell.edu/) to determine species' present status; when distribution maps were unclear, we considered a species present if three or more locations from the breeding bird survey were represented in the 100-km area surrounding La Brea.

We estimated the general LGM ranges of species using niche modeling and the 19 Bioclimatic variables [17]. Species modern localities were obtained from the breeding bird survey (https://www.pwrc.usgs.gov/bbs/; accessed multiple times); only localities west of -104° longitude were used to restrict analyses to areas likely most relevant to La Brea. We entered locality information into Maxent [18,19] to build a climatic niche model that was then projected onto the LGM climate layers using DIVA-GIS [20] (~20 ka; CCSM model); we used default parameters with the exception that we used 1000 iterations to assist model convergence. To explore the influence of default parameters, we reanalyzed 100 species at random (split between breeding and wintering) with 5000 iterations, and no clamping or extrapolation. We recognize that the specimens documented at La Brea might reflect entrapment of wintering and migrant species. To expand discovery of species occurrences at La Brea, we plotted potential winter
distributions by downloading January occurrences from the Global Biodiversity Information Facility (https://www.gbif.org; Appendix 2) and built niche models for each species using the same 19 Bioclim layers. If there were areas in the range with a high density of points, we randomly sampled up to 1500 breeding sites. We did not prune the climate layers for winter-only months [21–23] because we believe that for birds, the entire year is relevant to the existence of plant species at the site that in turn dictate avian presence. That is, if a plant species cannot survive the entire year, it will not be present at the site, nor will the birds that depend on it. Thus, for both breeding and wintering, we assume that all of the Bioclim layers are relevant. In addition, there is not a “summer” and “winter” seasonal period that is the same for all birds, especially for species that only migrate past La Brea. We note that very few studies delete winter months for estimating breeding distributions, in our opinion for the same reason. S1 and S2 Tables contain the breeding and wintering locality data, respectively, used in the models.

A myriad of different modifications have been proposed to tweak niche models [24–25]. Our goal in niche modeling was not to identify the exact range of a species at the LGM, instead we wished to estimate whether the 187 focal species were present at or within 100 km of La Brea. We used the 10% probability threshold to depict presence or absence at the LGM [26], and we recorded the distance from La Brea to the nearest predicted occurrence. We recognize there are multiple possible thresholds but in a comparison of a wide range of different threshold values for 50 species we found little change in our results. Some authors suggest using a correlation analysis to reduce the number of bioclimatic variables, by deleting one of two variables correlated at or above some level. We do not find this appropriate because any cutoff used is arbitrary. In addition, we analyzed species using the same bioclimatic variables; it is doubtful that all species would respond in the same way to a reduced set of variables (see below). For example, Zink and Gardner [27] analyzed multiple species using all 19 bioclim variables, and found that each variable contributed significant to at least one species, but if a correlation analysis had been used to eliminate variables, this explanatory information would have been lost. Hence, we kept all 19 variables in our analyses.

Nonetheless, to explore the possibility of bias in the above-described data sets and modeling approach, we made new niche models for 103 randomly chosen species using the MIROC-ESM LGM climate layers. For this random sample of the species we thinned the locality data to only include records > 20 km apart for each species to account for spatial sampling bias using the package spThinn [28]. To explore the effect of the background area selection for the model, we selected the study area for modelling each species niche as the minimum convex polygon of locality records surrounded by a 150 km buffer. We compared the results of these models with the previously described ones to determine if systematic bias stemming from differences in niche construction methods influenced our results.

The area surrounding La Brea includes a range of elevations from near sea level (La Brea = ca. 60 m) to over 1500 m, supporting differing habitats altitudinally. For example, southeast of La Brea the elevation is similar for 65 km, ranging from sea level to 100 m. Elevations reach 1500 m within 40 to 75 km of La Brea to the northeast and northwest, although there are intervening areas less than 150 m. This elevational heterogeneity complicates scoring a species as present at La Brea from niche models. Given the mobility of most birds [29], one might assume that if a LGM distribution map predicted presence within 100 km of La Brea, the species was likely present there. However, as noted above, some environments within 100 km from La Brea are very different in both elevation and habitat. We plotted the distribution of distances from La Brea to the closest predicted occurrence for each species in breeding and winter periods, and we considered a distance of 100 km or less as indicating presence at La Brea. Although 100 km might seem a large distance for species to traverse non-optimal habitat, over seasons and thousands of years, we considered it a biologically reasonable threshold.
distance. If a species is within 100 km in both breeding and wintering seasons, we considered them resident. As a control, one can examine the niche models for eastern species and observe that they do not predict presence at La Brea [27].

