Food Plant Biogeography of the Sonoran Desert

by

Carolyn Flower

A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Approved April 2019 by the
Graduate Supervisory Committee:

Benjamin Blonder, Chair
Wendy Hodgson
Andrew Salywon
Matthew Peeples

ARIZONA STATE UNIVERSITY

August 2019

ABSTRACT

There is an ongoing debate around the extent that anthropogenic processes influence both plant species distribution dynamics and plant biodiversity patterns. Past human food use may leave a strong legacy on not only the extent that food plants are dispersed and fill their potential geographic ranges, but also on food plant species richness in areas that have been densely populated by humans through time. The persistent legacy of plant domestication on contemporary species composition has been suggested to be significant in some regions. However, little is known about the effects that past human food use has had on the biogeography of the Sonoran Desert despite its rich cultural diversity and species richness. I used a combination of ecoinformatics, ethnobotanical, and archaeological data sources to quantitatively assess the impacts of pre-Columbian, and in some cases, more recent, human-mediated dispersal of food plants on the Sonoran Desert landscape. I found that (i) food plants do fill more of their potential geographic ranges than their un-used congeners, and that polyploidy, growth form, and life form are correlated with range filling and past food usage. I also found that (ii) both pre-Columbian and contemporary human population presence are correlated with relative food plant species richness. Thus, both past human food use and contemporary human activities may have influenced the geographic distribution of food plants at regional scales as well as species richness patterns. My research emphasizes that there is an interplay between ecological and anthropogenic processes, and that, therefore, humans must be considered as part of the landscape and included in ecological models.

ACKNOWLEDGMENTS

I would like to thank my advisor and mentor Benjamin Blonder for providing me the opportunity to attend graduate school as a member of the Macrosystems Ecology Lab. He cultivated a lab atmosphere that was equally fun and supportive as well as educational. I would also like to thank my committee members Wendy Hodgson, Andrew Salywon and Matthew Peeples for their encouragement and support. Thanks to Wendy Hodgson and Andrew Salywon for their enthusiasm and deep knowledge of Sonoran Desert ethnobotany. Thanks to Matthew Peeples for providing his expertise in Southwestern, U.S. archaeology.

I also want to thank postdoctoral researchers Luiza Aparecido and Pierre Gauzere and PhD students Courtenay Ray and Mickey Boakye from the Macrosystems Ecology Lab. They all guided me through many graduate school challenges ranging from conference presentations and grant proposals to statistical analyses. I also deeply appreciate the support of my parents Andrew and Susan Flower, and friends, Katie Hayes, Katie Delahoyde, Katie Miller, and Ashley Madera throughout this process.

I thank Edward Gilbert for helpful feedback on accessing botanical data within the SEINet Portal Network, as well as the Desert Botanical Garden librarian, Beth Brand, for her assistance finding references. I thank Dr. Robert Cámara Leret and Dr. Mauricio Diazgranados Cadelo of Kew Botanical Garden for their advice on digitizing the Sonoran Desert food plant’s dataset. I also thank archaeologist Sarah Oas, for her support and additional perspective on the analyses and discussion.

Finally, I would like to recognize all the indigenous people who have called the Sonoran Desert their home. Their intimate knowledge of plants and their environments is a reminder of the need to protect these useful and culturally important plants.

TABLE OF CONTENTS

CHAPTER Page

APPENDIX

LIST OF TABLES

LIST OF FIGURES

Figure Page

CHAPTER 1

INTRODUCTION

Drivers of Species' Geographic Ranges

A species geographic range is considered to be limited by the full range of biotic and abiotic conditions that influence its potential (i.e., or fundamental) and realized niche (Soberon & Peterson 2005, Soberon & Nakamura 2009). A recent review has suggested that studies on individual species' geographic ranges are predominantly considered in the context of climate factors (Tomiolio & Ward 2018). The "bioclimatic envelope hypothesis" is a backbone of many studies that operate under the assumption that species track their climatic envelope by shifting their distribution in order to match areas with favorable distributions (Tomiolio & Ward 2018). In particular, temperature and precipitation are two of the most frequently investigated drivers of range expansion and contraction (Tomiolio & Ward 2018).

Dispersal (e.g., seed, fruit, pollen) and species interactions may also influence species' geographic distributions (Soberon & Peterson 2005, Soberon & Nakamura 2009). The predominance of the "bioclimatic envelope hypothesis" has potentially caused a limited and biased understanding on what drives species range expansion (Tomiolio & Ward 2018). More research is emphasizing that the interspecific relationship between human and plant species has left a cumulative legacy on overall biodiversity patterns and species distribution dynamics (Boivin et. al. 2016). However, in many cases, anthropogenic factors (e.g., agriculture and urbanization) are overlooked and not considered as substantial drivers of range expansion i.e., a recent review found that only 4.3% of 109 papers addressed anthropogenic factors (Tomiolio & Ward 2018). It has been shown that multiple factors can be responsible for range expansion depending on habit and temporal and geographic scales (Tomiolio & Ward 2018). Although there are studies on range expansion that do account for both climate and anthropogenic factors, the percentage is quite low (Tomiolio & Ward 2018), and there is even less knowledge on their relative contribution to both range expansion and, in turn, richness patterns. The relationship between species distributions and species richness can be quite significant as the number of species in a given area is often influenced by each individual species' distribution.

Drivers of Richness Patterns

Humboldt was the first Western scientist to interpret the distribution of vegetation as being controlled by climate (Pausas & Bond 2018). Many of science's well-established hypotheses on species distributions and richness may be heavily biased toward Humboldt's forest-centric and climate-centric view of nature, dating back to the 1800s (Hawkins 2001, Pausas & Bond 2018). Europeans, like Humboldt, were accustomed to living in more forested environments and viewed alternative environments such as grasslands, savannas, and shrublands as fundamentally degraded (Pausas & Bond 2018). They did not necessarily consider how other factors in addition to climate (e.g., fire regimes herbivores, and megafauna dispersal, or humans) could have significantly shaped vegetation. This bias has arguably remained in ecology and biogeography with even a lack of recognition on the importance of certain plant consumers and/or disturbance variables (e.g., fire regimes and herbivores) in ecology and biogeography textbooks (Pausas & Bond 2018). Commonly, the distribution of species is explained in the more traditional terms of climate (e.g., the 'species-energy' hypothesis) and/or historical biogeography (e.g., the latitudinal diversity gradient, ‘out of the tropics’ hypothesis) at regional scales.

The climatically based species-energy hypothesis proposes that energy availability generates and maintains richness gradients (Hawkins et. al. 2003, Allen et. al. 2007). The latitudinal diversity gradient (LDG) is then potentially maintained as a direct consequence of greater energy availability towards the equator (Allen et. al. 2007). The LDG refers to the higher richness of species in the tropics compared to higher latitudes (Hawkins 2001, Willig et. al. 2003, Hillebrand 2004, Kerkhoff et. al. 2014). In terms of plants, the average species richness generally peaks where climate conditions are warm, wet and more seasonably stable and declines as conditions become colder, drier and more seasonably unstable (Janzen 1967, Gaston 2000, Ghalambor et. al. 2006, Kerkhoff et. al. 2014). Some studies have found that integrating both evolutionary and ecological processes is a promising framework for understanding biodiversity patterns (Kerkhoff et. al. 2014). The tropical conservatism hypothesis (TCH) proposes that part of the LDG could be explained due to niche conservatism; most clades originate in the tropics and then radiate outward, leading to higher diversification and lower extinction in the tropics (Weins & Donoghue 2004, Kerkhoff et. al. 2014). Plants in the tropics have also been observed to be limited in their ability to adapt to temperate climate conditions and are, therefore, also limited in their ability to disperse (Kerkhoff et. al. 2014).

Although the LDG is a very prominent pattern, species richness patterns can be very multifaceted. As a result, it is also important to consider underlying patterns that also influence species richness such as other spatial variables (e.g. longitude, elevation, depth) and environmental ones (e.g., topography, aridity) (Gaston 2000). The wide range of hypotheses proposed suggest that species richness is a complex pattern, and no single mechanism can adequately explain a given pattern especially at varying spatial scales (Gaston 2000). Studies show that not one of the major groups of biodiversity theories can explain the LDG alone (Lamanna et. al. 2014). Research also suggests that although modern climate has a very strong influence on species richness, it is not the only factor influencing species richness (Hawkins et. al. 2003). Importantly, climatic variables are sometimes insufficient in explaining richness gradients even over large spatial extents (Hawkins et. al. 2003). For example, differences in grain size and spatial extent can influence the relative contributions of climatic variables in regression models (Hawkins et. al. 2003). Studies also show that wildfires and anthropogenic fires as well as animal activity (e.g., grazing) can influence species richness patterns (Tomiolo & Ward 2018). It is important to be mindful of the Humboldtian bias and avoid overlooking other plant consumers, such as past humans, as significant environmental shapers and consider disturbance as a central mechanism in nature (Pausas & Bond 2018).

Alternative Hypotheses for the Drivers of Species' Geographic Ranges and Richness Patterns

Plants have been used by humans for food as well as for medicine, fiber, fuel, construction, and spiritual purposes for millennia (Boivin et. al. 2016). The lines between uses can be complex due to people's relationships with natural, social and spiritual domains (Gruca et. al. 2014). For example, often times, the spiritual framework (e.g., supernatural forces, mystic powers) is an inextricable part of traditional medicine (Gruca et. al. 2014). The ramifications of overall past plant use can also be seen in the architectural legacies of past pre-Columbian societies. The great houses of Chaco

Canyon, New Mexico are some of the largest pre-Columbian buildings in North America with over 240,000 trees used in construction (Guiterman, C.H. et. al. 2015). Recent research has shown that 70% of timbers likely originated over 75 km away from Chaco, suggesting an enormous investment in materials, labor, and human ingenuity partially due to plant resource availability (Guiterman, C.H. et. al. 2015). Collaborative research between ecologists and archaeologists have further expanded our knowledge on how plant resource availability can impact past human-mediated selection of plants for food. This interspecific relationship between plants and humans can also influence species richness patterns, emphasizing the importance of viewing landscapes as biocultural systems (Briggs et. al. 2006).

An explanation for plant richness patterns that has been gaining more attention is the past human-mediated dispersal and cultivation of food plants. There are significant instances globally that suggest that broad ecological dynamics such as plant species richness can be a product of past human farming and cultivation of wild plants (Ross, 2011, Boivin et. al. 2016, Levis et. al. 2017). Several lines of evidence suggest that this human-environment relationship in which humans influence ecosystems due to agricultural practices has been significant in certain regions since the late Pleistocene (e.g., Southwest Asia (Fuller et. al. 2012), South America (Clement et. al. 2010), North China (Bettinger et. al. 2010); and see Ellis et. al. 2013). In Southwest Asia, recent evidence suggests a higher species richness of food plants that were involved in early cultivation than originally thought (i.e., only eight founder crops). There are now considered to be 16 or 17 major food plant species such as *Avena sterilis* L. (wild oat), *Vicia peregrina* L. (vetch), and *Lathyrus sativus* L. (grass pea) (Fuller et. al. 2012). In

South America, at least 138 crops were being cultivated and managed by native Amazonians, and certain ones such as *Manihot esculenta* Crantz (manioc) and *Bactris gasipaes* Kunth. (peach palm) were widely dispersed by humans in Amazonia (Clement et. al. 2010). Charred macrofossils of *Panicum miliaceum* L. (broomcorn millet) and the increase in ceramic remains supports how intensive farming became in North China ca. 7000-5700 BP. Biocultural systems are products of both the choices people have made as well as the variety of factors (e.g. the physical environment, social conditions) that influence those choices.

The factors that drive species distributions and richness also depend on spatial scale (McGill 2010). Interdisciplinary research can provide a more balanced perspective on the relative importance of variables that potentially drive biodiversity patterns at these different scales. For example, for decades, researchers subscribed to the belief that plant species assemblages characterizing various regions (e.g., lowland Amazonian rain forest, Sonoran Desert) were nearly ‘pristine’ and untouched by past human populations (Bush et. al. 2015). Contemporary research that incorporates archaeological data and the archaeological perspectives suggest this is not the case. This research is further suggesting that the persistent legacy of past human impact can vary at different scales (see Levis et. al. 2017 for regional scale example, Hall et. al. 2013 for a local scale example, and Bush et. al. 2015 for overall discussion on the spatial heterogeneity of human settlement). Archaeology and paleoecology have enabled long-term reconstruction of population and land-use histories. These data can be integrated into ecological and geo-spatial studies on biodiversity patterns and species distribution dynamics (Ellis et. al. 2013).

Including more perspectives in both ecology and archaeology can encourage a variety of ideas and viewpoints in conservation policy and biogeography as a discipline. Collaborative research can help disentangle the drivers of biodiversity patterns. By incorporating multiple lines of thinking, we can avoid considering landscapes to be either completely ‘pristine’ and decoupled from human land-use legacies or as cultural parks, completely influenced by humans disregarding climatic effects and biotic interactions. In this way it may be easier to avoid extreme false dichotomies of either ‘no use’ or ‘all use’ (Bush et. al. 2015).

It can be challenging to ascertain the relative contributions of multiple impacts, and how well each contribution may be maintained on the landscape over time at varying spatial and temporal scales. Although in many regions there is indisputable evidence that past humans impacted the landscape through food use (Ross 2011, Hall et. al. 2013, Sedrez dos Reis et. al. 2014, Bush et. al. 2015, Levis et. al. 2017), it can be difficult to draw a distinction between the legacies of past people and contemporary human impacts (Bush et. al. 2015). In regard to anthropogenic factors, both past and modern agricultural practices as well as the encouragement of wild food plants can alter species’ dispersal regimes, impact soil quality and nutrient pools (Normand et. al. 2017).

Implications

Although the extent of pre-Columbian and historical human food use can differ depending on the region, these findings still have long-term implications for how biodiversity conservation is approached. Advocacy for conservation policy that includes Native American and other indigenous perspectives is being seen as more necessary to prevent the loss of biological, cultural, and food diversity (Foster et. al. 2003, Gavin et.

al. 2015). A recent study estimated that indigenous populations manage or have tenure rights over at least ~38 million km^2 in 87 countries or politically distinct areas on all inhabited continents (Garnett et. al. 2018). This represents over a quarter of the world's land surface (Garnett et. al. 2018). In many cases, these groups have long-standing relationships with the land, having used and modified landscapes for millennia. In this way, they can bring an important perspective to how contemporary land use is approached. As such, biocultural conservation recognizes that broad questions on biodiversity patterns cannot be taken on without collaborative partnerships amongst scientists and archaeologists, governments, conservation practitioners, and indigenous populations (Gavin et. al. 2015, Garnett et. al. 2018).

There are still challenges in regard to how biocultural conservation is approached. Even global and national conservation strategies that include indigenous communities still ignore local economic and infrastructure needs and the long-term implications for local populations. Misrepresentations and stereotyping of indigenous groups also remain, with mismatches between what the government and scientific community expects of indigenous groups and how indigenous groups view their role in conservation (Kohler & Brondizio 2016).

Despite the continued debate on how to implement biocultural conservation (Kohler & Brondizio 2016), researchers need to consider the social-ecological relationships that have been occurring for millennia (Boivin et. al. 2016). To be effective at understanding biodiversity patterns and conserving ecosystems, researchers need to go beyond the view of humans as only a recent disturbance. Similar to having more inclusive biodiversity conservation approaches (Gavin et. al. 2015, Garnett et. al. 2018), there also needs to be a continued focus on making the study of biogeography and, in turn, biodiversity patterns, more inclusive.

