RESEARCH ARTICLE

Human food use increases plant geographical ranges in the Sonoran Desert

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Abstract

Aim: Climate is usually regarded as the main determinant of plant species distributions. However, past human use of species for food might also have influenced distributions. We hypothesized that human-mediated dispersal has resulted in food plants occupying more of their potential geographical range. We also hypothesized that key ecological traits could predispose a species to occupy more of its potential climatic geographical range and be selected by humans for food.

Location: The Sonoran Desert of south-western North America.

Time period: Present day.

Major taxa studied: Food plants.

Methods: We used ethnobotanical data and data from large botanical ecoinformatics databases to estimate realized (dispersal- and climate-constrained) and potential (climate-constrained) ranges for food plants and their used and unused congeners.

Results: We found that food plants fill more of their potential geographical ranges than their unused congeners. We also found that succulence and annual growth interacted with food usage to increase range filling.

Main conclusions: Human food use has expanded the distribution of many plant species in the Sonoran Desert.

KEYWORDS
biogeography, dispersal, ethnobotany, geographical distribution, human–plant interactions, range filling, species distribution modelling, trait-based ecology

1 | INTRODUCTION

The reshaping of global biodiversity by humans has had a significant impact on Earth's ecosystems (Boivin et al., 2016; Levis et al., 2017; McKey et al., 2010). A key component often missing from species distribution modelling is the impact of human populations (McKey et al., 2010; Pausas & Bond, 2019). The geographical distribution of

any given species is influenced by three central processes: (a) biotic interactions, (b) abiotic factors, and (c) movement via dispersal (the biotic interactions, abiotic conditions and movement framework, or BAM; Peterson, 2011; Soberón & Nakamura, 2009; Soberon & Peterson, 2005). The biotic and abiotic factors are commonly studied as drivers of plant distributions, whereas the relative role of dispersal in influencing the geographical range of a species is less appreciated

but also frequently important (Hodkinson & Thompson, 1997; Normand et al., 2011; Primack & Miao, 1992). The impact of human populations on dispersal is often overlooked (Hodkinson & Thompson, 1997; Van Zonneveld et al., 2018). However, present-day species distributions cannot be understood fully without also addressing the past impacts of human movement of species on the landscape, whether direct (e.g., cultivation) or indirect (e.g., shifting habitats) (Boivin et al., 2016).

The use of plants for food is one of the most important ways in which humans can increase distributions, via propagation, wild harvesting and dispersal. Human populations have reorganized plant distributions at regional and continental scales (Crosby, 2003). In many landscapes, the legacy of humans is apparent today (Abrams & Nowacki, 2008; Levis et al., 2017; Shepard & Ramirez, 2011; Warren, 2016). Evidence for human impacts has been found in eastern North America (Abrams & Nowacki, 2008; Warren, 2016), Amazonia (Bitencourt & Krauspenhar, 2006; Clement et al., 2015; Clement & Junqueira, 2010; dos Reis et al., 2014; Shepard & Ramirez, 2011; Levis et al., 2017; but see McMichael et al., 2017), Southeast Asia (Barton & Denham, 2011; Brosius, 1991; Yang et al., 2013) and Central America (Ford & Nigh, 2016; Nesheim et al., 2010). However, evidence for human impacts in arid biomes is more limited.

We still lack an understanding of human impacts on the geographical distribution of the vast majority of food plants that are no longer a major component of human diets. This challenge can be addressed via studying range filling (Svenning & Skov, 2004), defined here as the ratio between the realized (R) and potential (P) geographical range. R/P is a measure of how well species have dispersed to fill their potential ranges. R/P is larger when high dispersal drives greater occupancy of the climate-determined potential range (Normand et al., 2011). Here, we ask: (a) does human food use in prehistoric and historic times increase R/P?; and (b) what ecological traits predisposed species to higher R/P via interactions with food use?

We hypothesized that past human utilization of food plant species has resulted in increased dispersal to favourable habitats, assuming that ranges are otherwise limited by dispersal (Guo et al., 2005; Primack & Miao, 1992; Svenning et al., 2008). As a result, in comparison to unused congeners and other unused species, food plants should fill more of their potential geographical range (i.e., have higher R/P) than their unused congeners, which presumably have otherwise similar phenotypes and life histories (hypothesis A). This hypothesis has been widely articulated (e.g., Abrams & Nowacki, 2008) and is consistent with descriptions of Native American land-use practices (Fowler & Lepofsky, 2011; Nabhan, 2016), but has not been tested formally across an entire flora in a biogeographical context.

We also hypothesized that certain plant traits, such as polyploidy, growth-form (herb, shrub or tree) and duration (perennial or annual) should predispose certain species to be selected for by humans and fill their potential climatic distribution range more (hypothesis B) (Meyer et al., 2012; Meyer & Purugganan, 2013). For example, both growth-form and life-form can play a significant role in predicting

the limits of a species range (Stahl et al., 2014; Violle et al., 2014) and human food use (Meyer et al., 2012; Whitehead et al., 2017). Additionally, certain traits associated with polyploidy could predispose these species to higher range filling and human food use (e.g., faster growth, larger size) (Meyer et al., 2012, Salman-Minkov et al. 2016). This hypothesis has been tested in the context of trait predictors of species use, but not in the context of range filling.

We quantified the extent to which past human populations have driven current species distribution and biodiversity dynamics through the domestication, cultivation and wild harvesting of food plants in the Sonoran Desert in south-western North America (Hodgson, 2001; Wiken et al., 2011; Figure 1). Our results indicate that humans have had a significant impact on the distribution of species and biodiversity in arid environments and highlight the role of human impacts on plant biogeography globally.