To explore whether species’ niche breadths changed over time, we selected a guild of bark-foraging species including Nuttall’s woodpecker, hairy woodpecker, downy woodpecker, black-backed woodpecker, acorn woodpecker, red-shafted flicker, Williamson’s sapsucker, red-breasted sapsucker, white-headed woodpecker, pileated woodpecker, Lewis’ woodpecker, red-breasted nuthatch, white-breasted nuthatch, and brown creeper. Niche breadth was estimated by applying the inverse concentration metric of Levins [30] as implemented in ENMTools [31–34], for both breeding and wintering periods at the LGM and present. To compare niche breadths we computed Pearson rank-order correlation coefficients to between scores from the two time periods to mitigate empirical differences. We computed Simpson’s [35] measure of species turnover as \( \frac{\min(b,c)}{a + \min(b,c)} \), where \( b \) = number of species unique to La Brea (19), \( c \) = number of species unique to present (2), \( a \) = number of species present at both time intervals (187–21 = 166).

**Results**

**Landbird species identified from La Brea during the LGM**

For the 63 documented extant species we examined (S1 Table), niche models showed that 36 species (58%) had ranges that overlapped La Brea at the LGM, 49 species (78%) were within 20 km, and 60 (95%) species were within 100 km (Fig 1). Of the 63 species, five are not present today within 100 km, suggesting range shifts, but less than 500 km. The LGM distribution of the Chihuahuan raven (\( C. \) cryptooleucus) was inconsistent with presence at La Brea but the possibility exists that the single specimen was misidentified. For specimens identified only
to genus from La Brea, we evaluated congeneric species occurring locally at the present time (Table 1), finding that 22 of 23 species were predicted to have been within 100 km of La Brea at the LGM.

For the 63 verified La Brea species that are extant, 41 (65%) species were predicted to have the same life history at the LGM and present, whereas 24 (35%) showed shifts, most involving shifts from resident status at the LGM, with the largest frequency being 11 residents that became winter visitants (Table 1). For example, in Fig 2 we show LGM breeding distributions for four species that currently only winter within 100 km of La Brea, but were breeding and

Fig 2. Predicted Last Glacial Maximum breeding distributions of four species. The triangle indicates the location of La Brea, and the five filled circles are 100 km from La Brea.

https://doi.org/10.1371/journal.pone.0227361.g002
wintering at the LGM, resulting in their shift to resident status. The Pacific wren and yellow-billed cuckoo are not present today near La Brea, whereas they were residents at the LGM (Fig 3). For the 23 species from genera identified from La Brea, a similar distribution of life history shifts was found, with 16 (70%) species being consistent across time, and seven species showing shifts (Table 2). Nineteen species that were present at the LGM are absent today (3 breeding, 1 wintering, 15 residents) and one species not present at the LGM is today a breeding species.

**Landbird species not identified from La Brea**

For the 97 species that have not yet been identified at La Brea, 95% were predicted to have occurred within 100 km during the breeding season and 91% in winter (Table 1). A total of
51 (54%) species were predicted to have the same life history at the LGM and present, whereas 38 (40%) showed shifts, most being shifts from resident status, with the largest frequency being 21 breeding species that became breeding-season only inhabitants (Table 1; excluding species that were not present at one or both times). Six species that were present at the LGM are absent today (2 breeding, 4 residents), and one species not present at the LGM is today a resident species. Across all categories, residents comprised 88% of the total species at the LGM and 60% at the present time.

Niche breadths of bark-gleaners

Our measure of niche breadth varied little between seasons and time periods (Fig 4), with the exception of downy woodpecker and hairy woodpecker, two of the more widespread woodpecker species. Overall, Pearson rank-order correlation coefficients were all > 0.7 and statistically significant (Table 3), suggesting no major shifts in niche breadth across time. Given 19 species unique to the La Brea record, and 2 unique to the present, and 166 species present at both time intervals, species turnover was low (Simpson’s [35] value = 2/168 = 0.012).

Comparison of different niche modeling assumptions

For the 103 species modeled under the MIROC–ESM_LGM conditions, we found that for five species (breeding season: yellow-billed cuckoo, warbling vireo; winter season: ash-throated flycatcher, yellow-billed magpie, Northwestern crow) our conclusions about presence or absence within 100 km of La Brea were altered (Fig 5). Therefore, the two different sets of niche modeling assumptions agreed on 95% of the species.