My study contributes to a growing body of research suggesting that it is also important to include past humans from biogeographical processes such as dispersal. I suggest that in semi-arid regions of the world (i.e., the Sonoran Desert and Southwest, U.S.) it is also important to consider the pre-Columbian and historic use of plants for food on biogeographic processes (i.e., dispersal) that can drive species richness on both large and smaller geographic scales. In this thesis I test the core idea that human activity is a major driver of plant species richness in the Sonoran Desert.

In Chapter 2, I investigate whether human food use in pre-Columbian and more recent times determine how well a species fills its potential geographic range. I also investigate whether there are certain ecological traits that predispose certain species to human food use and fill their potential range more than others. In Chapter 3, I investigate whether both pre-Columbian or contemporary human population presence predicts relative food plant species richness patterns for the Hohokam region (i.e., an area of the Sonoran Desert populated by sedentary pre-Columbian agriculturalists from 400-1450 A.D.). Together, these results suggest that both past human food use and contemporary human activities influence the geographic distribution of food plants at regional scales as well as species richness patterns. I argue that it is important to view landscapes as palimpsests, in which layers of ecological processes and human activity are etched on and erased temporally and spatially. My results also emphasize that the Sonoran Desert is a biocultural landscape, and that there needs to continue to be a cross-disciplinary approach to ecological research. This is the essential in order to address broad biogeographical questions on distribution and biodiversity patterns.

REFERENCES

Allen, A. P. Gillooly, J.F. & Brown, J.H. (2007). Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. Pages 283-299 in D. Storch, P.A. Marquet, and J.H. Brown, editors. Scaling Biodiversity. Cambridge University Press, Cambridge, U.K.

Bettinger, R.L., Barton, L. & Morgan, C. (2010). The origins of food production in North China: a different kind of agricultural revolution. *Evol. Anthropol*. 19. 9-21.

Bovin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denham, T. et. al. (2016). Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *PNAS*. 113, 6388-6396.

Briggs, J.M., Spielmann, K.A., Schaafsma, H., Kintigh, K.W., Kruse, M., Morehose, K. et. al. (2006). Why ecology needs archaeologists and archaeology needs ecologists. *Front Ecol. Environ*. 4, 180-188.

Bush, M.B., McMichael, C.H., Piperno, D.R., Silman, M.R., Barlow, J., Peres, C.A. et. al. (2015). Anthropogenic influence on Amazonian forests in pre-history: an ecological perspective. *J. Biogeogr*. 42. 2277-2288.

Clement C.R. & Junqueira A.B. (2010). Between a pristine myth and an impoverished future. *Biotropica*. 42(5). 534-536.

Ellis, E.C., Kaplan, J.O., Fuller, D. Q., Vavrus, S., Goldwijk, K.K. & Verburg, P.H. (2013). Used planet: a global history. *PNAS*. 110(20). 7978-7985.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D. et. al. (2003). The importance of land-use legacies to ecology and conservation. *Bioscience*. 53(1). 77-88.

Fuller, D.Q., Willcox, G., & Allaby, R.G. (2011). Early agricultural pathways: moving outside the ‘core area’ hypothesis in Southwest Asia. *J. Exp. Bot*. 63(2). 617-633.

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*. 405(6783). 220-227.

Garnett, S.T., Burgess, N.D., Fa, J.E., Fernandez-Llamazares, A., Molnar, Z., Robinson, C.J. et. al. (2018). A spatial overview of the global importance of Indigenous lands for conservation. *Nat. Sustain*. 1(7). 369-374.

Gavin, M.C., McCarter, J., Mead, A., Berkes, F., Stepp, J.R., Peterson, D. et. al. (2015). Defining biocultural approaches to conservation. *Trends Ecol Evol.* 30(3). 140-145.

Ghalambor, C. K., Huey, R.B., Martin, P.R, Tewksbury, J.J. & Wang. G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Intreg. Comp. Biol.* 46(1). 5-17.

Gruca, M., Camara-Leret, R., Macia, M.J. & Balslev, H. (2014). New categories for traditional medicine in the Economic Botany Data Collection Standard. *J. Ethnopharmacol.* 155(2). 1388-1392.

Guiterman, C.H., Swetnam, T.W. & Dean, J.S. (2015). Eleventh-century shift in timber procurement areas for the great houses of Chaco Canyon. *PNAS.* 113(5). 1186-1190.

Hall, S.J., Trujillo, J., Nakase, D., Strawhacker, C., Kruse-Peeples, M., Schaafsma, H. et. al. (2013). Legacies of prehistoric agricultural practices within plant and soil properties across an arid ecosystem. *Ecosystems*. 16(7), 1273-1293.

Hawkins, B.A. (2001). Ecology's oldest pattern? *Trends Ecol. Evol*. 16(8). 470.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J., Kaufman, D.M. et. al. (2003). Energy, water and broad-scale geographic patterns of species richness. *Ecology*. 84(12). 3105-3117.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat.* 163(2). 192-211.

Kerkhoff, A.J., Moriarty, P.E. & Weiser, M.D. (2014). The latitudinal species richness gradient in new world woody angiosperms is consistent with the tropical conservatism hypothesis. *PNAS*. 11(22). 8125-8130.

Kohler, F. & Brondizio, E.S. (2016). Considering the needs of indigenous and local populations in conservation programs. *Consrv.Biol.*. 31(2). 245-251.

Lamanna, C., Blonder, B., Violle, C., Kraft, N.J.B., Sandel, B., Simova, I. et. al. (2014). Functional trait space and the latitudinal diversity gradient. *PNAS*. 111(38) 13745-13750.

Levis, C., Costa, F.R.C, Bongers, F., Pena-Claros, M., Clement, C.R., Junqueira, A.B. et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*. 355(6329), 925-931.

McGill, B.J. (2010). Matters of scale. *Science*. 328(5978). 575-576.

Normand, S. Hoye, T.T., Forbes, B.C., Bowden, J.J., Davies, A.L., Odgaard, B.V. et. al. (2017). Legacies of historical human activities in arctic woody plant dynamics. *Annu. Rev. Environ. Resour*. 42(17). 541-567.

Pausas, J.G. & Bond, W.J. (2018). Humboldt and the reinvention of nature. *J. Ecol*. 10(11110. 1-7.

Ross, N.J. (2011). Modern tree species composition reflects ancient Maya "forest gardens" in northwest Belize. *Ecol. Appl*. 21(1). 75-84.

Sedrez dos Reis, M., Ladio, A. & Peroni, N. (2014). Landscapes with *Araucaria* in South America: evidence for a cultural dimension. *Ecol. Soc*. 19(2). 43.

Soberon, J. & Nakamura, M. (2009). Niches and distributional areas: concepts, methods, and assumptions. *PNAS*. 106. 19644-19650.

Soberon, J. & Peterson, A.T. (2005). Interpretations of models of fundamental ecological niches and species' distributional areas. *Biodiv. Inf.*. 2. 1-10.

Tomiolo, S. & Ward, D. (2018). Species migrations and range shifts: a synthesis of causes and consequences. *Perspect. Plant. Ecol. Syst.*. 33. 62-77.

Wiens, J.J. & Donoghue, M.J. (2004). Historical biogeography, ecology and species richness. *Trends Ecol. Evol*. 19(12). 639-644.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.*. 34. 273-309.

CHAPTER 2

FOOD USE EXPANDED PLANT SPECIES DISTRIBUTIONS IN THE SONORAN DESERT

ABSTRACT

Climate is usually regarded as the main determinant of plant species' distributions. However, past human use of species for food may have factored into regional and continental species' climatic geographic ranges. I hypothesized that increased human-mediated dispersal of food plants has resulted in species filling more of their potential climatic geographic range. I also hypothesized that key ecological traits could predispose a species to occupy more of its potential climatic geographic range and be selected by humans for food. By integrating ethnobotanical knowledge and ecoinformatics data for the Sonoran Desert, I found that food plants fill more of their potential geographic ranges than their un-used congeners. I also found that polyploidy, growth form, and life form are correlated with range filling and past food usage. This study demonstrates that human food preferences can leave a long-lasting impact on the distribution of plant species today.

INTRODUCTION

The reshaping of global biodiversity by humans has had a significant impact on Earth's ecosystems (McKey et al. 2010, Bovin et. al. 2016, Levis et. al. 2017). However, a key component missing from species distribution modeling, is the ecological legacy of past human populations (McKey et. al. 2010). Species distribution modeling typically assumes that any given species geographic distribution is influenced by three central processes: (**i**) biotic interactions (i.e., competition, predation, mutualisms, etc.); (**ii**) abiotic factors (i.e., temperature, precipitation, geographic space, etc.); (**iii**) movement via dispersal (i.e., seed, pollen, humans) (the BAM framework; Soberon & Peterson 2005, Soberon & Nakamura 2009, Peterson 2011). While biotic and abiotic factors are known important drivers of plant distributions, the relative role of dispersal in influencing a species geographic range is less clear (Soberon & Peterson 2005). In particular, the impact of prehistoric and historic human populations on this third process, movement via dispersal, is often overlooked. However, there is growing evidence that present-day species distributions cannot be fully understood without also addressing the past impacts of human movement of species on the landscape, whether direct (e.g., via cultivation) or indirect (e.g., via alteration of habitats) (Bovin et. al. 2016).

Including humans as potential drivers of species distributions is needed to forecast future changes in biodiversity. Collaborative research between ecologists and archaeologists is expanding our understanding of how past human land use has influenced ecosystem functioning and structure (e.g. Briggs et. al. 2006, Hall et. al. 2013). Ecological niche models (ENMs) that incorporate anthropogenic features (e.g. agricultural lands) can improve predictions relative to ENMs that are based solely on environmental variables because species’ distribution dynamics unfold within an ecological-cultural (i.e. biocultural) system (Kodis et. al. 2018). Assessing the role of human activity on landscapes is critical for accurate forecasting, as well as for data-driven policy-making around conservation. There is a long history of governmental agencies and NGOs placing greater conservation value on landscapes thought to be untouched by humans. This has caused negative social consequences via the exclusion of indigenous populations from protected areas and national parks (Denevan 1992, Brockington & Igoe 2006, Agrawai & Redford 2009, De Bont 2015, Anaya & Espírito-Santo 2018).

Plants have been used by humans for many purposes, such as medicine, ceremony, construction and food, for millennia and these uses tend to overlap. However, the use of plants for food is one of the most important ways humans may increase the distributions of plants, via propagation, wild-harvesting, and dispersal. Human populations have reorganized plant distributions at regional and continental scales (Crosby, Jr. 1972). In many landscapes, the legacy of humans remains apparent today (Abrams & Nowacki 2008, Shephard Jr. & Ramirez 2011, Warren II 2016, Levis et. al. 2017, but see also MacDougall 2003). The majority of evidence for this legacy comes from Amazonia (Bitencourt & Krauspenhar 2006, Clement & Junqueiria 2010, , Shephard Jr. & Ramirez 2011, Sedrez dos Reis, Ladio & Peroni 2014, Clement et. al. 2015, Levis et. al. 2017, Junqueira et. al. 2017, Levis et. al. 2018, but also see McMichael, C.H. et. al. 2017), Southeast Asia (Brosius 1991, Barton & Denham 2011, Yang et. al 2013), and Central America (Nesheim et al. 2010, Ford et. al. 2016). In South America, the geographic expansion of *Araucaria araucana* (Mol.) C. Koch (monkey puzzle tree) and *Araucaria angustifolia* (Bert.) O. Kuntze (Brazilian pine nut) was not only caused by more favorable climate conditions, but also past hunter-gathers (Bitencourt & Krauspenhar 2006, Sedrez dos Reis, Ladio & Peroni 2014). The expanded distribution of the *Bertholletia excelsa* Bonpl. (Brazil nut) has been facilitated by past human populations through cultivation and trade of the seeds (Shepard Jr. & Ramirez 2011). Across both island Southeast Asia and New Guinea, past inhabitants exploited plants such as *Eugeissona utilis* Becc. (sago), *Colocasia esculenta* (L.) Schott (taro), *Dioscorea* spp. (yam), and *Musa* spp. (banana) (Brosius 1991, Barton & Denham 2011, Yang et. al 2013 & Bovin et. al. 2016). In Central America, the Maya cultivated forest gardens, encouraging and farming numerous food plants (e.g. *Zea mays L.*) (Ford et. al. 2016).

Impacts of humans are best established for food plants that are economically important in the present day. However, biogeographers still lack understanding of the quantitative scope of human impacts on the geographic distribution of the vast majority of food plants that are no longer a major component of human diets. A key way to address this is through the concept of range filling (Svenning & Skov 2004), defined here as the ratio between the realized (R) and potential (P) geographic range. R/P is a measure of how well species have dispersed to fill their potential ranges (Svenning & Skov 2004). In order to examine the role humans have played in expanding plant species realized geographic ranges, I asked:

1) did human food use in prehistoric and historic times statistically influence R/P?
2) what ecological traits predisposed species to food use and high R/P?

I hypothesized that past human utilization of food plant species has resulted in increased dispersal to favorable habitats, assuming that ranges are otherwise limited by dispersal (Holt et. al. 2004, Guo et. al. 2005, Svenning et. al. 2008). As a result, compared to un-used congeners and other un-used species, food plants should maintain higher population densities and fill more of their potential geographic range (i.e., have higher R/P) than their un-used congeners, which presumably have otherwise similar phenotypes and life histories (Wiens & Graham 2005) (**Hypothesis A**).

I also hypothesized that certain plant traits like polyploidy, growth form (i.e., herb, shrub, tree), and life form (i.e., perennial or annual) should predispose certain species to be selected for by humans and/or fill their potential geographic distribution range more fully (**Hypothesis B**). (Meyer et. al. 2012, Meyer & Purugganan 2013). For example, both growth form and life form can play a significant role in predicting species' range limits (Violle et. al. 2014, Stahl et al. 2014) and human food use (Meyer et. al. 2012, Whitehead et. al. 2016). Additionally, certain traits associated with polyploidy could predispose these species to higher range filling and human food use (e.g., increased disease resistance, phenotypic plasticity) (Meyers et. al. 2012).

I focused my study on the Sonoran Desert in southwestern North America (Omernik 2004, Wiken et. al. 2011, USEPA 2016). The Sonoran Desert has immense plant diversity, with a long history of human occupation by both foraging and agricultural populations throughout the Holocene (Bell & Castetter 1937, Bohrer 1987, Bohrer 1991, Rea 1997, Hodgson 2001). The Sonoran Desert contains the oldest evidence for maize agriculture north of Mesoamerica dating to ca. 2100 B.P. (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 Sonoran Desert is perhaps most closely associated with the Hohokam archaeological culture (ca. A.D. 400-1450), which was characterized by large and long-lived settlements, intensive agriculture including hundreds of miles of irrigation canals along major rivers, and an exchange and market system extending throughout much of the region and beyond (Bayman 2001, Abbott et. al. 2007; Fish & Fish 2007, Hodgson et. al. 2018). The later prehistory of the Sonoran Desert saw substantial population declines (see Hill et. al. 2004) and an end to many of the hallmarks of the Hohokam system. However, there is evidence of continuity occupation and agricultural land use in some areas (see Loendorf et. al. 2013, Loendorf & Lewis 2017), and evidence of new arrivals in others as the diverse contemporary indigenous populations of the Sonoran Desert became recognizable in the archaeological record (e.g., O'odham, Seri, Apache, Maricopa, Yavapai, Cocopa, and others). The diets of these populations varied due to vegetational, faunal, and environmental differences, but they all used Sonoran Desert plants extensively for food and other uses (e.g., medicinal and ceremonial) (Castetter & Underhill 1935, Felger & Moser 1976, Crosswhite 1981, Bohrer 1991, Hodgson 2001, Rea 2007, Nabhan 2016).