2 | MATERIALS AND METHODS

2.1 | Regional context

The Sonoran Desert is a resource-rich environment, with a long history of human occupation by both foraging and agricultural populations throughout the Holocene (Bell & Castetter, 1937; Bohrer, 1981; Hodgson, 2001; Nabhan, 2016; Rea, 1997; Figure 2). The Sonoran Desert contains the oldest evidence for maize agriculture north of Mesoamerica, *c.* 2,100 yr BP (Merrill et al., 2009), and also saw the development of extensive agricultural settlements throughout the well-watered portions of the region in the pre-Hispanic period (Hill et al., 2004). The northern Sonoran Desert is perhaps most closely associated with the Hohokam archaeological culture (*c.* 400–1450 CE), which was characterized by large and long-lived settlements, intensive agriculture including hundreds of kilometres of irrigation canals along major rivers, and an exchange and market system extending throughout much of the region and beyond (Abbott et al., 2007; Bayman, 2001; Fish & Fish, 2008; Hodgson et al., 2018). The later prehistory of the Sonoran Desert saw substantial population declines (Hill et al., 2004). However, there is evidence of continued occupation and agricultural land use in some areas (Loendorf et al., 2013; Loendorf & Lewis, 2017) and evidence of new arrivals in others, because contemporary Indigenous peoples of the Sonoran Desert are recognizable in the archaeological record (e.g., O'odham, Seri, Apache, Maricopa, Yavapai, Cocopah). The diets of these peoples varied for cultural and ecological reasons, but they all used Sonoran Desert plants extensively for food and other purposes (Bohrer, 1991; Castetter & Underhill, 1935; Crosswhite, 1981; Felger & Moser, 1976; Hodgson, 2001; Nabhan, 2016; Rea, 1997).

Hundreds of plant species were, at the very least, wild harvested, and some were possibly domesticated or cultivated (Castetter & Underhill, 1935; Hodgson, 2001; Figure 1). For example, *Agave* spp., such as *Agave murpheyi* F. Gibson (Hohokam Agave) and *Agave delamateri* W.C. Hodgson & Slauson (Tonto Basin Agave) were domesticated and extensively cultivated in Arizona by Indigenous peoples

FIGURE 1 (a–d) Representative examples of Sonoran Desert food plants: (a) *Hordeum pusillum* Nutt., little barley; (b) *Chenopodium berlandieri* Moq., pit-seed goosefoot; (c) *Prosopis glandulosa* Torr., honey Mesquite; and (d) *Opuntia engelmannii* Salm-Dyck., Engelmann prickly pear. Images are reproduced under Creative Commons licenses and are credited to M. Lavin (a,b), J. Maughn (c) and D. Villafuela (d)
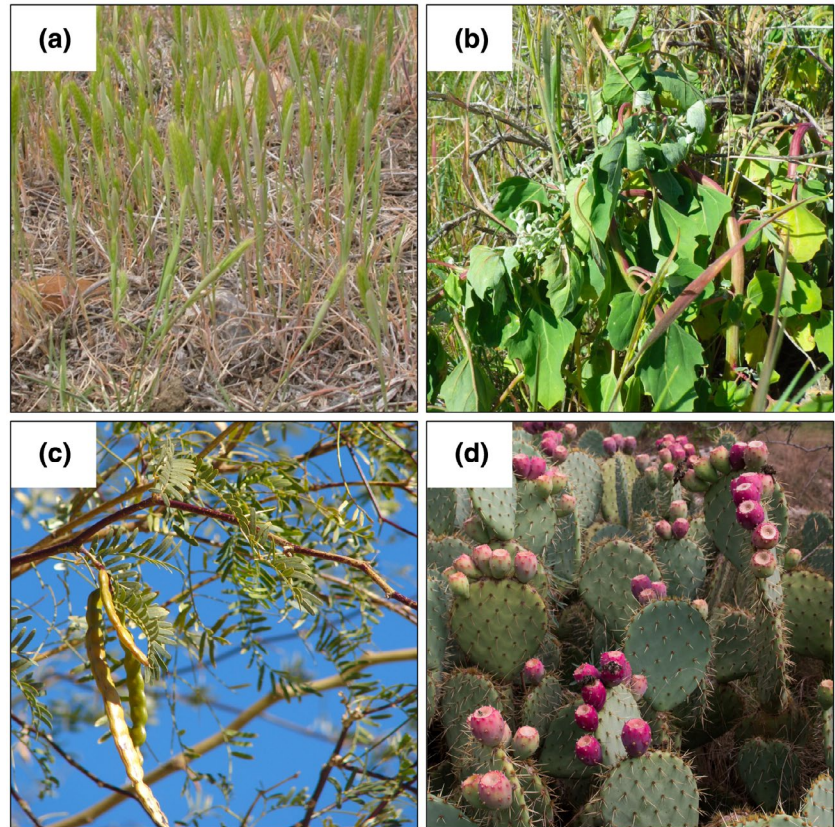
(Hodgson & Salywon, 2013; Hodgson et al., 2018; Parker et al., 2007). Mesquite (*Prosopis glandulosa* Torr., *Prosopis velutina* Wooton and *Prosopis pubescens* Benth.) was one of the most widespread and useful wild-harvested food plants in the Sonoran Desert (Bell & Castetter, 1937; Felger & Moser, 1976; Hodgson, 2001). *Prosopis velutina* (velvet mesquite) was so important to the Akimel O'odham that they referred to it as a the "tree of life" (Crosswhite, 1981; Rea, 1997).