Discussion

Many ecological principles were derived from lists of species of modern organisms from different continental areas or from different islands. Given our understanding of glacial history in
north temperate regions, it is obvious that species ranges changed with the onset and retreat of glaciers. Specifically how each species responded is not clear because in essence we lack field guides to the past distribution of species. Niche modeling provides a way to construct species lists for communities at different time periods [4], such as the LGM. However, niche models are hypotheses and not based on direct observational information, as are modern checklists. In this study, nearly all of the species identified from skeletal remains at La Brea were predicted to have occurred there or within 100 km by ecological niche models (S1 Table, Fig 1). Although this comparison represents a sample at just one geographical site, it nonetheless lends confidence to the ability of niche reconstructions to produce reasonably accurate LGM range estimates, at least for birds.

Table 3. Pearson product-moment correlation coefficients between measures of niche breadth for a guild of bark-foraging species.

|                  | LGM breeding | Present breeding | Present winter |
|------------------|--------------|------------------|----------------|
| Present breeding | 0.776**      |                  |                |
| LGM winter       | 0.868**      | 0.723**          |                |
| Present winter   | 0.754**      | 0.890**          | 0.701*         |

** $P < 0.01$

* $P < 0.05$

https://doi.org/10.1371/journal.pone.0227361.t003
The success of niche models in predicting species already known to occur at La Brea at the LGM makes it possible to predict which other species ought to have been present at the site. Of the 97 species currently unverified from La Brea, only two were predicted not to have occurred within 100 km of the site (Table 1). The lack of specimens of thrushes, hummingbirds, vireos, wrens, among others, suggests either that it was relatively rare for these birds to be trapped in the tar, their migratory habits resulted in short-term presence at La Brea, or they simply have not been identified from remains already or as yet to be recovered. A large proportion could be awaiting identification in the remains from La Brea. K. Campbell (email to RMZ on 3 June 2019) remarked "there are probably tens of thousands of passerine bones in the collection that have never seen the light of day". Our analysis (S1 Table) therefore provides a prospective checklist of land bird species at La Brea at the LGM, one of the first such checklists produced with the aid of niche modeling. Descriptions of species ranges at the LGM will facilitate comparison of changes in avifaunal composition over the last 21,000 years.

Of the 187 total species examined (including five extinct species), 183 were present at the LGM in one or more seasons, whereas 166 are present today. Thus, species richness decreased from the LGM to the present. In many studies of species turnover in birds (e.g., [1]), previous baseline surveys were judged inadequate. In the case of La Brea, we suggest that the species lists for both time periods are relatively robust, and there is relatively little turnover (Simpson’s [35] value = 0.012), and differences in species occurrence are due mostly to relatively local range shifts rather than species disappearance. On the other hand, the niche models (Table 2) commonly implied shifts in residency and life history status. Across all categories, and considering only species present at both time periods (169), 56 species (33%) shifted from one migratory state to another (Table 1), with the commonest being a larger number of resident species at the LGM (161; 88%) than at the present time (100; 60%). In particular, 27 species switched from resident at the LGM to being breeding-season only today, implying a suitable year around seasonal environment and the cessation of migration at the LGM (Table 2). These shifts resulted...
in greater species diversity in the breeding season (residents and breeding species), with 177 species estimated at the LGM and only 140 at the present. This suggests considerable plasticity in life history strategies, with frequent transitions from resident to migratory status [27].

Zink and Gardner [27] suggested that many current long-distance migrants reverted to being tropical sedentary residents during glacial maxima. However, most species that retained LGM breeding distributions in North America were in the western part of the continent. Peterson et al. [36] discovered that many niches do not change until well after speciation, which suggests niche conservatism over considerable periods. A greater percentage of resident species suggests a different niche structure than at present, such as narrower niches. However, we did not observe any strong trends in niche breadths in our sample of bark-foragers in any season or time period (Fig 4), although most were residents at both periods. This suggests that the LGM climate was suitable to a greater number of species, rather than changes in niche breadth that could allow greater species packing (e.g., niche partitioning). Warren (in litt.) suggested that niche breadth metrics are affected by the fact that environmentally suitable habitat for birds was more common or more uniformly distributed at the LGM. Thus, although niche conservatism may well be a characteristic of many birds [37], these niches can be seasonally variable. Future studies should consider a null model approach to account for the expected differences based on available habitat.

It is unclear what the vegetation at La Brea might have been at the times most of the specimens were deposited. Fragomeni and Prothero [38] wrote that study of offshore sea cores by Heusser [39] suggested that “the region changed from oak and chaparral vegetation around 59 ka to pine-juniper-cypress woodlands by 24 ka, then to a closed-cone juniper-ponderosa forest with abundant winter snow during the last glacial maximum (24–14 ka).” This could be inconsistent with our suggestion that there were more residents than migrants in the La Brea avifauna; however, if the dates given for the duration of this environment are actually older, there could be no inconsistency. Given changes in community vegetation structure, it is of interest that stasis in the size and shape of La Brea mammals has been noted [38, 40].