There has been limited quantitative analysis on the distributions of the many native plants that were utilized for food by various prehistoric and historic populations in the Sonoran Desert. Such analysis would provide a key test case for understanding the prevalence of human impacts on plant distributions in semi-arid regions. It seems likely that hundreds of species were, at the very least, wild harvested, and some were possibly domesticated or cultivated (Castetter & Underhill 1935, Hodgson 2001, Hodgson et. al. 2018). Archaeological, morphological, and molecular evidence leaves little doubt that

Agave spp. such as *A. murpheyi* F. Gibson (Hohokam Agave), *A. delamateri* W.C. Hodgson & L. Slauson (Tonto Basin Agave), and *Agave sanpedroensis* (San Pedro Agave) W. C. Hodgson & Salywon are pre-Columbian domesticates extensively cultivated in Arizona by indigenous peoples (Parker et. al. 2007, Hodgson & Salywon 2013, Hodgson et. al. 2018). Mesquite, (*Prosopis glandulosa* Torr., *P. velutina* Woot., and *P. pubescens* Benth.), was one of the most widespread and useful wild-harvested food plants in the Sonoran Desert (Bell & Castetter 1937, 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). Other examples of plants moved by past people include *Cylindropuntia fulgida* (Engelm.) Knuth (chain-fruit cholla) and *Stenocereus thurberi* (Engelm.) Buxbaum (organ-pipe cactus) by the Seri and *Hordeum pusillum* Nutt. (little barley), a pre-Columbian domesticate of the Hohokam (Hodgson 2001).

Some researchers also argue that crops moved as part of "ecological packages" that included non-domesticated or "weed" species (Bovin et. al. 2016). The Hohokam took up prolonged residence in which successive generations continued to irrigate land as well as farm and harvest a variety of plants, including weedy species (Fish & Fish 2007, Bayman 2001). Weedy annuals, especially *Chenopodium* spp.(goosefoot), are frequently recovered at archeological sites as well as *Amaranthus* spp. (amaranth), *Descurainia* spp. (tansy mustard), *Astragalus* spp. (milk vetch), and *Hordeum pusillum* Nutt. (little barley) (Gasser 1981, Bohrer 1987, Gasser & Kwiatkowski 1991, Bohrer 1991, Fritz et. al. 2009).

Historic Akimel O'odham populations managed both cultivated fields and "second gardens" that were comprised of wild and semi-wild greens (Crosswhite 1981). These "weeds" included *Amaranthus palmeri* S. Watson (Palmer's amaranth), *Portulaca oleracea* L. (little hogweed), *Descurainia pinnata* (Walter) Britton (western tansy mustard), and *Salvia columbariae* Benth. (desert chia) (Rea 2007). Any weeds 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, Rea 1997). These are just a few examples of a much broader history of food plant usage that was a significant part of past indigenous peoples' (e.g., O'odham, Apache, Yavapai, Seri, Mohave, Cocopah) livelihoods in the Sonoran Desert region.

To assess my hypotheses, I quantified the extent at which past human populations have driven current species distribution and biodiversity dynamics through the domestication, cultivation, and wild harvesting of Sonoran Desert food plants. These results explore the extent of human impacts in a more arid region (i.e. an understudied region for this kind of research) and provide an example case for exploring human impacts on plant biogeography elsewhere.

MATERIALS AND METHODS

Ethnobotanical Dataset

I developed an ethnobotanical dataset of Sonoran Desert food plants based on Hodgson (2001) comprising 356 food plants that have been used by multiple past human populations. These plants were selected based on their native origin and available documentation (i.e., ethnographies, voucher specimens) that could contextualize their food usage as being part of the history, physical, and social environments of indigenous populations (Hodgson 2001). Populations include the Hohokam, Akimel O’odham, Western Apache, Tohono O’odham, Hia C-eḍ O'odham, Maricopa, Kevelchadon, Quechan, Halchidhoma, Mohave, Kumeyaay, Cahuilla, Cupeño, Cocopah, Seri, Yaqui (and Mayo combined under the name Cahita), and Pima Bajo. Non-native food plant species (e.g., *Erodium cicutarium* (L.) L'Hér. ex Aiton, *Sonchus* spp.) were not included in this study to focus the analysis on native, food plants of the Sonoran Desert. Species such as *Cyperus rotundus* L. (sedge), *C.esculentus* L. (sedge) were included due to being quite naturalized and cosmopolitan in the region. *Lantana camara* L. (lantana) and *Bidens pilosa* L. (hairy beggarticks) were also included as they also are considered to be relatively naturalized and originate in the Americas. As the study of ethnobotany is continually evolving, there may still be food plants with inferred uses that are not yet documented. For this reason, I decided to focus on a core set of food plants with the understanding that this plant list may be updated in the future. It is also important to note that cultural groups can have their own folk taxonomy, describing and organizing their natural surroundings from collective social knowledge (Rea 1997). Sometimes Linnaean taxonomy and folk taxonomy do not fit conveniently together because a group or person may combine what they consider to be similar plants together, referring to them with the same name. The potential inconsistencies between folk taxonomy and scientific names is another aspect to keep in mind when considering my results (Wendy Hodgson, per. comm., April 22, 2019).

For each food plant, I identified the closest relatives that were used and those that were un-used by pre-Columbian peoples (see **Appendix A:** List of Food Plants and Congeners Excel Spreadsheet). I refer to these species as congeners and note that they may or may not include sister species. Used and un-used congeners were selected through a systematic review of phylogenetic publications (see **Appendix B:** Phylogenetic Literature Review). Species were considered "used" if they were documented as being utilized for any purpose (e.g., ceremonial, medicinal, construction, food) by pre-Columbian peoples. Species that were not documented to have been used for any purpose were designated "un-used". The North American Native American Database (Moerman 2003) as well as IUCN species lists, SEINet, (SEINet Portal Network 2018) and ethnobotanical articles were queried to ascertain the proper category for each species. Un-used congeners were selected for the comparative analysis with the core Sonoran Desert food species. Sometimes it was necessary to select a congener that was significantly less documented as being utilized or was not primarily used for food but for other purposes (e.g., medicinal, fiber, fuel).

I excluded *Agave* spp. from this study. It was not possible to model *Agave* because of large uncertainties around the phylogenetic relationships amongst the domesticates and their wild progenitors within the Sonoran Desert; moreover, nearly all *Agave* species have documented uses, limiting ability to make comparisons to unused congeners (Parker et. al. 2007, Hodgson & Salywon 2013, Parker et. al. 2014, Hodgson et. al. 2018, Wendy C. Hodgson, Andrew M. Salywon, per. comm.March 28, 2018). In total, *n*=801 food plants and used/un-used congeners were included in the R/P analysis.

Estimating range filling

I used the realized/potential range size ratio (R/P) as a measure of how well species fill their potential ranges based on rasterized geographic distribution data. 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. Both R and P were calculated for North America as well as clipped to the Sonoran Desert. R was then calculated as the number of cells with at least one observation, while P was calculated as the number of cells predicted as suitable (above a threshold value) by a species distribution model. For the Sonoran Desert analysis, both R and P were calculated using a 10km x 10km pixel grain size. The North America R and P were estimated at a much coarser resolution of 50 km x 50 km to account for this being a continental scale analysis. As there is no single natural scale that ecological patterns should be studied, these scales were chosen to account for the varying geographic extents (e.g., regional and continental) of the analysis (Dungan et. al. 2002, Elith & Leathwick 2009).

I first compared distributions using the Commission for Environmental Cooperations's (CEC) Sonoran Desert Level III Eco-Region as the extent (Omernik 2004, Wiken et. al. 2011, USEPA 2016). This regional-scale analysis included Arizona, California, northern Baja California, and Sonora (Wiken et. al. 2011), comprising desert and thornscrub biomes. This analysis excluded higher elevation areas above 1219 m. based on clipping to a Global Multi-resolution Terrain Elevation Data 2010 elevation raster (Danielson & Gesch 2011) in order to exclude montane areas where ethnobotanical records were not available. I then analyzed the geographic ranges of these core Sonoran Desert food plants for North America, defined as the entirety of the continent (i.e., Canada, United States, Mexico, Central America), to capture the geographic differences between food plants and their un-used congeners across a larger geographic extent and to include congeners that may have had at least part of their distributions outside of the Sonoran Desert.

I combined species occurrence data from several biodiversity databases: BIEN 4 (Maitner et. al. 2017, accessed May 2018), SEINet (SEINet Portal Network 2018, accessed May 2018), and GBIF (Chamberlin 2017, accessed May 2018). This approach may suffer from undersampling biases but is the best option given the lack of available gridded atlas data for species in this region. Analyses were conducted at coarse grain sizes to mitigate these biases. Occurrence data for each species was downloaded through the R statistical software program APIs for each database. Only herbarium specimens were included (to be as accurate as possible and conservative) and all duplicated coordinates were removed. Data cleaning for GBIF was performed using the ‘CoordinateCleaner’ package in R (Zizka 2018). Records with suspicious individual counts were removed (i.e., very high occurrence counts may indicate inappropriate data or data entry problems). Very old records (before 1945) were removed as these were more likely to be unreliable with regards to location. Coordinates were also removed if they were within 0.5 degrees radius around the GBIF headquarters in Copenhagen, DK, and if they were assigned to the location of zoos, botanical gardens, herbaria, universities, museums, or open ocean.

To estimate P, I used generalized linear models (GLM) to generate a threshold suitability surface for each species (Thuiller et. al. 2003) using the ‘sdm’ package in R (Naimi & Araujo 2016). I then used kappa threshold (via the ‘dismo’ package (Hijmans et. al. 2007)) to transform the model predictions into a binary presence/absence. Specific bioclimatic variables from WorldClim (Ficke & Hijmans 2017) were chosen to prevent overfitting of the species distribution models. The bioclimatic variables chosen were BIO1=Annual Mean Temperature, BIO5=Maximum Temperature of Warmest Month, BIO6=Mininum Temperature of Coldest Month, BIO12=Annual Precipitation, BIO13=Precipitation of Wettest Month, and BIO14=Precipitation of Driest Month. I focused on climatic variables as, at a coarser scale, potential distributions are thought to be determined more by indirect, large-scale variables such as climate (Thuiller, et. al. 2003, Bahn & McGill 2007, Wisz et. al. 2013).

Statistical Analysis for R/P

The Sonoran Desert food plant R/P ratios were first compared to the R/P ratios of their un-used congeners within the Sonoran Desert geographic extent (**Fig. 1**). I also compared the relative change in R/P between the food plants and both their used and un-used congeners (**Fig. 2**). I created two proportional indexes (PI): (**i**) a PI that compared the food plants (FP) to their used congeners (UC) and (**ii**), a PI that compared the food plants (FP) to their un-used congeners (UUC):

$$PI.UC = \frac{\left(\left(\frac{R_{FP}}{P_{FP}}\right) - \left(\frac{R_{UC}}{P_{UC}}\right)\right)}{\left(\frac{R_{FP}}{P_{FP}}\right)}$$

$$PI.UUC = \frac{\left(\left(\frac{R_{FP}}{P_{FP}}\right) - \left(\frac{R_{UUC}}{P_{UUC}}\right)\right)}{\left(\frac{R_{FP}}{P_{FP}}\right)}$$

I then assessed each proportional index relative to the null expectation of zero. A more positive PI value indicated a greater difference in R/P ratios between the food plant and congener with the food plant having a higher R/P ratio (i.e. higher range filling). The proportional index used the R and P values from the North America analysis (i.e. not clipping to the Sonoran Desert) in order to use as many phylogenetically related congeners as possible. Wilcoxon unpaired tests were conducted to compare food plants and their congeners. Conducting statistical analyses on the R/P ratios at both regional (i.e. Sonoran Desert; **Fig. 1**) and continental (i.e. North America; **Fig. 2**) scales allowed us to investigate food plant range filling from two different biogeographical perspectives.

Ecological trait dataset

I created a trait dataset for all the above species. Traits included growth form (e.g., herb vs. shrub), life form (annual vs. perennial) and polyploidy (binary, yes/no). Growth form and life form data was synthesized from the SEINet Portal Network (SEINet Portal Network 2018, accessed July 2018) as well as the USDA Plant Database (USDA 2018, accessed July 2018) and the Flora of North America (eFloras 2008, accessed July 2018). Information on polyploidy was gathered from published studies as well as the Chromosome Counts Database (Rice et. al. 2015, accessed July 2018). I obtained complete data for all traits except polyploidy, for which 59% of species had data available (i.e., including the food plants, un-used congeners, as well as the used congeners).

I then determined whether these traits or their interactions with food usage predicted R/P by conducting two multiple linear regression analyses. The first model (G.L.Model) focused solely on growth form and life form for the complete dataset of food plants and un-used congeners (See **Fig. S1** in **Appendix C**, *n*=534 species). The second model (G.L.P.Model) was a dataset of food plants and un-used congeners for all traits including only cases for which ploidy data was available (**Fig. 3**, *n*=329 species). Model forms were:

$$G.L.Model = \ R/P \sim Food.Usage * (Growth\ Form + Life\ Form)$$

$$G.L.P.Model = R/P \sim Food.Usage * (Growth\ Form + Life\ Form + Polyploidy)$$

Used congeners were excluded from both models so that the food plants were directly compared to their un-used congeners. The R/P ratios for North America were chosen for this analysis because the dataset had a more comprehensive selection of un-used congeners to compare with the food plants. Type III ANOVAs were conducted for both multiple linear regression analyses to test for significance of each predictor variable.

RESULTS

I found that Sonoran Desert food plants do fill their potential range more than their un-used congeners in an unpaired analysis (**Fig. 1**, Wilcoxon: W =16999, P = 1.03e-12, median R/P ratio for food plants=0.21, median R/P ratio for Un-used congeners =0.07). Additionally, the proportional indexes (PI) revealed in a paired analysis that Sonoran Desert food plants compared directly to their un-used congeners fill more of their potential distribution range across North America (**Fig. 2**, Wilcoxon: W=77549, P<2.2e-16, median PI for FP-UUC=0.49, median PI for FP-UC=0.06).

R/P was predicted by several traits and as well as an interaction between polyploidy and food usage. Both regression models were statistically significant overall (G.L.P.Model=Adjusted R^2=0.20, F-statistic=8.61, P=2.47e-13; See **Fig. 3** for G.L.P.Model and **Fig. S1** for G.L.Model). Both regression models also indicated that lower range filling of the un-used congeners was significant (G.L.P.Model Un-used Congener coefficient= -0.07, SE= 0.02, t statistic= -3.16, P=1.0e-03, ANOVA P=1.0e-03; see **Fig. 3;** See **Fig. S1** for G.L.Model;). G.L.P.Model revealed that species with succulent growth forms (e.g. species in the Cactaceae family) had lower R/P ratios across North America (Succulent coefficient=-0.05, SE=0.02, t statistic=-2.8, P=5.62e-03, ANOVA Growth Form: P=6.2e-03; see **Fig. 3**). In contrast, polyploid species had overall higher R/P ratios across North America (Polyploidy coefficient = 0.02, SE=0.01, t statistic= 2.15, P= 3.0e-02; ANOVA Polyploidy: P= 3.0e-02; see **Fig. 3**). There was also a significant interaction between polyploidy and the un-used congeners. The mean and median R/P ratios for polyploid un-used congeners were higher than the mean and median R/P ratios for the un-used congeners not documented as polyploid (G.L.P.Model: Un-used:Polyploidy coefficient=0.05, SE=0.02, t statistic= 2.0, P=4.6e-02; ANOVA: P=4.6e-02; see **Fig. 3** and see **Appendix D**: Median and Mean R/P Ratios for Polypoidy **Table S1**). The mean and median R/P ratios for the polyploid food plants were also higher compared to the food plants that were not documented as polyploid, but the difference was not statistically significant (see **Appendix D**: Median and Mean R/P Ratios for Polypoidy **Table S1**).