Crops may have moved as part of "ecological packages" that included non-domesticated or "weed" species (Boivin et al., 2016). The Hohokam took up prolonged residence, in which successive generations continued to irrigate land and to farm and harvest a variety of plants, including weedy species (Bayman, 2001; Fish & Fish, 2008). Weedy annuals, especially *Chenopodium* spp. (goosefoot), are frequently recovered at archeological sites, as are *Amaranthus* spp. (amaranth), *Descurainia* spp. (tansy mustard), *Astragalus* spp. (milk vetch) and *Hordeum pusillum* Nutt. (little barley) (Bohrer, 1991; Fritz et al., 2009; Gasser, 1982).

Historic Akimel O'odham populations managed both cultivated fields and "second gardens" that were composed of plants providing greens or seeds (Crosswhite, 1981). These species included *Amaranthus palmeri* S. Watson (Palmer's amaranth), *Descurainia pinnata* (Walter) Britton (western tansy mustard) and *Salvia columbariae* Benth. (desert chia). Species that were not edible were eliminated, and older plants that had not been picked in time were intentionally allowed to go to seed for the following year (Crosswhite, 1981). These are a few examples of a much broader history of food plant usage that was a significant part of the livelihoods of Indigenous peoples.
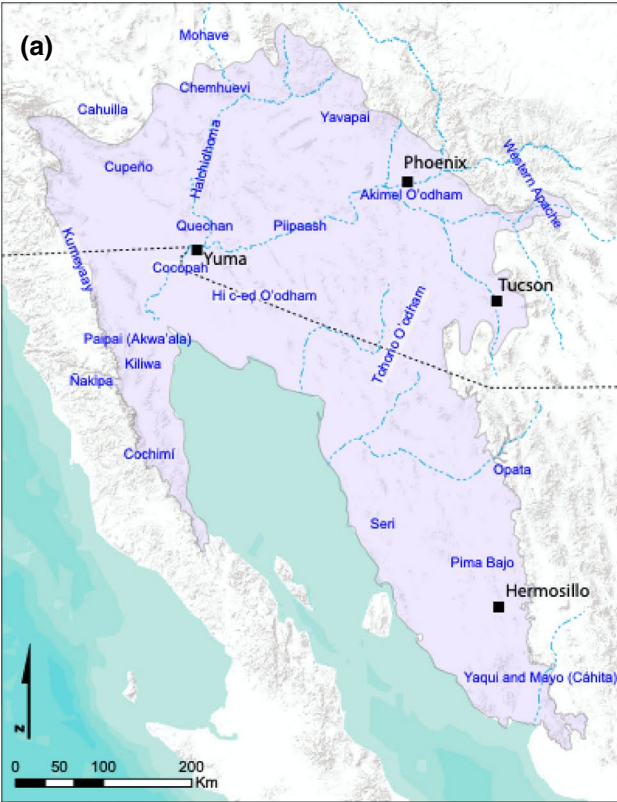
2.2 | Study region

The boundaries of the Sonoran Desert were defined using the Commission for Environmental Cooperations's Sonoran Desert Level III Eco-Region (Omernik, 2004; Wiken et al., 2011), which encompasses the desert and thornscrub biomes in southern Arizona, south-eastern California, north-eastern, north- and south-central Baja California, and north-central and western Sonora. The boundary excluded higher-elevation areas, based on clipping to a Global Multi-resolution Terrain Elevation Data 2010 elevation raster (Danielson & Gesch, 2011), in order to omit a small fraction of land area (1.1%–3.3% depending on grain size) representing montane areas where ethnobotanical records were not available. A threshold elevation of 1,219 m was chosen as an approximate boundary with higher-elevation grassland and woodland, based on upper elevation limits of saguaro cacti (Shreve & Wiggins, 1964).

2.3 | Ethnobotanical data

We developed an ethnobotanical dataset of Sonoran Desert food plants comprising $n = 349$ food plants that have been used by multiple past human populations. These plants were selected based on

their native origin and extensive available documentation (i.e., ethnographies and voucher specimens) that could contextualize their food usage as being part of the history and physical and social environments of Indigenous peoples. This information was synthesized through systematic reviews and interviews (Abbott et al., 2007; Bell & Castetter, 1937; Bohrer, 1981, 1991; Castetter & Underhill, 1935; Crosswhite, 1981; Felger & Moser, 1976; Fish & Fish, 2008; Fritz et al., 2009; Gasser, 1982; Hodgson, 2001; Moerman, 2003; Rea, 1997) and necessarily represents a partial but substantial effort toward summarizing millennia of accumulated knowledge.

Indigenous peoples included in this study comprise the Akimel O'odham, Western Apache, Tohono O'odham, Hia C-eḍ O'odham, Maricopa, Kevelchadon, Quechan, Halchidhoma, Mohave, Kamia, Cahuilla, Cupeno, Cocopah, Seri, Yaqui (and Mayo combined under the name Cahita) and Pima Bajo, in addition to the ancestral populations of these groups, including populations that archaeologists recognize as Hohokam.

For each food plant, we identified closely related species that were selected through a systematic review of papers presenting relevant phylogenies (Supporting Information Appendix S1). Species were first categorized into usage types, as "used" if they were documented as being used for any purpose (e.g., ceremonial, medicinal, construction, food) by Indigenous peoples and "unused" if not. Species were also categorized separately into contrast types, as "sister" (most closely related) or as "congener" (i.e., other congeners), in order to provide a proxy for the utility of the comparison, under the premise that more closely related species are more likely to share traits and niches. If possible, multiple closely related species were chosen for each food plant species.