Because of the many different assumptions used in published niche models [41–44], we explored the effects of LGM climate projections from different Global Climate models (CCSM, MIROC--ESM_LGM), as well as the effect of background (accessible) area selection, and spatial sampling bias. Our criterion was simply whether each model predicted occurrence within 100 km of La Brea, and we found that 95% of the models led to the same conclusions, showing our results are robust to varying climatic data and niche modelling approach. There is, however, clearly differences in the projected distributions at scales less than 100 km (Fig 5), which could be further explored for answering different questions. Nonetheless, it appears that these differences stem mainly from differences in the Global Climate Models.

Supporting information

S1 Table. Locations (longitude, latitude) for each specimen used in breeding niche models. (XLSM)

S2 Table. Locations (longitude, latitude) for each specimen used in wintering niche models, including information on downloads from Global Biodiversity Information Facility. (XLSM)

Acknowledgments

We thank Blake McGeorge for assistance with wintering niche models. K. Campbell provided advice and information. D. Shepard, N. Najar and an anonymous reviewer provided helpful comments on the manuscript.
Author Contributions

Conceptualization: Sebastian Botero-Cañola.

Data curation: Robert M. Zink, Helen Martinez, Katelyn M. Herzberg.

Formal analysis: Robert M. Zink.

Methodology: Robert M. Zink, Sebastian Botero-Cañola.

Project administration: Robert M. Zink.

Writing – original draft: Robert M. Zink.

Writing – review & editing: Robert M. Zink, Sebastian Botero-Cañola.

References

1. Lynch JF, Johnson NK. Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. Condor 1974; 76:370–384.

2. Gotelli NJ, Colwell RK. Estimating species richness. Biol. Div.: frontiers in measurement and assessment 2011; 12:39–54.

3. Peterson AT. Predicting species’ geographic distributions based on ecological niche modeling. Condor 2011; 103:599–605.

4. Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, et al. Ecological niches and geographic distributions. Princeton: Princeton Univ. Press; 2011.

5. Maguire KC, Nieto-Lugilde D, Fitzpatrick MC, Williams JW, Blois JL. Modeling species and community responses to past, present, and future episodes of climatic and ecological change. Ann. Rev. Ecol. Evol. Syst, 2015; 46:343–368.

6. Ribeiro V, Werneck FP, Machado RB. Distribution dynamics of South American savanna birds in response to Quaternary climate change. Austral Ecol. 2016; 41:768–777.

7. Yannic G, Pellissier L, Ortego J, Lecomte N, Couturier S, Cuyler C, et al. Genetic diversity in caribou linked to past and future climate change. Nat Clim Change 2014; 4:132.

8. Myers CE, Stigall AL, Lieberman BS. PaleoEN M: applying ecological niche modeling to the fossil record. Paleobio. 2015; 41:226–244.

9. Howard H. A census of the Pleistocene birds of Rancho La Brea from the collections of the Los Angeles Museum. Condor 1930; 32:81–88.

10. Howard H. Further studies upon the birds of the Pleistocene of Rancho La Brea. Condor 1936; 38:32–36.

11. Howard H. A comparison of avian assemblages from individual pits at Rancho La Brea, California. Contributions in Science. Nat. Hist. Mus. Los Angeles Co. 1962; 58:1e24.

12. Miller AH. A new genus of icterid from Rancho La Brea. Condor 1947; 49:22–24.

13. Miller AH. The passerine remains from Rancho La Brea in the paleontological collections of the University of California. Univ. Cal. Pub., Bull. Dep. Geol. Sci. 19, 1–22 (1929).

14. Dawson WR. Records of fringillids from the Pleistocene of Rancho La Brea. Condor 1948; 50:57–63.

15. Campbell KE Jr, Bochenkski ZM. A new genus for the extinct Late Pleistocene owl Strix breas Howard (Aves: Strigiformes) from Rancho La Brea, California. In Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution, ed. W. E. Boles and T. H. Worthy. Records of the Australian Museum 2010; 62:123–144.

16. Johnston DW. The biosystematics of American crows. Seattle: University of Washington Press, 1961.

17. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 2005; 25:1965–1978.

18. Phillips SJ, Anderson RP, Schapire RE. Maximum entropy modeling of species geographic distributions. Ecol. Model. 2006: 190:231–259.