DISCUSSION

I found that the Sonoran Desert species documented as being used for food filled their potential geographic range more than un-used congeners, consistent with **Hypothesis A** (i.e., the human utilization of food plant species has resulted in increased dispersal to favorable habitats, assuming that ranges are otherwise limited by dispersal). This pattern was statistically significant for my regional analysis (i.e., the Sonoran

Desert) that compared R/P ratios between the food plants and un-used congeners (**Fig. 1**). In the more stringent test using the proportional indexes (i.e. comparing species pairs that were highly related and presumably ecologically very similar), I found a similar overall pattern in which the food plants had higher R/P ratios than their un-used congeners (**Fig. 2**), also consistent with **Hypothesis A** (i.e., food plants should maintain higher population densities and fill more of their potential geographic range than their unused congeners, which presumably have otherwise similar phenotypes and life histories). My results provide evidence that it is important to include past human dispersal of food plants when predicting current plant species distributions.

The higher R/P ratios of the food plants (**Figs. 1 & 2**) suggests that economically and culturally significant plant species are also likely to be influenced by non-environmental factors. There were instances of wild and semi-wild greens, mentioned in the literature as being encouraged or managed by past humans, having higher range filling ratios than their unused congeners. For example, *S. columbariae* (i.e., approx. 55%) filled its potential range more than its unused congener, *Salvia leucophylla* (i.e, approx. 8%). *A. palmeri* (i.e. approx. 56%) also filled its potential range more than its unused congener *A. wrightii* (i.e., approx. 1%). *A. palmeri*, one of the most abundant weedy plants, was quite popular and harvested by groups such as the River Pima and Tohono O'odham (Hodgson 2001). *D. pinnata*, another one of the semi-wild greens that was encouraged in "second gardens" by groups such as the Akimel O'odham, was also possibly cultivated by the Hohokam (Bohrer 1970, Hodgson 2001). *D. pinnata*'s range filling ratio was approximately 67% compared to one of its unused congeners, *D. incisa* (Engelm. Ex. A. Gray) Britton (mountain tansy mustard) which had a range filling ratio of approximately 1%. Legumes such as *Phaseolus acutifolius* (tepary bean) have been an important source of protein for over 5,000 years in the Americas (Hodgson 2001). *P. acutifolius* had a range filling ratio of approximately 20% while its unused congener, *P. grayanus* Woot. & Standl. (Gray's bean) had a range filling ratio of approximately 2%. Other probable domesticated plants such as *H. pusillum* (i.e., 12%) had only a very small difference in range filling than its unused congener, *Hordeum arizonicum* Covas. (Arizona barley) (i.e., 10%). There were also instances of food plants, with no unused congeners in the Sonoran Desert, such as mesquite all having relatively robust range filling ratios (i.e., *P. glandulosa* approx. 62%, *P. pubescens* approx. 38%, *P. velutina* approx. 54%). Although there is general consensus that both environmental filtering (i.e., abiotic constraints) and dispersal filtering (e.g., chance colonization, differences in dispersal abilities) play a role in community assembly and distribution dynamics (Guo et. al. 2005, Fraaije et. al. 2015), my research suggests that past human-mediated dispersal of food plants is also a major driver of community assembly and distribution dynamics.

Ecological traits provide some limited insight into which species are more likely to have geographic ranges modified by humans (Meyer et. al. 2012). I identified trait predictors of food use and R/P in both regression models (G.L.P.Model, **Fig. 3**; see **Appendix C**: G.L.Model **Fig. S1**), consistent with **Hypothesis B** (i.e., certain plant traits like polyploidy, growth form, and life form should predispose certain species to be selected for by humans and/or fill their potential geographic distribution ranges more). Polyploidy and succulence influenced R/P ratios (i.e., range filling) (G.L.P.Model, **Fig. 3)**. The higher range filling for polyploidy species (**Fig. 3;** see **Appendix D:** Median and Mean R/P Ratios for Polyploidy, **Table S1)** is potentially indicative of their higher phenotypic plasticity (Meyers et. al. 2012, Minkov et. al. 2016). Increased genetic diversity (i.e. genotypic plasticity) could result in these species' morphology and physiology being better adapted to different environmental niches (i.e. phenotypic plasticity) (Leitch & Leitch 2008). This phenotypic plasticity may result in the polyploid plants filling their potential distribution range more in my analysis (see **Appendix D:** Median and Mean R/P Ratios for Polyploidy **Table S1**). The greater tendency for polyploids to have phenotypic plasticity compared to diploid taxa may have also made some of these plants more appealing to past humans (i.e., easier to cultivate, larger fruits or bigger plant parts in general). This legacy of past human selection combined with greater phenotypic plasticity could be a potential factor in why the polyploid food plants had higher R/P ratios compared to food plants that were not documented as polyploid (see **Appendix D:** Median and Mean R/P Ratios for Polyploidy **Table S1**)

Succulents had lower R/P ratios across North America (G.L.P.Model, **Fig. 3;** and see **Appendix C**: G.L.Model **Fig. S1**). The median R/P ratios for succulents was higher for the Sonoran Desert analysis than the North America analysis (see **Appendix E**: Median and Mean R/P Ratios for Succulents **Table S2**). Succulent species found in the Cactaceae and Asparagaceae families have been culturally important for many prehistoric and historic Sonoran Desert indigenous populations. The Sonoran Desert overlaps with some of the regions (e.g., Southwestern United States) that are thought to be where the Cactaceae lineage is most prominent (Arakaki et. al. 2011). This could contribute to human populations having greater access to a variety of useful cacti species.

There are more perennials (378 out of 534) than annuals (156 out of 534) in the G.L.Model's ecological trait dataset. Although there are many annual food plants that were important to past human populations in the Sonoran Desert (e.g., *H. pusillum* Nutt., *Amaranthus* spp.), 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). The collective abundance and richness of both succulents and other perennials perhaps suggests that there were more opportunities to use these plants by pre-historic and historic people because of the historical plant biogeography (e.g., phylogenetic and distributional history of the plants across time scales) of the region. For example, the Akimel O'odham journeyed into the hills to gather the fruits of *Y. baccata* Torr. (banana yucca) (Bell & Castetter 1941) and received its preserved fruit of banana yucca in trade with the Tohono O'odham (Hodgson 2001).

It is essential to view landscapes as biocultural landscapes, linking ecological and cultural systems. Research reveals a long history of pre-Columbian modification in the Amazon, Southeast Asia, and Central America, with impacts on biodiversity at regional scales (Yang et. a. 2013, Ford. et. al. 2016, Levis et. al. 2017). The Sonoran Desert is also known for its rich biodiversity and ethnobotanical history (Hodgson 2001). Although there is growing evidence that the Sonoran Desert was a hotspot for *Agave* domestication and cultivation, less research has been conducted on species that were managed in semi-cultivated systems, wild-harvested or directly and indirectly transported (Briggs et. al. 2006). This research demonstrates that the impacts of past human food use in semi-arid environments can also be significant.

Other factors beyond human dispersal could explain my findings that Sonoran Desert food plants generally fill their potential ranges more than their un-used congeners. Many species attractive to humans as food are also attractive to megaherbivores

(Guimaraes, Galetti & Jordano, 2008, Gill 2014, Doughty et. al. 2015, van Zonneveld et. al. 2018, Bocherens 2018). Megaherbivores behaved as ecosystem engineers, changing the structure of vegetation through mechanisms such as dispersing very large seeded and fleshy fruits (Bocherens 2018). Many of these large fruits tend to be rich in nutritious pulp which would be attractive to both past humans and megaherbivores. Unraveling these factors remain challenging as extant animals such as livestock, deer, coyote and birds continue to disperse some of these fruits such as *Opuntia* spp. (prickly-pear cactus) (Majure & Ervin 2007). However, there is evidence that pre-Columbian human harvesting has been central to the maintenance of the geographic ranges of a variety of fleshy-fruited species (Guimaraes, Galetti & Jordano, 2008). Some Native Americans were cactus seed predators and dispersers. The Seri practiced "second harvest" of *Pachycereus pringlei* (S. Watson) Britton & Rose (*cardón*) seeds, and all of the Baja California groups who utilized *Stenocereus gummosus* (Engelmann) Gibson & Horak and *S. thurberi* (Engelmann) Buxbaum (*Pitahaya*) practiced this second type of harvest as well (del Barco 1981, Hodgson 2001). They would leave their fecal 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 1981, Hodgson 2001). *Proboscidea parviflora* (Woot.) Woot. & Standl. (devil's claw) most likely had its populations severely reduced after megaherbivore extinction. Although cattle are good dispersers, keeping plants like devil's claw from going extinct, Native Americans also kept it growing as a source of fiber for basketry and bred horticultural varieties (Janzen 1986, Bretting 1986). These interspecific human and plant interactions encouraged human-mediated dispersal of food plants and perhaps plants of other uses too (i.e., fiber) (Janzen 1986).

Colonial or industrial uses of plants by non-indigenous people could have also affected the distribution of plants. While I have suggested impacts of indigenous peoples, Spanish colonists and/or European settlers may have also had an impact on species distribution dynamics and biodiversity as well (Crosby, Jr. 1972). Not only did European settlers cultivate New World food plants, they also brought with them many of their own culturally significant plants as well as domesticated animals. The legacies of herbivore introduction include browsing, grazing, and trampling of herbaceous species which can increase the probability of survival by perennial species (Janzen 1986). While my spatial datasets cannot directly uncover the timescales over which human impacts have occurred, it is likely that current patterns have been shaped by both indigenous peoples and European settlers.

My work has shown that food plants do fill more of their potential geographic range than their un-used congeners, and that certain ecological traits can have an influence on range filling and potentially human selection. Results further challenge the myth of ‘pristine’ landscapes, especially in semi-arid environments. Better quantifying the impacts of human-mediated dispersal of useful plants will be important for predictive modeling of biodiversity dynamics.

FIGURES

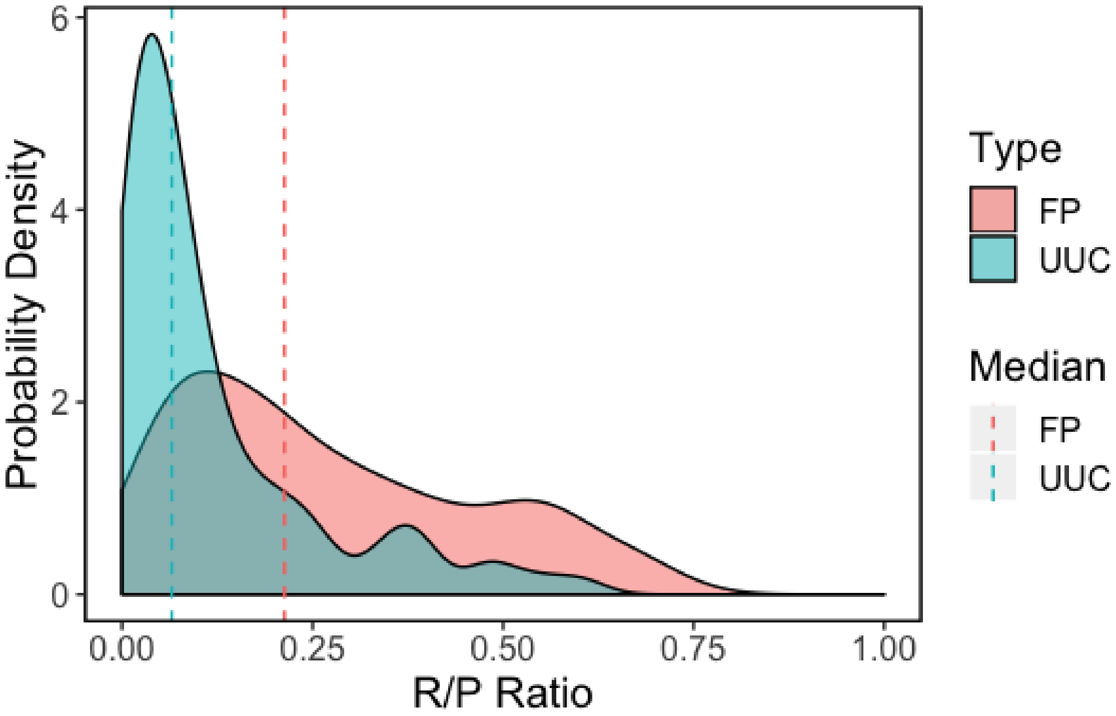


Figure 1 Density plots of food plant (FP) (red) R/P ratios compared to the R/P ratios of their un-used congeners (UUC) (blue) in the Sonoran Desert. The dashed vertical lines indicate the overall median R/P ratio for the food plants (red) and the overall median R/P ratio for the un-used congeners (blue). The food plants (red) had a significantly higher overall median R/P ratio compared to the overall median R/P ratio for the un-used congeners (blue) (Wilcoxon: W=16999, P=1.03e-12).

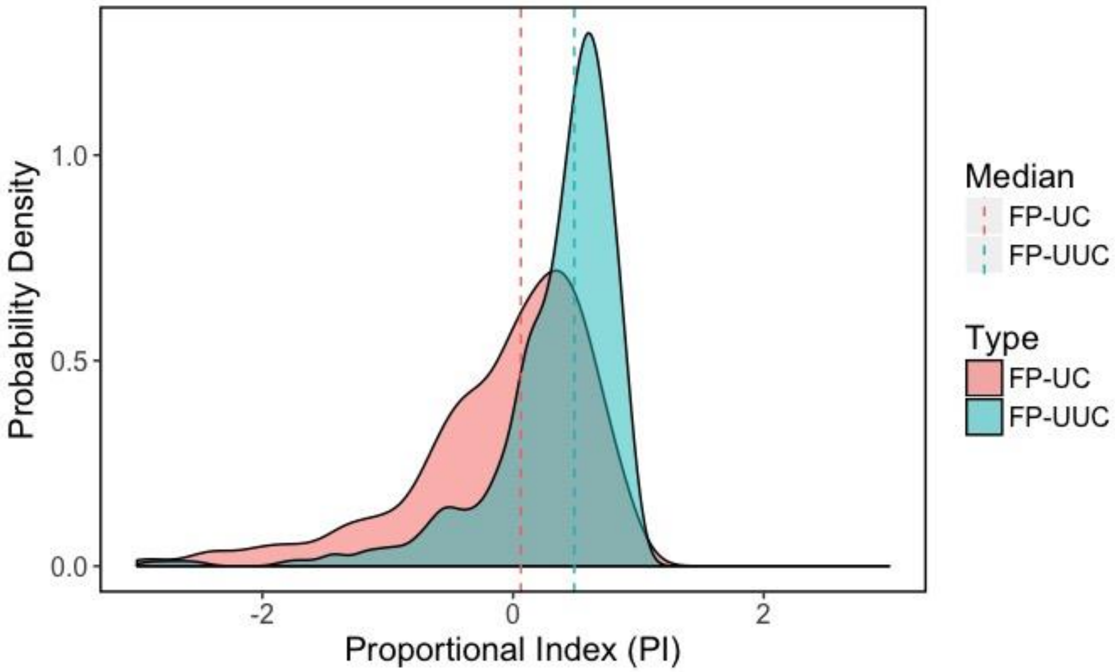


Figure 2. Density plots of proportional indexes (PI) that compared the relative change in R/P between the food plants (FP) to their used congeners (UC) (FP-UC) (red), and to their un-used congeners (UUC) (FP-UUC) (blue). The dashed vertical lines indicate the overall median R/P ratio for the FP-UUC density plot (blue) and the FP-UC density plot (red). The FP-UUC PI overall median R/P ratio was significantly higher than the overall median R/P ratio for the FP-UC PI (Wilcoxon: W=77549, P<2.2e-16).