Only closely related species with at least one occurrence in the Sonoran Desert were included in the study, in order to limit issues of comparison to species that occur primarily outside the region. Given that this study focuses on the ratio, R/P, rather than R or P alone, there are no intrinsic biases in including species that might have only small portions of their ranges in the focal region, because R/P standardizes small realized ranges against small potential ranges.

Sometimes it was necessary to select a closely related species that was significantly less documented as being used or was not primarily used for food but for other purposes (e.g., medicinal, fibre, fuel), because many used species may have been locally extirpated or knowledge of these uses may have been lost in recent centuries (Bohrer, 1978; Hodgson, 2001). In some cases (92 of 349), no closely related species with ranges in the Sonoran Desert were identified, or no used closely related species was identified (2 of 349). These species were still used in the unpaired and trait analyses.

We excluded *Agave* spp. from this study, although they are common in the Sonoran Desert. Nearly all *Agave* species have documented uses, limiting the ability to make comparisons to unused congeners. Additionally, there are large uncertainties around the phylogenetic relationships amongst the domesticates and their wild progenitors within the Sonoran Desert.

2.4 | Estimating range filling

We used the realized/potential range size ratio (R/P) as a measure of how well species fill their potential ranges. Analyses were based on first mapping geographical distributions across North America, then clipping R and P to the extent of the Sonoran Desert. The clipping was carried out because the focus of the study was not on widely versus narrowly distributed species, but rather on the differential effect of human food use on range filling within this region. P was defined as the total number of pixels predicted to be suitable habitat using a species distribution model. R was defined as the number of pixels containing at least one occurrence point.

We built species distribution models using presence-only occurrence data using the "dismo" R package. Although such data are limited by potentially uneven sampling effort and prevalence (Hastie & Fithian, 2013), they represent the most reasonable option for these analyses. Systematic vegetation censuses of the Sonoran Desert are not available, and plant atlas maps do not exist. To overcome these limitations, we made several further methodological decisions.

First, to minimize spatial undersampling and to maximize representation of realized niches, we combined species occurrence data from several biodiversity databases: BIEN 4 (Maitner et al., 2018), SEINet (http://www.swbiodiversity.org/) and GBIF (https://www.gbif.org/). All databases were accessed between 11 and 14 September 2020. SEINet is focused on the Arizona region and contains numerous records not included in other databases. For BIEN only, only non-cultivated data were included. For GBIF, records were removed for non-herbarium sources, and for sources before 1945 owing to less reliable geolocation. Across databases, records were also removed if they were outside North America or corresponded to the location of zoos, botanical gardens, herbaria, universities, museums or open ocean. Data cleaning was performed using the CoordinateCleaner package in R (Zizka et al., 2019).

Second, to assess the effects of undersampling of some regions and oversampling of others, the analyses were conducted at both 25 and 50 km grain sizes, on a Lambers equal-area projection centred at 45° N, −100° E (Connor et al., 2018; Dungan et al., 2002; Elith & Leathwick, 2009).

Third, to standardize sampling effort as best as possible, we resampled (with replacement) all raw datasets to a total of 500 occurrences. We then grid sampled these resampled data to include a single

randomly selected record per pixel. We also omitted species from analyses if the grid-sampled data contained fewer than five occurrences or if the occurrence data resulted in an estimate of R of zero. A map of total raw, resampled and grid-sampled occurrence counts per pixel is shown in the Supporting Information (Figure S1). Across all species, there were a mean $\pm$ *SD* of $n = 913 \pm 1{,}687$ raw occurrences and $n = 133 \pm 104$ grid-sampled occurrences (across grain sizes).

To estimate R, we summed the areas of cells containing at least one presence record. This approach is sensitive to undersampling issues, but is ameliorated by the methodological choices described above.

To estimate P, we summed the areas of cells whose suitability exceeded a threshold value. Suitability was estimated for each species using species distribution models. We first generated pseudo-absence data with the same number of points as the grid-sampled data and sampled from the extent of North America. We then fitted each model using three methods: general additive model (gam), random forest (rf) and generalized boosted regressions model (gbm) (Elith & Leathwick, 2009). Each model was replicated 10 times, using 80% of the data randomly selected for training and 20% for testing. An ensemble model was then generated using a weighted average based on the area under the curve (AUC) statistic of each submodel (Araújo & New, 2007). The ensemble was then thresholded, based on the full input dataset, either to maximize the sum of sensitivity and specificity [max($se + sp$)] or to make sensitivity equal to specificity ($se = sp$) (Liu et al., 2005). We discarded species for which the ensemble mean AUC was < 80%. Ultimately, of the 20 models per species (two threshold choices multiplied by two spatial scales multiplied by five replicates), we retained a mean $\pm$ *SD* of $n = 17.7 \pm 4.3$ models that satisfied all of the above criteria.

Each model was based on the same small set of climate predictors, in order to develop a proxy for the potential distribution of each species in the absence of non-climatic factors (Bahn & McGill, 2007; Elith & Leathwick, 2009; Wisz et al., 2013). We chose a small set of variables to avoid model overfitting, in order to capture precipitation and temperature variation likely to be relevant to a broad range of species (Tomiolo & Ward, 2018). Climate data were obtained from the CHELSA database at 10 arc-min resolution (Karger et al., 2017). Predictors comprised: BIO1 = annual mean temperature, BIO5 = maximum temperature of warmest month, BIO6 = minimum temperature of coldest month, BIO12 = annual precipitation, BIO13 = precipitation of wettest month and BIO14 = precipitation of driest month (Supporting Information Figure S2).