19. Elith J, Phillips SJ, Hastie T, Dudik M, Chee YE, Yates CJ. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 2011; 17:43–57.

20. Hijmans RJ, Guarino L, Bussink C, Mathur P, Cruz M, Barrentes I, et al. DIVA-GIS. Version 7.1.7. A geographic information system for the analysis of species distribution data. Manual http://www.diva-gis.org/ (2004).
21. Nakazawa Y, Peterson AT, Martinez-Meyer E, Navarro-Siguénza AG. Seasonal niches of Nearctic-Neotropical migratory birds: implications for the evolution of migration. Auk 2004; 121:610–618.
22. Peña-Peniche A, Ruvalcaba-Ortega I, Rojas-Soto O. Climate complexity in the migratory cycle of Ammodramus bairdii. PLoS ONE 2018; 13(8): e0202678. https://doi.org/10.1371/journal.pone.0202678 PMID: 30148886
23. Pérez-Moreno H, Martínez-Meyer E, Soberón J, Rojas-Soto O. Climatic patterns in the establishment of wintering areas by North American migratory birds. 2016. Ecol. an Evol; 6:2022–2033.
24. Varela S, Lima-Ribeiro MS, Terribile LC. A short guide to the climatic variables of the last glacial maximum for biogeographers. PloS one 2015.; 10e0129037.
25. Title PO, Bemmels JB. ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. Ecography 2018: 4:291–307.
26. Escalante T, Morrone JJ, Rodríguez-Tapia G. Biogeographic regions of North American mammals based on endemism. Biol. J. Linn. Soc. 2013; 110:485–499.
27. Zink RM, Gardner AS. Glaciation as a migratory switch. Science advances 2017; 3p.e1603133.
28. Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP. spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 2015; 38:541–545.
29. Grinnell J. The role of the “accidental”. Auk 1922; 39:373–380.
30. Levins R. Evolution in changing environments: some theoretical explorations. Princeton Univ. Press. Princeton, 1968.
31. Warren DL, Glor RE, Turelli M. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 2010; 33:607–611.
32. Glor RE, Warren DL. Testing the ecological basis of biogeographic boundaries. Evolution 2011; 65:673–683.
33. Warren DL, Glor RE, Turelli M. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 2008; 62:2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x PMID: 18752605
34. Nakazato T, Warren DL, Moyle LC. Ecological and geographic modes of species divergence in wild tomatoes. Am. J. Bot. 2010; 97:680–693. https://doi.org/10.3732/ajb.0900216 PMID: 21622430
35. Simpson GG. Mammals and the nature of continents. Am. J. Sci. 1943; 24:1–31.
36. Peterson AT, Soberon J, Sanchez-Cordero V. Conservatism of ecological niches in evolutionary time. Science 1999; 285:1265–1267. https://doi.org/10.1126/science.285.5431.1265 PMID: 10455053
37. Zink RM. Homage to Hutchinson, and the role of ecology in lineage divergence and speciation. J. Biogeog. 2014; 41:999–1006.
38. Fragomeni A, Prothero D.R. Stasis in late Quaternary birds from the La Brea tar pits during the last glacial-interglacial cycle. New Mexico Mus. Nat. Hist. Bull. 2011. 53:511–516.
39. Heusser L. Direct correlation of millennial-scale changes in western North American vegetation and climate with changes in the California Current system over the past ~ 60 ky. Paleoceanography and Paleoclimatology 1998; 13:252–262.
40. Prothero DR, Syverson VJ, Raymond KR, Madan M, Molina S, Fragomeni A, et al. Size and shape stasis in late Pleistocene mammals and birds from Rancho La Brea during the Last Glacial-Interglacial cycle. Quat. Sci. Rev. 2012; 56:1–10.
41. Barve N, Barve V, Jiménez-Valverde A, Lira-Noriega A, Maher SP, Peterson AT, et al. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol. Model. 2011; 222:1810–1819.
42. Warren DL, Wright AN, Seifert SN, Shaffer HB. Incorporating model complexity and spatial sampling bias into ecological niche models of climate change risks faced by 90 California vertebrate species of concern. Diver. Distrib. 2014; 20:334–343.
43. Kramer-Schadt S, Niedballa J, Pilgrim JD, Schröder B, Lindenborn J, Reinfelder V, et al. The importance of correcting for sampling bias in MaxEnt species distribution models. Diversity Distrib. 2013; 19:1366–1379.
44. Norris D. Model thresholds are more important than presence location type: Understanding the distribution of lowland tapir (Tapirus terrestris) in a continuous Atlantic forest of southeast Brazil. Tropical Cons. Sci. 2014; 7:529–547.