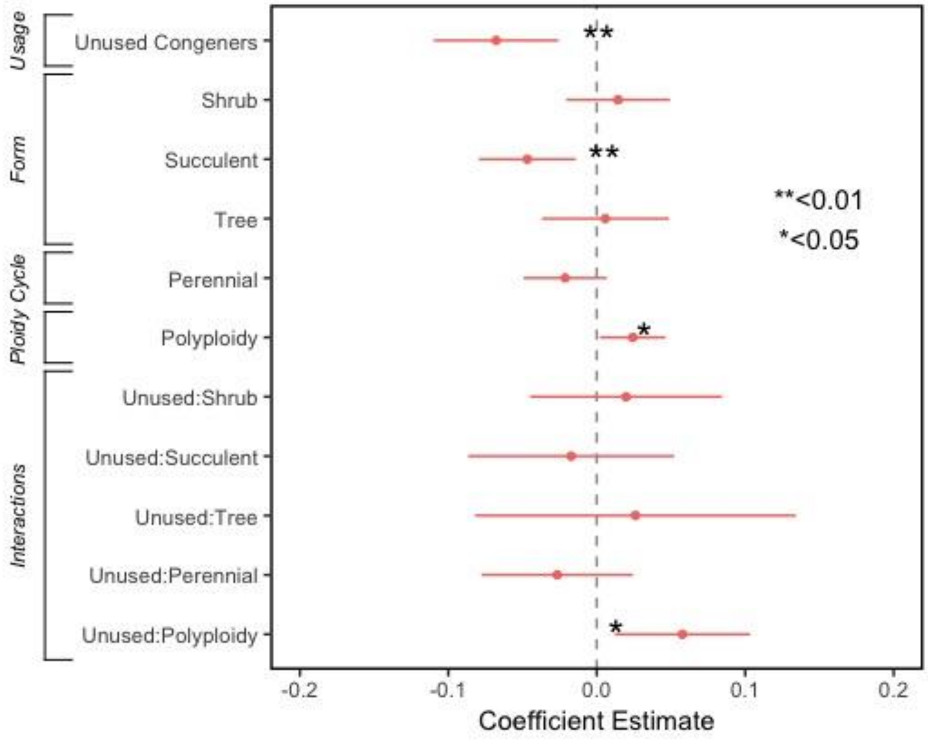


Figure 3 Coefficient estimates for the predictors of R/P in North America (G.L.P.Model). Data included species for which ploidy data was available (*n* =329). (*), P <0.05; (**) P <0.01). Ecological traits such as succulence and polyploidy were statistically significant, correlating with R/P. Food usage was also statistically significant, correlating with R/P.

REFERENCES

Abbott, D.R., Smith, A.M., Gallaga, E. (2007). Ballcourts and ceramics: the case for Hohokam marketplace in the Arizona Desert. *Am. Antiquity*. 72, 461-484.

Abrams, M.D. & Nowacki, G.J. (2008). Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. *The Holocene*. 18, 1123-1137.

Agrawai, A. & Redford, K. (2009). Conservation and displacement: an overview. *Conservat. Soc.* 7, 1-10.

Anaya, F.C. & Espírito-Santo, M.M. (2018). Protected areas and territorial exclusion of traditional communities: analyzing the social impacts of environmental compensation strategies in Brazil. *Ecol. Soc*. 8, 1-13.

Arakaki, M., Christin, P., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R.M, et. al. (2011). Contemporaneous and recent radiations of the world's major succulent plant lineages. *PNAS*. 108, 8379-8384.

Bahn, V. & McGill, B.J. (2007). Can niche-based distribution models outperform spatial interpolation. *Glob. Ecol. and Biogeogr*. 1-10.

Barton, H. & Denham, T. (2011). Prehistoric vegeculture and social life in Island Southeast Asia and Melanesia. *Why cultivate? Anthropogenic and archaeological approaches to foraging-farming transitions in Southeast Asia*. In. G. Barker & M. Janowski (Eds.). McDonald Institute for Archaeological Research, Cambridge, UK. pp. 17-25.

Bayman, J.M. (2001). The Hohokam of Southwest North America. *J. World Prehist*. 15, 257-312.

Bell, W.H. & Castetter, E. F. (1937). The Utilization of Mesquite and Screwbean by the Aborigines in the American Southwest. *Ethnobiological Studies in the American Southwest*. University of New Mexico Bulletin, Biological Series, University of New Mexico Press, Albuquerque, 5.

Bell, W.H. & Castetter, E.F. (1941). The Utilization of Yucca, Sotol, and Beargrass by the Aborigines in the American Southwest. *Ethnobiological Studies in the American Southwest*. The University of New Mexico Bulletin, Biological Series, University of New Mexico Press, Albuquerque, 5.

Bitencourt, A.L.V. & Krauspenhar, P.M. (2006). Possible prehistoric anthropogenic effect on *Araucaria angustifolia* (Bert.) O. Kuntze expansion during the late Holocene. *Rev. Bras. Paleontolog.,* 9, 109-116.

Bocherens, H. (2018). The rise of the anthroposphere since 50,000 years: an ecological replacement of megaherbivores by humans in terrestrial ecosystems? *Front Ecol. Evol*. 6, 1-8.

Bohrer, V.L. (1987). Methods of recognizing cultural activity from pollen in archaeological sites. *The Kiva*. 46, 135-142.

Bohrer. V.L. (1991). Recently recognized cultivated and encouraged plants among the Hohokam. *The Kiva*. 56, 227-235.

Bovin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denham, T. et. al. (2016). Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *PNAS*. 113, 6388-6396.

Bretting, P.K. (1986). Changes in fruit shape in *Proboscidea parvifora* ssp. *parviflora* (Martyniaceae) with domestication. *Econ. Bot*. 40, 170-176.

Briggs, J.M., Spielmann, K.A., Schaafsma, H., Kintigh, K.W., Kruse, M., Morehose, K. et. al. (2006). Why ecology needs archaeologists and archaeology needs ecologists. *Front Ecol. Environ*. 4, 180-188.

Brockington, D. & Igoe, J. (2006). Eviction for conservation: a global overview. *Conservat. Soc.* 4, 424-470.

Brosius, J.P. (1991). Foraging in tropical rain forests: the case of the Penan of Sarawak, East Malaysia (Borneo). *Hum. Ecol*. 19, 123-150.

Castetter, E.F. & Underhill, R.M. (1935). The Ethnobiology of the Papago Indians. *Ethnobiological Studies in the American Southwest*. University of New Mexico. Bulletin, Biological Series, 4, 1-84.

Chamberlain, S. (2017). rgif: Interface to the Global 'Biodiversity' Information Facility API. R package version 0.9.8. https://cran.r-project.org/web/packages/rgbif/index.html

Clement, C.R., Denevan, W.M., Heckenberger, M.J., Junqueira, A.B., Neves, E.G., Teixeira, W.G. et. al. (2015). The domestication of Amazonia before European conquest. *Proc. R. Soc. B*. 282, 1-9.

Clement, C.R. & Junqueira A.B. (2010). Between a pristine myth and an impoverished future. *BioTropic*a. 42, 534-536.

Crosby, Jr. (1972). The Columbian Exchange: The biological and cultural consequences of 1492. Praeger Publishers. Westport, CT. 1-268.

Crosswhite, F.S. (1981). Desert plants, habitat, and agriculture in relation to the major pattern of cultural differentiation in the O'odham people of the Sonoran Desert. *Desert Plants.* 3, 47-76.

Danielson, J.J. & Gesch, D.B. (2011). Global multi-resolution terrain elevation data 2010 (GMTED2010). U.S. Geological Survey Open-File Report 2011-1073, 1-26.

De Bont, R. (2015). "Primitives" and protected areas: international conservation and the "naturalization" of indigenous people, ca. 1910-1975. *JHI*. 2, 215-236.

del Barco., M. (1981). Ethnology and linguistics of Baja California. F. Tiscareno, trans. Dawson's Book Shop, Los Angeles, Calif.

Denevan, W.M. (1992). The pristine myth: the landscape of the Americas in 1492. *Ann. Assoc. Am. Geogr.* 82, 369-385.

Doughty, C.E. Wolf, A., Morueta-Holme, N., Jorgensen, P.M., Sandel, B., Violle. et. al. (2015). Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography*. 38, 001-010.

Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Jakomulska, A., et. al. (2002). A balanced view of scale in spatial statistical analysis. *Ecography*. 25, 626-640.

eFloras. (2008). Published on the Internet http://www.efloras.org (accessed July 2018). Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA.

Elith, J. & Leathwick, J.R. (2009). Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677-697.

Felger, R.S. & Moser, M.B. (1976). Seri Indian food plants: desert subsistence without agriculture. *Ecol. Food Nutr*. 5, 13-27.

Fick, S.E. & Hijmans, R.J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol*. 37, 4302-4315.

Fish, S.K. & Fish, P.R. (2007). The Hohokam millennium. 1-12. Fish, S.K. & Fish, P.R. (Eds.). *The Hohokam Millenium*. School for Advanced Research Press. Santa Fe, New Mexico. 1-151.

Ford, A. & Nigh, R. (2015). *The Maya forest garden: eight millennia of sustainable cultivation of the tropical woodlands*. Routledge. New York, NY. 1-187.

Fraaije, R.G.A., ter Braak, C.J.F., Verduyn, B, Verhoeven, J.T.A. & Soons, M.B. (2015). Dispersal versus environmental filtering in a dynamic system: drivers of vegetation patterns and diversity along stream riparian gradients. *J. Ecol.* 103, 1634-1646.

Fritz, G.J., Adams, K.R., Rice, G. E. & Czarzasty, J.L. (2009). Evidence for domesticated amaranth from a sedentary period Hohokam house floor at Las Canopas. *KIVA.* 74, 393-419.

Gasser, R.E. (1981). Hohokam use of desert food plants. *Desert Plants*. 3, 216-234.

Gasser, R.E. & Kwaitkowski, S.M. (1991). Regional signatures of Hohokam plant use. *KIVA*. 56, 207-226.

Gill, J.L. (2014). Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytol*. 201, 1163-1169.

Guimaraes Jr., P.R., Galetti, M. & Jordono, P. (2008). Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE*. 3, e1745.

Guo, Q., Taper, M., Schoenberger, M., Brandle, J. (2005). Spatial-temporal population dynamics across species range: from centre to margin. *OIKOS*. 108, 47-57.

Hall, S.J., Trujillo, J., Nakase, D., Strawhacker, C., Kruse-Peeples, M., Schaafsma, H. et. al. (2013). Legacies of prehistoric agricultural practices within plant and soil properties across an arid ecosystem. *Ecosystems*. 16, 1273-1293.

Hijmans, R.J, Phillips. S., Leathwick, J. & Elish, J. (2007). dismo: species distribution modeling. R package version 1.1-4. http://CRAN.R-project.org/package=dismo

Hill, J.B., Clark, J.J., Doelle, W.H., Lyons, P.D. (2004). Prehistoric demography in the Southwest: migration, coalescence, and Hohokam population decline. *Am. Antiq*. 69, 689-716.

Hodgson, W.C. (2001). *Food Plants of the Sonoran Desert*. The University Arizona Press. Tucson, Arizona. 1-299.

Hodgson, W.C. & Salywon, A.M. (2013). Two new *Agave* species (Agavaceae) from central Arizona and their putative pre-Columbian domesticated origins. *Brittonia*. 65, 5-15.

Hodgson, W.C., A.M., Salywon, Doelle, W.H. (2018). Hohokam lost crop found: a new *Agave* (Agaveceae) species only known from large-scale pre-Columbian agricultural fields in southern Arizona. *Syst. Bot.* 43, 734-740.

Holt, R.D., Keitt, T.H, Lewis, M.A., Maurer, B.A., Taper, M.L. (2005). Theoretical models of species' borders: single species approaches. *OIKOS*. 108, 18-27.

Janzen, D.H. (1986). Chihuahuan desert nopaleras: defaunated big mammal vegetation. *Annu. Rev. Ecol. Syst*. 17, 595-636.

Junqueira. A.B., Levis. C., Bongers, F., Pena-Claros, M., Clement, C.R., Costa, F. et. al. (2017). Response to comment on "persistent effects of pre-Columbian plant domestication on Amazonian forest composition'. *Science*. 358, 1-2.

Kodis, M., Galante, P., Sterling, E.J. & Blair, M.E. (2018). Ecological niche modeling for a cultivated plant species: a case study on taro (*Colocasia esculenta*) in Hawaii. *Ecol. Appl*. 28, 967-977.

Leitch A.R. & Leitch, I.J. (2008). Genome plasticity and the diversity of polyploid plants. *Science*. 320, 481-483.

Levis, C., Costa, F.R.C, Bongers, F., Pena-Claros, M., Clement, C.R., Junqueira, A.B. et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*. 355, 925-931.

Levis, C., Flores, B.M., Moreira, P.A., Luize, B.G., Alves, R.P, Franco-Moraes, J. et al. (2018). How people domesticated Amazonian forests. *Front. Ecol. Evol*. 5, 1-21.

Loendorf, C. & Lewis, B.V. (2017). Ancestral O'odham: Akimel O'odham cultural traditions and the archaeological record. *Am. Antiq*. 82, 123-139.

Loendorf, C.R., Fertelmes, C.M., Lewis, B.V. (2013). Hohokam to Akimel O'odham: obsidian acquisition at the historic period Sacate Site (GR-909), Gila River Indian Community, Arizona. *Am. Antiq*. 78, 266-284.

MacDougall, A. (2003). Guest editorial: did Native Americans influence the northward migration of plants during the Holocene? *J. Biogeogr*. 30, 633-647.

Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue II, J., Duran, S.M. et. al. (2017). The BIEN R package. A tool to access the Botanical Information and Ecological Network (BIEN) database. *Methods Ecol. Evol*. 91, 373-379.

Majure, L.C. & Ervin, G.N. (2007). The opuntias of Mississippi. *Haseltonia*. 14, 111-126.

McKey, D., Rostain, S., Iriarte, J., Bruno, G., Birk, J.J., Holst, I. et. al. (2010). Pre-Columbian agricultural landscapes, ecosystem engineers, and self-organized patchiness in Amazonia. *PNAS*. 107, 7823-7828.

McMichael, C.H., Feeley, K.J., Dick, C.W., Piperno, D.R. & Bush, M.B. (2017). Comment on ‘Persistent effects of pre-Columbian plant domestication on Amazonian forest composition’. *Science*. 358, 1-2.

Merrill, W.L., Hard, R.J., Mabry, J.B., Fritz, G.J., Adams, K.R., Roney, J.R. et. al. (2009). The diffusion of maize to the southwestern United States and its impact. *PNAS*. 50, 21019-21026.

Meyer, R.S. & Purugganan, M.D. (2013). Evolution of crop species: genetics of domestication and diversification. *Nature Rev. Genet*. 14, 840-852.

Meyer, R.S., Duvual, A.E. & Jensen, H.R. (2012). Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytol.* 196, 29-48.