2.5 | Ecological trait dataset

We assembled functional trait data for all species in the dataset, across usage and contrast types. Traits included growth-form (e.g., herb versus shrub), life-form (annual versus perennial) and polyploidy (binary, yes/no). Growth-form and life-form data were synthesized from the SEINet Portal Network (accessed July 2018; http://www.swbiodiversity.org/) and from the USDA Plant Database (accessed July 2018; https://plants.sc.egov.usda.gov/) and the Flora of North America (accessed July 2018; http://www.efloras.org/flora_page.aspx?flora_id=1). Information on polyploidy was gathered from published studies (Supporting Information Appendix S1) and from the Chromosome Counts Database (Rice et al., 2015) (accessed July 2018; http://ccdb.tau.ac.il/). We obtained complete data for all traits except polyploidy, for which 59% had data available.

2.6 | Phylogeny

We assembled a phylogeny for all species used in the study. We first assigned family names to each species using the Taxonomic Name Resolution Service (http://tnrs.iplantcollaborative.org/). We then constructed a phylogeny using the V.PhyloMaker R package (Jin & Qian, 2019), using the "GBOTB.extended" backbone tree and the "scenario 3" algorithm for binding tips to nodes.

2.7 | Methodological analyses

We first determined whether R, P or R/P at 25 km grain size was correlated with the same statistic at 50 km grain size, across all species, for both threshold choices and across all species distribution model replicates. All of R, P and R/P were strongly correlated with themselves across grain sizes (Supporting Information Figure S3; mean $\pm$ *SD* $R^2 = 0.80 \pm 0.12$ across all methodological combinations), indicating that analyses at either scale would yield similar conclusions. We, therefore, present main text results for only 25 km spatial grain size. Variation across threshold choices and replicates was minimal; therefore, we averaged R/P to species level for all analyses hereafter.

Next, to determine whether methodological choices and undersampling influenced our conclusions, we also conducted additional regression analyses with potentially conflating variables. We built additional linear models determined with either the sampling intensity (number of grid-sampled presence records) or the success of the modelling procedure (mean AUC score) as the predictor and $\log_{10}$ R/P as the response, at both 25 and 50 km grain size. The effect of both variables was minimal [mean $\pm$ *SD* R^2 of 0.10 ± 0.01 for number of grid-sampled presence records (Supporting Information Figure S4); 0.0009 ± 0.0005 for AUC (Supporting Information Figure S5)]; therefore, we do not include these predictors in further main text analyses.

2.8 | Main analyses

We compared the distribution of R/P across all usage types and contrast types. A linear model of the form $\log_{10}$ R/P ~ Usage + Contrast Type was fitted. R/P was $\log_{10}$-transformed before analysis to meet error distribution assumptions. Data were summarized at the species-mean level (i.e., aggregating across species distribution model thresholds and replicates) before analysis. ANOVA (type II) was used to assess the significance of each predictor.

In a more stringent analysis, we also compared the change in the difference in R/P between each food plant and each of its used and unused contrasts, for both sister and congener contrast types. Data were summarized at the species-mean level (i.e., aggregating across species distribution model thresholds and replicates) before analysis. A linear model of the form $\log_{10}$ R/P ~ Usage + Contrast Type was fitted, and ANOVA (type II) was used to assess the significance of each predictor. The above two sets of analyses were not carried out with phylogenetic correction, because the units of analysis are species-contrast pairs and not species.

To determine whether the measured traits influenced R/P particularly for food plants, we built a generalized least squares model of the form $\log_{10}$ R/P ~ Usage × (Growth-Form + Life-Form + Polyploidy), incorporating a Brownian correlation structure based on the phylogeny for these species. In this case, the analysis was carried out with phylogenetic correction, because the units of analysis are species. This model specification includes an interaction between usage and traits, which is necessary to test the hypothesis that range filling is greater for species that are used and that have certain traits. The analysis was carried out for all usage types and contrast types but was restricted to cases where polyploidy data were available. We then used type II ANOVA to determine whether any of the trait predictors had a statistically significant effect on results. A Nagelkerke pseudo-R^2 (one minus the ratio between the log-likelihood of the full model and the equivalent intercept-only model) was used to report goodness-of-fit.

3 | RESULTS

3.1 | Range filling

Sonoran Desert food plants in unpaired analyses had higher R/P than their used and unused contrasts overall, regardless of whether the contrasts were sisters or congeners (overall model $F_{3,509} = 12.6$, $p = 6.6 \times 10^{-8}$, $R^2 = .07$; Figure 3; at 50 km grain in Supporting Information Figure S6). ANOVA indicated that usage was a significant

predictor ($p = 1.2 \times 10^{-8}$), whereas contrast type was not ($p = .96$). The model estimated that unused contrasts had R/P 32% lower than food plants, and used contrasts had R/P 10% lower than food plants.

In a more stringent paired analysis, we also found that Sonoran Desert food plants had higher R/P than their used and unused contrasts, each within the same genus (overall model $F_{2,414} = 15.0$, $p = 5.3 \times 10^{-7}$, $R^2 = .07$; Figure 4; at 50 km grain in Supporting Information Figure S7). As before, ANOVA indicated that usage was significant predictor ($p = 8.3 \times 10^{-8}$), whereas contrast type was not ($p = .7$). The model estimated that differences in R/P between food plants and their unused same-genus contrast were 10% lower than between food plants and their used same-genus contrasts. There was little effect from whether the contrast was either sister or congener (1% lower).