Milla, R., Morente-Lopez, J., Alonso-Rodrigo, Miguel, Martin-Robles, N & Chapin III, F.S. (2014). Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proc. R. Soc. B.* 281, 1-9.

Minkov, A. S., Sabath, N. & Mayrose, I. (2016). Whole-genome duplication as a key factor in crop domestication. *Nat. Plants*. 2, 1-4.

Moerman, D. (2003). Native American ethnobotany. A database of plants used as drugs, foods, dyes, fibers and more, by natives of North America. http://naeb.brit.org/about

Nabhan, G.P. (2016). *Gathering the Desert.* University of Arizona Press. Tucson, Arizona. 1-221.

Naimi, B. & Araujo, M.B. (2016). sdm: a reproducible and extensible R platform for species distribution modeling. *Ecography*. 39, 368-375.

Nesheim, I., Halvorsen, R. & Nordal, I. (2010). Plant composition in the Maya Biosphere Reserve: natural and anthropogenic influences. *Plant Ecol.* 208, 93-122.

Omernik, J.M. (2004). Perspectives on nature and definition of ecological regions. *Environ. Manage*. 34, Suppl. 1, S27-S38.

Parker, K.C., Trapnell, D.W., Hamrick, J.L. & Hodgson, W.C. (2014). Genetic and morphological contrasts between wild and anthropogenic populations of *Agave parryi* var. *huachucensis* in south-eastern Arizona. *Ann. Bot.* 113, 939-952.

Parker, K.C., Hamrick, J.L., Hodgson, W.C., Trapnell, D.W., Parker, A.J. & Kuzoff, R. K. (2007). Genetic consequences of Pre-Columbian cultivation for *Agave murpheyi* and *A. delamateri* (Agavaceae). *Am. J. Bot*. 94, 1479-1490.

Peterson, A. T. (2011). Ecological niche conservatism: a time-structured review of evidence. *J. Biogeogr*. 38, 817-827.

Rea, A.M. (1997). *At the desert's green edge: an ethnobotany of the Gila River Pima*. The University Press. Tucson, Arizona. 1-413.

Rice, A., Glick, L., Abadi, S., Einhorn, M., Kopelman, N.M, Salman-Minkov, A. et. al. (2014). The chromosome counts database (CCDB)- a community resource of plant chromosome numbers. *New Phytol*. 206, 19-26.

Sedrez dos Reis, M, Ladio, A. & Peroni, N. (2014). Landscapes with Araucaria in South America: evidence for a cultural dimension. *Ecol. Soc*. 19, 43.

SEINet Portal Network. 2018. http://:swbiodiversity.org/seinet/index.php.

Shepard Jr., G.H. & Ramirez, H. (2011). "Made in Brazil": human dispersal of the Brazil Nut (*Bertholletia excelsa*, Lecythidaceae) in ancient Amazonia. *Econ. Bot*. 65, 44-65.

Soberon, J. & Peterson, A.T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodiversity Informatics*. 2, 1-10.

Soberon, J. & Nakamura, M. (2009). Niches and distributional areas: concepts, methods, and assumptions. *PNAS*. 106, 19644-19650.

Stahl, U., Reu, B., Wirth, C. (2014). Predicting species' range limits from functional traits for the tree flora of North America. *PNAS*. 38, 13739-13744.

Svenning, J.C., Normand, S., Scov, F. (2008). Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography*. 31, 316-326.

Svenning, J.C. & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecol. Lett*. 7, 565-573.

Thuiller, W., Miguel B., A. & Sandra, L. (2003). Generalized models vs. classification tree analysis: predicting spatial distributions of plant species at different scales. *J. Veg. Sci*. 14, 669-680.

USDA, NRCS. (2018). The PLANTS Database (http://plants.usda.gov, July 2018). National Plant Data Team, Greensboro, NC 27401-4901 USA.

USEPA: United States Environmental Protection Agency. (2016). *Ecoregions of North America*. Available at: https://www.epa.gov/eco-research/ecoregions-north-america. Last accessed 03 August 2018.

Violle, C., Reich, P.B., Pacala, S.W., Enquist. B.J., Kattge, J. (2014). The emergence and promise of functional biogeography. *PNAS*. 38, 13690-13696.

Warren II, R.J. (2016). Ghosts of cultivation past- Native American dispersal legacy persists in tree distribution. *PLoS ONE*. 11, 1-16.

Whitehead, S.R., Turcotte, M.M., Poveda, K. (2016). Domestication impacts on pant-herbivore interactions: a meta-analysis. *Phil. Trans. R. Soc. B*. 272, 1-9.

Wiens, J.J. & Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Syst*. 26, 519-529.

Wiken, E., Nava, F.J. & Griffith, G. (2011). North American terrestrial ecoregions-level III. Commission for Environmental Cooperation, Montreal, Canada. 1-145.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenior, J., Damgaard, C.F. et. al. (2013). The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modeling. *Biol. Rev. Camb. Philos. Soc*. 88, 15-30.

Yang, X, Barton, H.J, Wan, Z., Li, Q., Ma, Z., Li, M. et. al. (2013). Sago-type palms were an important plant food prior to rice in southern subtropical China. *PLoS ONE*. 8, 1-8.

Van Zonneveld, M. Larranaga, N., Blonder, B., Coradin, L., Hormaza, J.I. & Hunter. D. (2018). Human diets drive range expansion of megafauna-dispersed fruit species. *PNAS*. 10, 1-6.

Zizka, A. (2018). CoordinateCleaner: automated cleaning of occurrence records from biological collections. R. package version 1.0-7. http://CRAN-R-project.org/package=CoordinateCleaner

CHAPTER 3

PRE-COLUMBIAN AND CONTEMPORARY POPULATION INFLUENCE ON FOOD PLANT SPECIES RICHNESS IN THE SONORAN DESERT

ABSTRACT

Human activity may leave a persistent legacy on biodiversity (i.e. species richness) through dispersal of useful plants for food and other important uses (e.g., medicine, construction, ceremony). The consequences of human activities on plant biogeography are poorly understood in arid regions despite a rich history of indigenous populations using an extensive assemblage of native plants especially for food, and the deep footprint of settler-driven land use. I investigated the influence that pre-Columbian populations and contemporary populations had on the richness of food plants in the Sonoran Desert. I found that: (**i**) the ratio of food plant richness to total species richness is greater with higher contemporary population density and pre-Columbian population density based on pre-Columbian population density at spatial scales consistent with foraging-by-food distances. I also found (**ii**) an influence of contemporary population density but a weaker legacy of pre-Columbian population density at smaller spatial distances consistent with intensive land use. Thus, the primary impact on biodiversity appears to be consistent with broader-scale wild-harvesting and dispersal, rather than through intensive agricultural propagation, and also consistent with strong effects of contemporary settlement. With the limited extant archaeological data, these findings suggest that areas with high population density (pre- and post- colonization) retain legacies of these uses through increases in useful species' geographic ranges.

INTRODUCTION

There are many hypotheses for the drivers of species richness patterns. At broad scales, species richness patterns are traditionally explained in terms of climate (e.g., the 'species-energy' hypothesis) (Hawkins et. al. 2003, Allen et. al. 2007) and/or historical biogeography (e.g., the 'out of the tropics' hypothesis, the tropical niche conservatism hypothesis) (Janzen 1967, Jablonski et. al. 2006, Ghalambor et. al. 2006, Kerkhoff et. al. 2014, Lamanna et. al. 2014). At regional scales, topographic complexity (Coblentz & Riitters 2004), as well as elevation (Parker 1991) are also considered to play an important role in plant distributions and species richness patterns (Merriam 1890, Merriam 1894, Coblentz & Riitters 2004). The wide range of hypotheses proposed and still studied (Stevens 1989, Currie 1991, Currie et. al. 1999, Currie et. al. 2004. Hillebrand 2004, Wiens & Donoghue 2004) clearly show that species richness is a complex pattern with explanations varying across spatial scales (Gaston 2000).

These hypotheses do not extensively consider biotic factors via dispersal, genetic/phenotypic plasticity and competition as well as how humans, throughout time, have influenced biodiversity patterns (Crosby, Jr. 1972, Denevan 1992, Clement & Junqueira 2010, Sedrez et. al. 2014, Piperno et. al. 2015, Warren II 2016, Levis et. al. 2017, Junqueira et. al. 2017). Species richness patterns can be more fully understood by viewing biodiversity patterns as a product of interactions between human cultures and ecology, the study of how organisms react with one another and with their physical environment (Malhi 2017, Levis et. al. 2017). Many environments once assumed to be "pristine" are now acknowledged to be at least partially structured by past and present human activity (Piperno et. al. 2015) which some researchers refer to as biocultural landscapes. Biocultural landscapes can also be viewed as palimpsests, i.e. temporal and spatial layers of successive activities that are partially destroyed and reworked (Bailey 2007, Bovin et. al. 2016). This framework has a long history of being applied to archaeology, but only more recently to ecology (Bailey 2007, Bovin et. al. 2016). Thus, species richness, could be the outcome of both ecological processes and human activities that are erased and etched on the landscape over time.

Although studies in Southeast Asia (Brosius 1991, Barton & Denham 2011, Yang et. al. 2013), Central America (Ross 2011, Ford et. al. 2016), and the Amazon Basin (Bitencourt & Krauspenhar 2006, Mckey et. al. 2010, Clement & Junqueira 2010, Sedrez et. al. 2014, Clement et. al. 2015, Junqueira et. al. 2017, Levis et. al. 2017, Levis et. al. 2018show that past humans modified landscapes, the biogeographic consequences of these human actions are poorly known. In some regions, past human-mediated dispersal and cultivation of food plants may have played an important role in structuring species richness, for example, via pre-Columbian farming and cultivation of wild plants (Abrams & Nowacki 2008, Ross 2011, Levis et. al. 2017). In a few cases, there is evidence for regional expansion of particular species distribution through food use. For example, in the Amazon Basin, forests closer to archaeological sites have greater relative and absolute abundance and richness of domesticated species on a regional scale (Levis et. al. 2017). There is also evidence that Neotropical fruit species that were once megafauna-dispersed are also thought to have had their geographic and environmental ranges maintained and expanded through human-mediated dispersal and management (van Zonneveld et. al. 2018).

It is important to consider both past and present human populations in understanding richness patterns (Bush et. al. 2015, McMichael et. al. 2017). For instance, there is also evidence of impacts from 500 years of colonization by European settlers and recovering, indigenous populations in the Amazon on plant distribution and richness (McMichael et. al. 2017). For example, the Amazonian rubber boom of 1850-1920 resulted in enrichment of forests with deliberately sown *Hevea.Brasiliensis* Willd. ex A.Juss.) Müll.Arg. (rubber tree) and edible palms (McMichael et. al. 2017), accompanying other kinds of modification such as deforestation, agroforestry and agriculture. Contemporary human populations are also found clustered around the same major river channels as pre-Columbian populations (Piperno et. al. 2015, McMichael et. al. 2017). These cumulative impacts can still be discernible on the landscape at varying levels and spatial scales (Bush et. al. 2015, McMichael et. al. 2017, Junqueira et. al. 2017, Levis et. al. 2017, van Zonneveld et. al. 2018). However, causality can be uncertain -do people influence plant richness, or does richness influence people to inhabit species rich habitats? Even though it is difficult to answer this question, I can still use the presence of people as an effective indicator; in others, I can conjecture that active dispersal occurred and that people can drive richness patterns. There is significant evidence for this in regard to isolated species such as *Quercus* spp. (oak), *Carya* spp. (hickory) and *Castanea* spp. (chestnut) in eastern North American forests (Abrams & Nowacki 2008) and *Gleditsia triacanthos* L. (honey locust) by the Cherokee in the Southern Appalachian Mountain Region (U.S.) (Warren 2016), but there has not been a test of this for whole species assemblages outside of the Amazon (Junqueira et. al. 2017, Levis et. al. 2017, McMichael et. al. 2017).

Here I asked whether pre-Columbian and/or contemporary human activity shapes species richness patterns. I hypothesized that pre-Columbian populations altered biodiversity patterns at the landscape scale through cultivation, wild-harvesting, and dispersal of food plants. As a result, I predicted that there would be higher food plant species richness in areas that had high pre-Columbian populations (**Hypothesis A**). I also hypothesized that contemporary populations would have a significant effect on food plant species richness patterns. I predicted that urbanization and settlement for ranching, agriculture, etc. also lead to increased dispersal of useful native plants (Janzen 1986, Stuart et. al. 2006), and/or that areas with high utility for these activities also have high habitat value for useful native plants (Hope et. al. 2003, McMichael et. al. 2017, Howard n.d.). Given that people settle in areas that are favorable for high plant diversity, or specifically select places because of their high plant diversity (Goncalves et. al. 2016, Gaoue et. al. 2017), I predicted there would be higher food plant species richness in areas of high contemporary population density (**Hypothesis B**). The arguments for past and contemporary human effects on the landscape are not mutually exclusive. There is a need to tease apart the separate and combined effects on regional plant species richness of both pre-Columbian and contemporary populations.

I focused my work on the Sonoran Desert of southwestern North America as defined by Omernik 2004 and USEPA 2016. The Sonoran Desert is rich in plant species diversity and cultural history (Hodgson 2001 Nabhan 2016). Not only does the Sonoran Desert region possess a long legacy of past indigenous populations using plants for food

(Castetter & Underhill 1935, Bell & Castetter 1937, Bell & Castetter 1941, Gasser 1981, Crosswhite, 1981, Bohrer 1987, Bohrer 1991, Gasser & Kwiatkowski 1991, Rea 1997, Hodgson 2001, Fritz et. al. 2009), but the arid conditions help preserve the archaeological evidence of past settlements, and thus, it can be easier to perceive (Matthew Peeples per. comm. March 2019). Pre-Columbian human impacts on plants may be both direct and indirect through activities such as encouraging propagation and/or trade between individuals and larger social groups (Bayman 2001, Fish & Fish 2007). The Phoenix and Tucson metropolitan areas currently have a combined population of approximately 8 million people. Contemporary human direct and indirect impacts on native plant distributions may include seed dispersal via road networks (Ansong & Pickering 2013, Auffret et. al. 2014), and other animals that disperse seeds through man-made “linear gaps” like roadways, trails, and powerlines (Suárez-Esteban et. al. 2016). Land clearance for both agriculture (Hope et. al. 2003) and cities (Walker et. al. 2009), as well as residential homeowner landscaping preferences (Walker et. al. 2009, see Hope et. al. 2003 and Hope et. al. 2006 for ‘luxury effect’ hypothesis) could also influence plant species richness.

The most likely source of pre-Columbian influence on biodiversity during the more recent Anthropocene in the Sonoran Desert are the Hohokam people. The Hohokam is an archaeological cultural designation for sedentary agriculturalists who resided in the Sonoran Desert and adjacent areas ca. 400-1450 A.D. (Bayman 2001, Abbott et. al. 2007, Fish & Fish 2007). They inhabited approximately 80,000 km^2 in the southern half of Arizona and adjacent northern Sonora, Mexico (see **Appendix K**: Hohokam Defined

Region). The Hohokam's subsistence practices were multifaceted and included direct cultivation of cultigens as well as the encouragement and dispersal of native, wild plants (Bohrer 1987, Bohrer 1991, see **Appendix G**: Hohokam Food Production and Cultivation and **Appendix L**: Examples of Hohokam Plants Used). I analyzed Hohokam effects on food plant species richness at two different buffer distances, reflecting the distances populations would travel for transplanting, transporting, and dispersing food plant species (i.e., 36 km buffer distance; **Figs. 4-7**), as well as farming (i.e., 7 km buffer distance; See **Appendix H:** Hohokam 7 km Buffer Distance **Figs. S2-S5**). Cross-cultural studies suggest that these distances equate to the rough distance that could be covered on foot in one day (36 km) and the typical range of intensive agricultural land use in similar arid environments (7 km; see Varien 1999, Wilcox et al. 2007, Hill et. al. 2015)

The impacts of Hohokam food use have historically been analyzed for particular archaeological sites and complexes (Briggs et. al. 2006, Hall et. al. 2013). Pollen records reflect intensive use and transport of a wide variety of native plant species ranging from succulents to weedy annuals and the more well-researched cultigens (See **Appendix F:** Hohokam Food Plant Use). Despite extensive archaeobotanical data, little is known on how these diverse uses have impacted regional species richness patterns. There are elevated frequencies of Chenopodiaceae-*Amaranthus* and other weedy pollen types around agricultural land in this region (Stuart et. al. 2006), possibly overlapping with the elevated concentrations of pre-Columbian pollen samples of signature weedy taxa that the Hohokam used for food (Fish 1984, Stuart et. al. 2006). Thus, it seems more also likely that in addition to settling in areas of high plant richness, the Hohokam actively enriched their settlements with food plants, influencing species richness.

MATERIALS AND METHODS

Ethnobotanical Dataset

I compiled an ethnobotanical dataset of Sonoran Desert food plants based on Hodgson (2001) comprised of 356 plants that have been used by past human populations. They were selected for this analysis based on their native origin and available documentation (i.e. ethnographies, preserved specimens) that contextualize their food use as being part of the history, physical and social environments of indigenous populations. I then identified the food plants that had occurrences within the study area of the Hohokam (n=253). This was based on BIEN4 (Maitner et. al. 2017), SEINet Portal Network (SEINet Portal Network 2018) and GBIF data (Chamberlin 2017).

Hohokam Study Area

My study uses archaeological information from the Heritage Southwest Database (HSW) study area for the Hohokam region (i.e. comprising the geographic extent of the Hohokam populations in the Sonoran Desert). The HSW is a digital geodatabase containing information on more than 10,000 pre-Columbian and more recent archaeological sites across the U.S. Southwest and Mexican Northwest, maintained by the non-profit Archaeology Southwest in Tucson (Peeples et. al. 2006, Hill et. al. 2002). This database contains information on more than 1,000 settlements occupied across the Hohokam region between A.D. 700 and 1450 (see Doelle 1995, Doelle 1980, Hill et. al. 2004, Peeples 2006). This database includes estimates of the sizes and occupation spans of individual sites based on available archaeological information including counts of structures from surface or excavations, dated archaeological materials, and the classes of public architectural features present. These data have been used to estimate population across the Hohokam region (Doelle 1995, Hill et. al. 2004, Mills et. al. 2013, 2015).

Species Distribution Modeling

Species distribution modeling was used to estimate the potential areas of distributions for the food plants. This was done on the basis of each species observed presences and pseudo-absences. The species occurrence data was then combined from several biodiversity databases: BIEN 4 (Maitner et. al. 2017), SEINet (SEINet Portal Network 2018), and GBIF (Chamberlin 2017). Although this approach can suffer from undersampling, it is the best option given the lack of available gridded atlas data for species for this region, or of available regional plot data (pers. comm. 2018, R. Madera; pers. comm. 2018, B. Maitner). Although there are no herbarium records from the pre-Columbian time period, herbarium species occurrences were used to capture the most accurate plant occurrence records for the Hohokam region. The 'CoordinateCleaner' package in R (Zizka 2018) was used to perform data cleaning on GBIF data, removing duplicate records. Records with suspicious individual counts were removed (i.e., very high occurrence counts may indicate inappropriate data or data entry problems). Very old records (i.e., before 1945) were removed as these were more likely to be unreliable with regards to location, and if they were assigned to the location of zoos, botanical gardens, herbaria, universities, museums, or open ocean.

Potential range estimates were defined as the total number of pixels predicted to be suitable habitat using a species distribution model. I used the 'dismo' package

(Hijmans et. al. 2007) to choose pseudo-absence points at random from the extent of the Sonoran Desert. I then used general additive models (GAM) to generate a threshold suitability surface for each food plant species using the ‘sdm’ package in R (Naimi & Araujo 2016). GAMs provide added flexibility for fitting more ecologically realistic relationships in SDMs (Elith et. al. 2006, Elith & Leathwick 2009). I then used the ‘spec_sens’ threshold (via the ‘dismo’ package) to transform the model predictions into a binary presence/absence. The spatial scale of 2 km x 2 km was chosen given the geographic extent of the study area, the scale of available data, and the goals of the study (Elith & Leathwick 2009). Finer resolution can provide better predictions for fixed or very locally mobile organisms (Guisan & Thuiller 2005).

Elevation, topographic and climatic variables were used as predictors for the SDMs. Specific climatic variables from WorldClim (Fick & Hijmans 2017) were chosen to prevent overfitting of the species distribution models. The bioclimatic variables chosen were BIO1- Annual Mean Temperature, BIO5- Maximum Temperature of Warmest Month, BIO6=Mininum Temperature Coldest Month, BIO12=Annual Precipitation, BIO13= Precipitation of Wettest Month, and BIO14= Precipitation of Driest Month. Potential distributions are thought to be determined primarily by indirect, large-scale variable such as climate (Thuiller et. al. 2003, Bahn & McGill 2007, Wisz et. al. 2013). I chose a small set of variables to avoid model overfitting to capture precipitation and temperature variation likely to be relevant to a broad range of species (Tomiolo & Ward 2018). I also included elevation (USGS GMTED10) (Danielson & Gesh 2011) and topography (USGS 2013) data which are thought to contribute to plant distribution at more intermediate scales (Elith & Leathwick 2009). Although I used these climate variables for the SDMs, due to the wide variety of food plant species analyzed, there was an inability to create models more sensitive to soil type, slope exposures and other more nuanced habitat requirements of the plants. It is also important to note that these climate variables are recent and do not necessarily reflect the exact climate during the pre-Columbian Hohokam time period.

Response and Predictor Variables

The response variable (i.e., the variable I analyzed and tried to explain) in the models was relative food plant species richness. I first calculated a total richness for the food plants (i.e., food plant richness) by overlaying maps of species distributions from the above models. I then estimated total richness by overlaying distributions of all known species, using data available from BIEN3 (Maitner et. al. 2017). The richness values in these two raster datasets were divided to derive a relative food plant species richness raster. The BIEN3 species range maps (Maitner et. al. 2017) are currently the most comprehensive set of land plant range maps available and include 98,829 species across North and South America (Brian Maitner per comm. Jan. 2019). I downloaded range maps for all available species as GIS shapefiles using the package ‘BIEN’ for R (Maitner et. al. 2017). Analyses were carried out for each 100 km x 100 km resolution cell in North and South America. The species richness map was then resampled to the Hohokam study area (i.e., my geographic extent) and 2km x 2km resolution.

Predictor variables (i.e., variables that may explain changes in the response variable) comprised river distance, Hohokam maximum population and contemporary population density. I used the ‘raster’ package to create a river distance layer using river data from major rivers in the Hohokam region. I consider distance from river as a driver of food plant species richness, with potentially higher richness closer to rivers. In order to estimate Hohokam population, I used the HSW data from the Hohokam region and created buffers around every settlement in the study area at both the 7 km (farming) and 36 km (wild-harvesting) distance. I then used the maximum estimated population for any interval for every site. This measure of population is a measure of the relative intensity of population throughout the Hohokam sequence. Areas that had either more sites or larger sites would provide high values and areas with few sites or smaller sites during the period between A.D. 700 and 1450 would have lower values. Contemporary population data was downloaded from NASA's Socioeconomic Data and Applications Center (SEDAC) (CIESIN 2017).

The spatial extent of the study was delineated by setting a 36 km buffer around each archaeological site. This is estimated to be a day's walk from a major settlement (Wilcox et. al. 2007, Hill et. al. 2015) and defines a potential zone of plant use. (e.g., exchange, transplant, dispersal, propagation) amongst Hohokam settlements (**Fig.1**). I also repeated analyses using a 7 km buffer around each archaeological site which is estimated to be the distance people will travel to specifically farm (see Wilcox et. al. 2007, Varien 1999; See **Appendix H:** Hohokam & km Buffer Distance **Fig. S1**).

Regressions and Spatial Autocorrelation

I built a spatial GAM using the 'mgcv' package (Wood 2011, Wood 2017) to predict the response variables using the explanatory variables, accounting for spatial autocorrelation of the data. GAMs with spatial terms are useful to account for spatial autocorrelation (Leathwick 2001) and are commonly used to implement non-parametric smoothers in regression models (Jones & Wrigley 1995, Guisan & Zimmerman 2000). I also included two interaction terms (**i**) Hohokam population and contemporary population and, (**ii**) Hohokam population and distance from river to further test how pre- and post-Columbian settlement patterns impact relative food plant species richness. I power-transformed (lambda=1/4) the population and river distance data to improve normality of the model residuals. I then scaled the explanatory variables to account for differences in variance. A smoothing term was applied to the spatial term (i.e., the latitude and longitude coordinates) for a full smooth of the interaction (Jones & Wrigley 1995, Guisan & Zimmerman 2000). I also used a smoothing term on the other explanatory variables as well as the interaction terms. I used the 'visreg' package (Breheny & Burchett 2017) to create partial residual plots and interaction plots to ascertain variable importance for relative food plant species richness. It is important to note that I did not include the climate variables in the GAM in order to avoid circular results as the climate variables were used to create the SDMs. However, I did conduct a supplementary analysis at the 36 km distance that included the climate variables for transparency (See **Appendix I** Hohokam 36 km Buffer Distance with Climate Variables).

RESULTS

At distance scales consistent with wild-harvesting (36 km), the model including all the explanatory variables for relative food plant species richness was statistically significant (Adjusted R^2 = 0.827, -REML=-78134) with a deviance explained at 82.8%. High relative food plant species richness was partially predicted by high pre-Columbian and contemporary populations. There was higher relative food plant species richness in areas that had the highest pre-Columbian populations using a GAM regression analysis (**Fig 4**, **Fig. 5**, GAM: s(Hohokam.Pop.) F=37.46, P=<2e-16). Additionally, I found that there was higher relative food plant species richness in areas of high contemporary population density (**Fig. 5**, GAM: s(Contemporary.Pop.) F=14.05, P=0.000178). These results suggest that high population density of pre-Columbian and contemporary populations may have had a persistent positive effect on the enrichment of food plant species richness.

In addition to pre-Columbian and contemporary population, spatial dependence was also found to be a driver for the enrichment of food plant species richness. Modeling the spatial dependence in the systematic part of the model did account for spatial autocorrelation. The spatial term was statistically significant (**Fig. 5**, GAM: s(x,y) F=1423.06, P=<2e-16). Relative food plant species richness was not influenced by distance from river except for a decrease in food plant richness at the furthest distance from rivers (**Fig. 5**, GAM: s(River.Distance) F=14.14, P=<2e-16).

I found that relative food plant species richness was also partially predicted by two interactions terms. The highest centers of contemporary population density (i.e., Phoenix and Tucson) and the areas of highest pre-Columbian populations (i.e., which also include Phoenix and Tucson but extend outward) tended to also have some of the highest instances of relative food plant species richness. The combined effects between Hohokam population and contemporary population were statistically significant (**Fig. 5**, GAM: s(Hohokam.Pop., Contemporary. Pop.) F=37.49, P=<2e-16; **Fig. 6**). There were also instances of high relative food plant species richness in areas of jus high contemporary population or just high Hohokam population estimates (**Fig. 6**). The interaction between Hohokam population and distance from river was found to also be statistically significant (**Fig. 5**, GAM: s(Hohokam.Pop, River.Distance) F=31.03, P=<2e-

16; **Fig. 7**). There appears to be higher food plant richness both in areas close and further from the river at different pre-Columbian population maximums (**Fig. 7**) This is potentially indicative of how, in certain cases, the Hohokam would inhabit areas close to rivers and then expand their settlements outward, possibly engaging in exchange and dispersal of food plants away from the river via harvesting as well as caring techniques.

At distance scales consistent with agriculture (7 km) the model, including all predictor variables, was statistically significant (Adjusted R^2=0.852, -REML=-26181) with a deviance explained at 85.4%. Although there were some instances of higher relative food plant species richness within areas of higher pre-Columbian populations, the results were not statistically significant at this buffer distance (see **Appendix H:** Hohokam 7 km Buffer Distance **Fig. S2**, **Fig. S3**, GAM: s(Hohokam.Pop.) F=0.637, P=0.698). However, similar to the 36 km distance results, I did find that there was higher relative food plant species richness in areas of high contemporary population density and this was statistically significant (see **Appendix H**: Hohokam 7 km Buffer Distance **Fig. S3**, GAM: s(Contemporary.Pop.), F=17.026, P=3.79e-05).

Both distance from river and spatial dependence of the values are also found to be drivers for the enrichment of food plant species richness. Similar to the 36 km distance results, modeling the spatial dependence in the systematic part of the model did account for spatial autocorrelation. The spatial term was statistically significant (see **Appendix H:** Hohokam 7 km Buffer Distance **Fig. S3**, GAM: s(x,y) F=602.924, P=<2e-16). Relative food plant species richness was not influenced by distance from river (richness remains relatively constant (see **Appendix H:** Hohokam 7 km Buffer Distance **Fig. S3**, GAM: s(River.Distance), F=10.814, P=<2e-16).

Relative food plant species richness was also partially predicted by the interaction between Hohokam and contemporary population at the 7 km buffer distance. This was also statistically significant (see **Appendix H:** Hohokam 7 km Buffer Distance **Fig. S3**, GAM: s(Hohokam.Pop., Contemporary. Pop.) F=13.650, P=<2e-16; **Fig. S4**). Similar to the 36 km buffer distance, there was enrichment of food plant species richness in areas where high contemporary population density and high Hohokam population density overlap, and also areas of high contemporary population density but low Hohokam populations (**Fig. S4**). The interaction between Hohokam population and distance from river was also statistically significant (see **Appendix H:** Hohokam 7km Buffer Distance **Fig. S3**, GAM: s(Hohokam.Pop., River.Distance) F=3.982, P=<2e-16; **Fig. S5**). However, highest enrichment of food plant species richness was found further from rivers at both lower and higher Hohokam population estimates potentially suggesting other drivers as an influence at this distance.

DISCUSSION

This study used archaeological and ecological data to provide evidence for both prehistoric and contemporary human influence on plant biogeography. My results show that, at distances consistent with wild-harvesting (36 km), both pre-Columbian and contemporary population have shaped patterns of relative food plant species richness. However, the importance of each factor in the GAM varied depending on buffer scale See **Appendix H:** Hohokam 7 km Buffer Distance). Therefore, both hypotheses received partial support. I found that, when basing my analysis on a day’s walk from a major settlement (i.e., the 36 km buffer distance), there was higher relative food plant species richness in areas that had the highest pre-Columbian populations, partially consistent with

Hypothesis A (i.e., there would be higher food plant species richness in areas that had high pre-Columbian populations) (**Fig. 5**).