3.2 | Trait predictors of range filling

We found that there were minor interactive effects of traits and food usage on R/P (d.f. = 265, residual d.f. = 247, pseudo-R^2 = .04; Figure 5; at 50 km grain in Supporting Information Figure S8). ANOVA indicated that there was a significant main effect of usage ($p < .001$). There was also a significant interaction effect of usage × form ($p = .0001$) and a marginally significant effect of usage × perenniality ($p = .052$). R/P was higher for shrubs, succulents and trees that were also used for food or other purposes, or for annuals that were also used for food or other purposes, than for unused species.

## 4 | DISCUSSION

4.1 | Range filling

Sonoran Desert species that have been documented as being used for food filled their potential geographical range more than unused congeners, consistent with hypothesis A. This result was consistent across both an unpaired analysis, comparing all food plants and a

FIGURE 3 Variation in range-filling ratio, R/P, among food plants (red) and their unused (teal) and used (yellow) contrast species. Sister contrast species are shown with long-dashed lines and congener contrast species with short-dashed lines. Vertical lines indicate the group medians. Note that the x axis has been square root-transformed for visual clarity. Density plots aggregate data over different threshold choices and species distribution model replicates and reflect models run at 25 km spatial grain
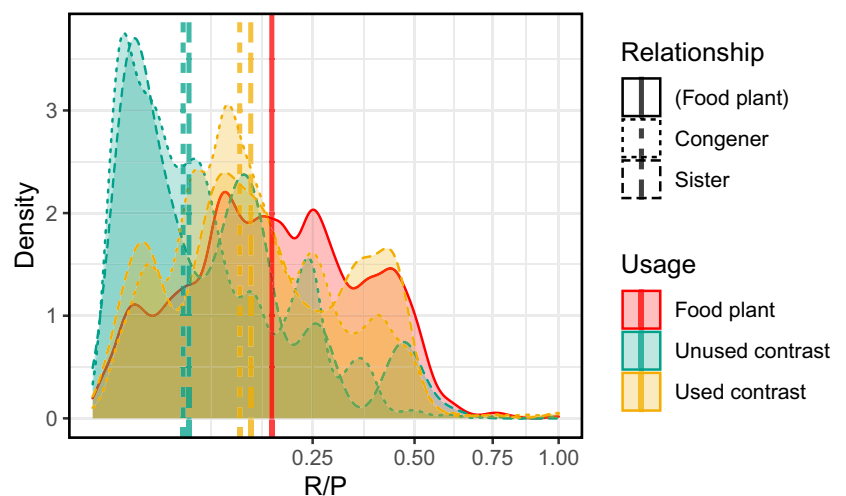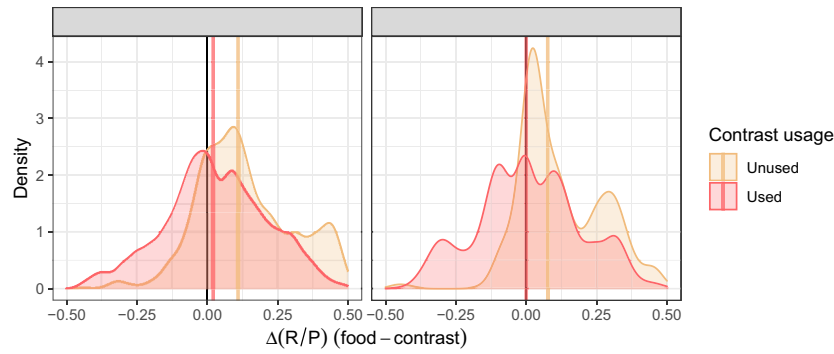
FIGURE 4 Differences in range-filling ratio, Δ(R/P), between food plants and either an unused contrast species (orange) or a used contrast species (red). Contrast species include those with realized ranges in the Sonoran Desert that are either sister species (right panel) or other congeners (left panel). Vertical lines show the null expectation of no difference (black), food plant–unused contrast median (orange) and food plant–used contrast median (red). Density plots aggregate data over different threshold choices and species distribution model replicates and reflect models run at 25 km spatial grain
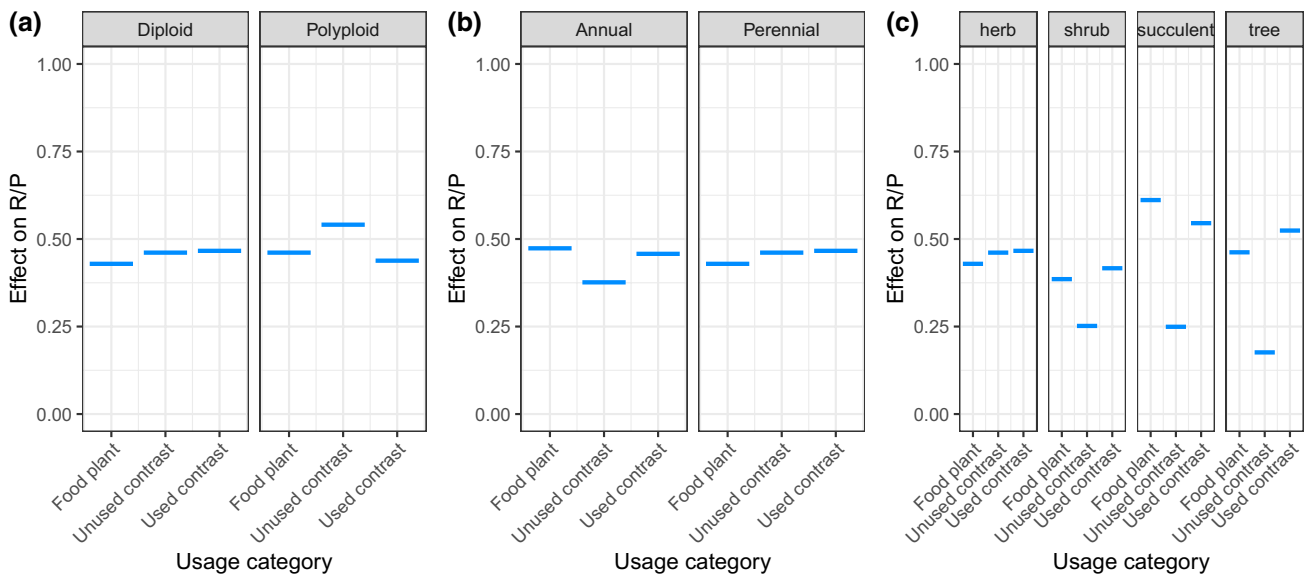
FIGURE 5 Effects of traits and usage on range filling (R/P) for all species in the dataset, for models of: (a) polyploidy, (b) duration and (c) growth-form. Effects have been back-transformed from a logarithmic to a linear scale for plotting. Confidence intervals are not shown owing to limitations of the visualization package

broad set of other species, and in a paired analysis, comparing differences in R/P between food plants and each of their sister and congeneric species.

Thus, the geographical ranges of economically and culturally significant plant species are likely to be influenced by non-environmental factors, that is, by human food usage. Although there is general consensus that both environmental filtering (i.e., abiotic constraints) and dispersal (e.g., chance colonization, differences in dispersal abilities) play a role in community assembly and distribution dynamics (Fraaije et al., 2015; Guo et al., 2005), our research suggests that past human-mediated dispersal of food plants is also a major driver of community assembly and distribution dynamics. However, the relatively low explained variation in the statistical models indicates that human use is not the only factor explaining range-filling patterns; for example, as seen in North American trees (Seliger

et al., 2021). Our results, therefore, provide an alternative and complementary explanation for previously described patterns of range filling (e.g., Seliger et al., 2021; Svenning & Sandel, 2013; Svenning & Skov, 2004) and build on prior studies of biogeographical consequences of human dispersal of plants (Abrams & Nowacki, 2008; Van Zonneveld et al., 2018; Warren, 2016) to provide flora-wide analyses and to carry out these analyses in an arid biome.

4.2 | Trait predictors of range filling

Ecological traits provide limited additional insight into which species are more likely to have geographical ranges modified by humans (Meyer et al., 2012). We found that food plant species had higher range filling among annual or non-herbaceous species, suggesting

that the effect of human use on geographical ranges is likely to have been greatest for these types of species. This result weakly supports hypothesis B, because the explained variation was low in this model.

We found that succulent food plants had higher R/P. Succulent species found in the Cactaceae and Asparagaceae families have been culturally important for many prehistorical and historical Sonoran Desert cultural populations, and the Sonoran Desert overlaps with some of the regions (e.g., arid Mexico and southwestern USA) where the Cactaceae lineage is prominent (Arakaki et al., 2011).

We also detected an interaction between annual growth-form and usage on R/P. There are many annual food plants that were important to past human populations in the Sonoran Desert (e.g., *Hordeum pusillum*). However, the region has an extensive amount of culturally and economically useful perennial species that range from perennial herbs to succulents (e.g., cacti, yucca, trees). It might be the case that these perennial species were already widely dispersed and thus there was less opportunity for additional human dispersal. The collective abundance and richness of these species suggests that there were more opportunities to use these plants because of the historical plant biogeography of the region. For example, the Akimel O'odham journeyed into the hills to gather the fruits of *Yucca baccata* Torr. (banana yucca) (Bell & Castetter, 1941), and they received the preserved fruit of *Y. baccata* var. *brevifolia* (Schott ex. Torr.) L. Benson & Darrow (Spanish dagger) and banana yucca in trade with the Tohono O'odham (Hodgson, 2001).

4.3 | Other explanations

Other factors beyond dispersal of plants by people could explain our findings. The most concerning possibility is methodology, if food plants either had more extensive sampling in the herbaria records we consulted or were associated with species distribution models with different thresholds. We showed that our results were robust to a number of methodological factors, including species distribution model grain size, threshold choice and goodness-of-fit, in addition to dataset sampling intensity. Thus, methodological choices are unlikely to drive our results.

It is also possible that the assumed causality is not correct, that is, that higher range filling causes human use, rather than human use causing higher range filling. Our data cannot distinguish between these possibilities, because we do not have the ability to infer the Pleistocene and Holocene range dynamics of hundreds of species from temporally resolved evidence (e.g., middens or phytoliths). It is difficult to imagine a mechanism by which people could select species based on P or R/P, because only R is directly observable. Additionally, extensive archaeological and phylogeographical evidence for selected species indicates a long history of humans moving food plants; for example, corn, chile and squash, all of which were domesticated in Mesoamerica and later widely spread (Pickersgill, 2007). Other archaeological evidence is also

consistent with human dispersal of plants; for example, palms from low-elevation coastal areas to higher-elevation north-central areas of what is now Mexico as early as during the Last Glacial Maximum (Ardelean et al., 2020).

It is possible that R/P is determined not by dispersal, but rather by species interactions among plants (Peterson, 2011; Soberon & Peterson, 2005; Wisz et al., 2013). Competitive interactions can set range limits in trailing-edge populations, whereas mutualistic interactions can set range limits in leading-edge populations. Such processes could lead to variability in R/P. We are unable to rule out this possibility without carrying out an infeasible number of large-scale experiments (Alexander et al., 2015), but suggest that these impacts are likely to be weak at large scales (Wisz et al., 2013).

Alternatively, R/P could be determined by dispersal mediated by species interactions among plants and animals. Food plants attractive to humans were also attractive to other dispersers, such as megaherbivores (Bocherens, 2018; Doughty et al., 2016; Gill, 2014; Guimarães Jr et al., 2008; Van Zonneveld et al., 2018). Megaherbivores can drive long-distance dispersal of species, often those with very large-seeded and fleshy fruits (Bocherens, 2018). Disentangling human and animal dispersal of plants is challenging, because extant animals, such as livestock, deer, coyotes and birds, continue to disperse some of these fruits, such as *Opuntia* spp. (prickly pear cactus) (Majure & Ervin, 2008). However, there is evidence that pre-contact human harvesting has been central to the maintenance of the geographical ranges for a variety of fleshy-fruited species (Guimarães Jr et al., 2008). Some Native Americans were cactus seed predators and dispersers. The Seri practised "second harvest" of *Pachycereus pringlei* (S. Watson) Britton & Rose (*cardón*) seeds, and several of the Baja California groups who used *Stenocereus gummosus* (Engelmann) Gibson & Horak and *Stenocereus thurberi* (Engelmann) Buxbaum (*pitahaya*) also practised this second type of harvest (del Barco 1980; Felger & Moser, 1976; Hodgson, 2001). They would leave their faecal material on a flat rock in the sun to dry, return to glean the seeds, and then clean and cook the seeds to be prepared for food, such as flour (del Barco 1980; Hodgson, 2001). *Proboscidea parviflora* (Woot.) Woot. & Standl. (Devil's claw) most probably had its populations severely reduced after megaherbivore extinction, but Native Americans maintained populations as a source of fibre for basketry and bred horticultural varieties (Bretting, 1986; Janzen, 1986). These interspecific human and plant interactions encouraged human-mediated dispersal of food plants and, perhaps, plants with other uses, such as fibre provisioning.

Last, R/P could also be impacted by colonial or industrial uses of plants by non-Indigenous peoples, that is, European settler-colonialists, especially via the establishment of missions. Not only did European settlers cultivate North American food plants, they also brought with them many of their own plants and domesticated animals (Crosby, 2003). The legacies of these animal introductions (e.g., horses) include browsing, grazing and trampling of herbaceous species, all of which can have complex impacts on species distributions (Bohrer, 1978). Although our spatial datasets cannot directly

uncover the time-scales over which human impacts have occurred, it is likely that current patterns have been shaped by both Indigenous peoples and settlers.

4.4 | Conclusion

Collaborative research between ecologists and archaeologists can expand our understanding of how past human land use has influenced ecosystem functioning and structure (Briggs et al., 2006; Hall et al., 2013). Here, we have shown that the impacts of past human food use in arid environments can also be significant, extending findings for pre-contact humans in the Amazon, Southeast Asia and Central America (Ford & Nigh, 2016; Levis et al., 2017; Yang et al., 2013). Indeed, the Sonoran Desert is already known for its rich biodiversity and ethnobotanical history (Hodgson, 2001).

Our work has shown that food plants fill more of their potential geographical range than their unused congeners, and that certain ecological traits can have an influence on range filling. Human dispersal of food plants is a key explanation for these patterns. Better quantification of the impacts of human-mediated dispersal of plants will be important for predictive modelling of biodiversity dynamics.

Assessing the role of human activity on species distributions is crucial for accurate forecasting and for data-driven conservation policy. There is a long history of governmental agencies and non-governmental organizations placing greater conservation value on landscapes thought to be untouched by humans (Denevan, 1992). This has resulted in negative social consequences via the exclusion of Indigenous peoples from protected areas and national parks (Agrawal & Redford, 2009; Anaya & Espírito-Santo, 2018; Brockington & Igoe, 2006; De Bont, 2015). Our work adds to a growing consensus that people and nature must be considered together in the Anthropocene, and that traditional use of plants has positive effects on ecosystems broadly (Anderson, 2013; Fowler & Lepofsky, 2011; Kimmerer, 2013). Furthermore, the documentation of human–plant relationships over the long term in the Sonoran desert across centuries strengthens Native claims on their homelands and helps to translate Indigenous statements of long-term presence on and relationship with the land in terms that intersect with ongoing discussions in the realm of governmental land management and planning. Recognizing the impacts of past land use on species distributions and community compositions helps to counter the colonialist views of Indigenous landscapes as 'pristine' people-free wilderness and can play a role in advocating for Indigenous sovereignty.

AUTHOR CONTRIBUTIONS
B.B. conceived the project. B.B. and C.F. designed research. C.F. performed research. C.F. and B.B. wrote the manuscript. W.C.H. and A.M.S. contributed ethnobotanical data and insight on Sonoran Desert food plants and cultural history. B.S.M. and B.J.E. provided ecoinformatics data and guidance on its usage. M.A.P. contributed information on Sonoran Desert prehistorical/historical human populations. All authors provided feedback on the manuscript.

DATA AVAILABILITY STATEMENT
The data and code underlying this study are available at: https://doi.org/10.6078/D1PH79

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BIOSKETCH

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SUPPORTING INFORMATION

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