At the 36 km buffer distance, I also identified contemporary population as potentially an important influence on relative food plant species richness, consistent with **Hypothesis B** (**Fig. 5**) (i.e., there would be higher food plant species richness in areas of high contemporary population density). It is a challenge to understand if food plant distributions are shaped by both contemporary populations and pre-Columbian populations, or if there are one or more common drivers that could cause high population and high relative food plant richness. One common factor could be the canal networks in the Phoenix Basin and the interest in continuing to settle in areas where water remains available (e.g. the Santa Cruz River) in the Tucson Basin (Fish & Fish 1992). For example, in the mid-1800s, Piman Indian farmers and Mormon pioneers of the Lehi settlement used the ancient canals as a model for modern irrigation in the Phoenix area (Howard n.d.). The early historic canals were formed largely by cleaning out the Hohokam canals (Howard n.d.). This could have helped maintain remnant populations of food plants that were originally encouraged and dispersed by the Hohokam. There is generally higher relative food plant species richness in areas of both high Hohokam populations and contemporary population (**Fig. 6**), suggesting that it is important to address the combination of pre-Columbian and contemporary human effects on a landscape scale.

Climate variables were found to be significant drivers of relative food plant species richness as well (see **Appendix I:** Hohokam 36km Buffer Distance with Climate Variables **Fig S6 & S7**). However, it is important to consider that the extent of this significance may be due to the climate variables also being used for the food plant SDMs. In order to account for this, I added the climate variables into the GAM for the 36k m distance in the Supplementary section. Even with the addition of the climate variables in the model, the conclusions remain qualitatively very similar (see **Appendix I:** Hohokam 36 km Buffer Distance with Climate Variables **Fig S6 & S7**). Namely, Hohokam population and the interaction between Hohokam population and contemporary population as well as Hohokam population and distance from river remain significant. This suggests that the persistent effects of population could also be a driver of food plant species enrichment patterns.

There are also instances of higher relative food plant species richness in areas of high contemporary population, but lower Hohokam population estimates (see **Appendix I:** Hohokam 36 km Buffer Distance with Climate Variables **Fig. S8**). Although it is in the best interest of contemporary human populations in water-limited areas to also be close to canals, technological advances do make it easier to expand even further outward than the Hohokam potentially could have expanded. Additionally, studies have shown in the Phoenix area that there is an overall trend for native and introduced plant diversity to be higher (i.e., higher generic species richness) in the contemporary, human-managed, urban landscape where there is higher available nutrients and water due to fertilization and irrigation (Hope et. al. 2003). This could also be a possibility in the Tucson area, which is also comprised of neighborhoods of varying income levels and access to human-controlled nutrients and irrigation (Halper et. al. 2012). However, there are also instances of higher relative food plant species richness with high Hohokam populations and low contemporary population (see **Appendix I:** Hohokam 36 km Buffer Distance with

Climate Variables **Fig. S8**). This suggests that it is equally as important to consider how human impacts in pre-Columbian times can persist on the landscape scale as well. I argue that both pre-Columbian and recent management of plants continues to shape patterns of plant species richness in the Sonoran Desert today.

It was also found that the relative impacts of pre-Columbian and recent populations can differ depending on buffer distance (i.e., how many points I included in the study where there were no humans, but where there potentially could have been). At the 7 km buffer distance (see **Appendix H:** Hohokam 7 km Buffer Distance), there is actually a general decrease in relative food plant species richness as Hohokam population increases (see **Appendix H:** Hohokam 7 km Buffer Distance). This suggests that although this zone is the nearest available by pre-Columbian people for agricultural use, it does not necessarily capture the entire zone or continuum of food plant use (i.e., agricultural as well as wild-harvesting, dispersal through exchange and transport). Similar to the 36 km buffer distance, the analysis suggests high relative food plant species richness in areas of both high contemporary population and high Hohokam populations (see **Appendix H:** Hohokam 7 km Buffer Distance, **Fig.S4**). When I considered the combined effect of distance from river and Hohokam population, it appeared that there was only high relative food plant species richness in areas of high Hohokam population estimates regardless of distance from river (see **Appendix H:** Hohokam 7 km Buffer Distance, **Fig. S5**). This could suggest that the Hohokam increased food plant species richness through the management and dispersal of these plants around their settlements.

The Hohokam were gatherers and consumers of desert food plants, dispersing and encouraging populations of both woody perennials as well as weedier species beyond their settlements (Gasser 1981, Crown 1987, Bohrer 1987, Gasser & Kwaitkowski 1991, Bohrer 1991, Fish 1993, Fish & Fish 1994). In more recent times, leguminous trees such as mesquite (e.g., *Prosopis glandulosa, P. velutina,* and *P. pubescens*) were considered desirable for their nutritious beans and would be left standing in cleared fields, sometimes also growing densely in hedgerows that were sustained through agricultural water. Identified seeds and charcoal from pre-Columbian settlements supports the availability of these trees through time as well (Fish & Fish 1992). It is also thought that weedy plants such as *Chenopodium* spp. (goosefoot), *Amaranthus* spp. (amaranth), and *Boerhavia* spp (spiderling). were encouraged within agricultural fields as secondary resources by the Hohokam. These species were less water intensive compared to the cultigens (e.g., *Zea mays*, *Cucurbita* spp., *Phaseolus* spp.) (Fish & Fish 1992). *Hordeum pusillum* (little barley) as well as *Descurainia pinnata* (tansy mustard) also grew well on disturbed ground (Bohrer 1991). *Phaseolus* spp. (bean) as well as *Opuntia* spp. (prickly pear) and *Cylindropuntia* spp. (cholla) were most likely tended to and transplanted amongst settlements (Fish & Fish 1992).

One of the limits of my analysis was my inability to quantify the impact of subsequent human populations after the pre-Columbian Hohokam but before contemporary times. In order to more fully capture a continuum of use and investigate the legacy of food use through time on the landscape, population estimates of other cultural groups will be needed (e.g., Pima, Apache, Tohono O’odham). It is also important to consider the legacy of European settlers in the Hohokam region. In the late 1700s, Spanish soldiers began to farm in areas in proximity to the Tohono O’odham in the Tucson Basin (Darling & Lewis 2007). The arrival of the railroad in the 1800s allowed for large amounts of non-native foods to be imported into Tucson, also altering the suite of crops cultivated on farmland (e.g., water-intensive crops such as lettuce and watermelon). By the late 1800s, the combination of drought, ground-water pumping, and digging a deeper canal had led to the degradation of the river and disrupted traditional farming (Thiel 2010).

Limited archaeological and population data mean that this study is a first effort in arid regions to investigate on the relative influence of human food use on biodiversity patterns (i.e. food plant species richness) by considering pre-Columbian and contemporary populations on the landscape scale. This is in contrast to analyses that solely focus on past human food use and the resulting richness and distribution legacies on the landscape (Levis et. al. 2017). The results strongly suggest that in general, species richness patterns and biogeography of useful species are not necessarily primarily driven by environment, but also have large human signatures –even in ‘pristine’ areas or those that were apparently abandoned for long periods of time. I argue that it can be limiting to consider distribution and richness patterns solely from a climate-centric perspective (Pausas & Bond 2018). My analysis contributes to a growing body of research suggesting for a more integrative view of nature in which disturbance plays a central role (Pausas & Bond 2018). This approach may begin to form the basis of an inclusive biogeography that includes more human effects.

FIGURES

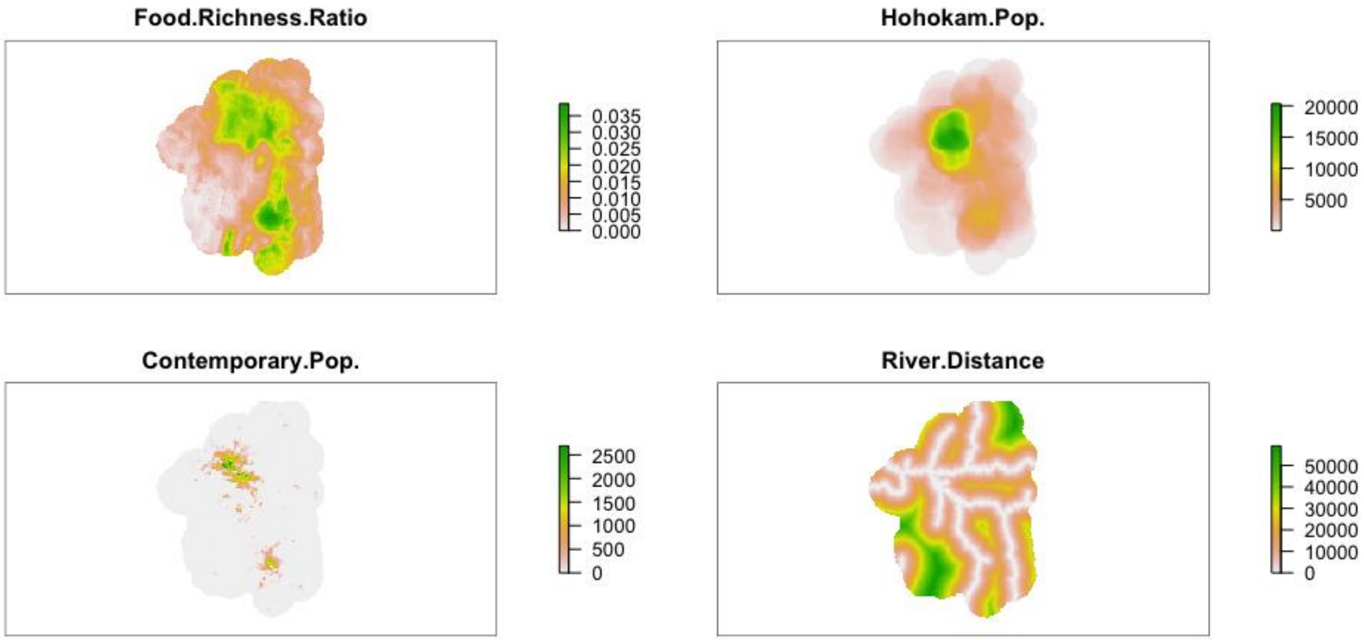


Figure 4. Response variable (i.e. Food.Richness.Ratio) and explanatory variables (i.e. Hohokam.Pop., Contemporary.Pop., and River.Distance) that were used in the GAM at the 36 km buffer distance, consistent with the distance Hohokam would travel in the Sonoran Desert for wild-harvesting. Green represents the highest food plant species richness, the highest human populations, and the farthest distance from rivers.

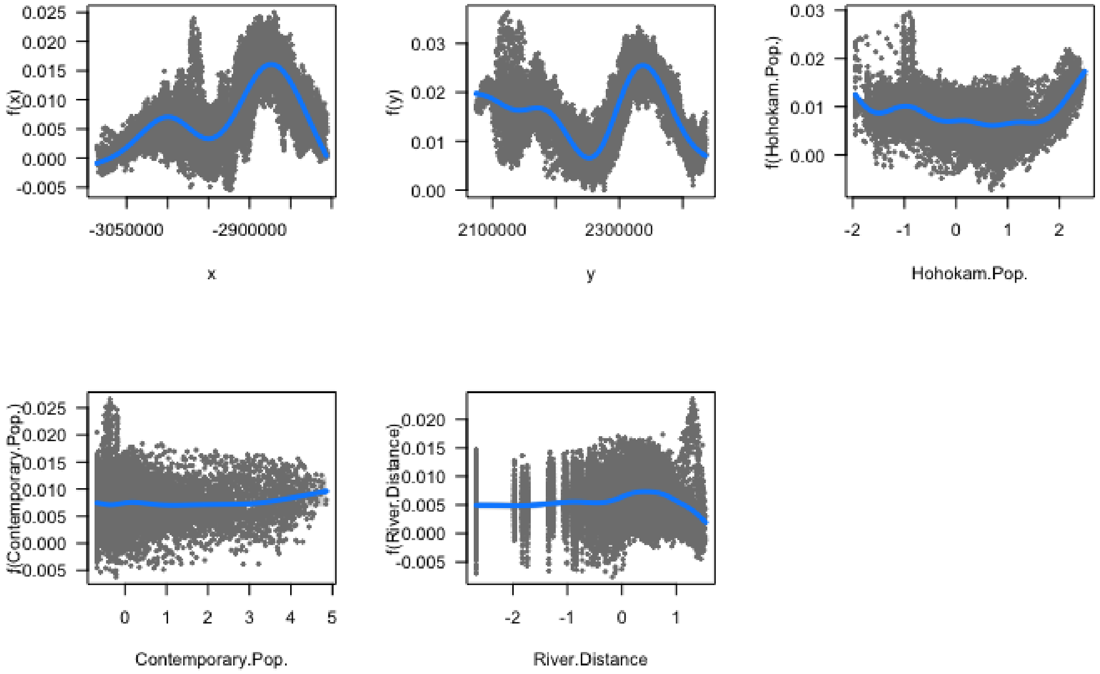


Figure 5. Partial residuals for each explanatory variable used in the GAM for the 36 km buffer distance (Adjusted R^2 = 0.827, -REML=-78134 with a deviance explained at 82.8%). Partial residual plots show the relationship between each predictor variable and the response variable given that the other predictor variables are in the model. This is useful for understanding the relative importance of each predictor variable. Hohokam and Contemporary population increase correlates with higher relative food plant species richness.

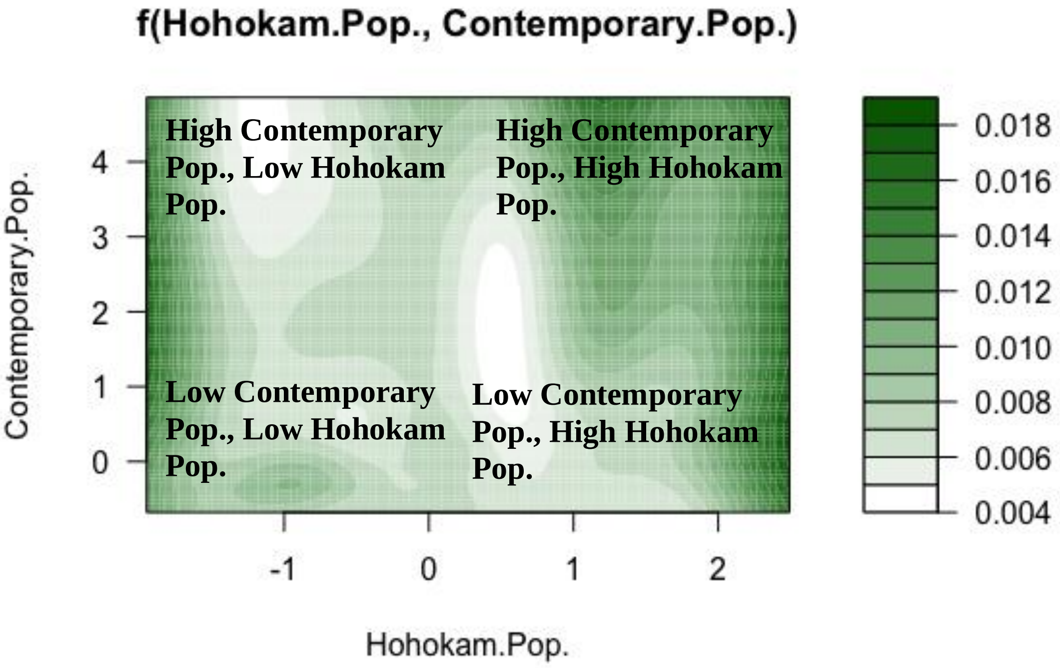


Figure 6 Relative food plant species richness was partially predicted by an interaction between Hohokam.Pop. and Contemporary.Pop in the GAM using the 36 km buffer distance (GAM: s(Hohokam.Pop., Contemporary. Pop.) F=37.49, P=<2e-16). The red represents higher relative food plant species richness. There is higher relative food plant species richness with instances of higher contemporary and Hohokam populations, high Hohokam populations and low contemporary populations, as well as high contemporary populations and low Hohokam populations.

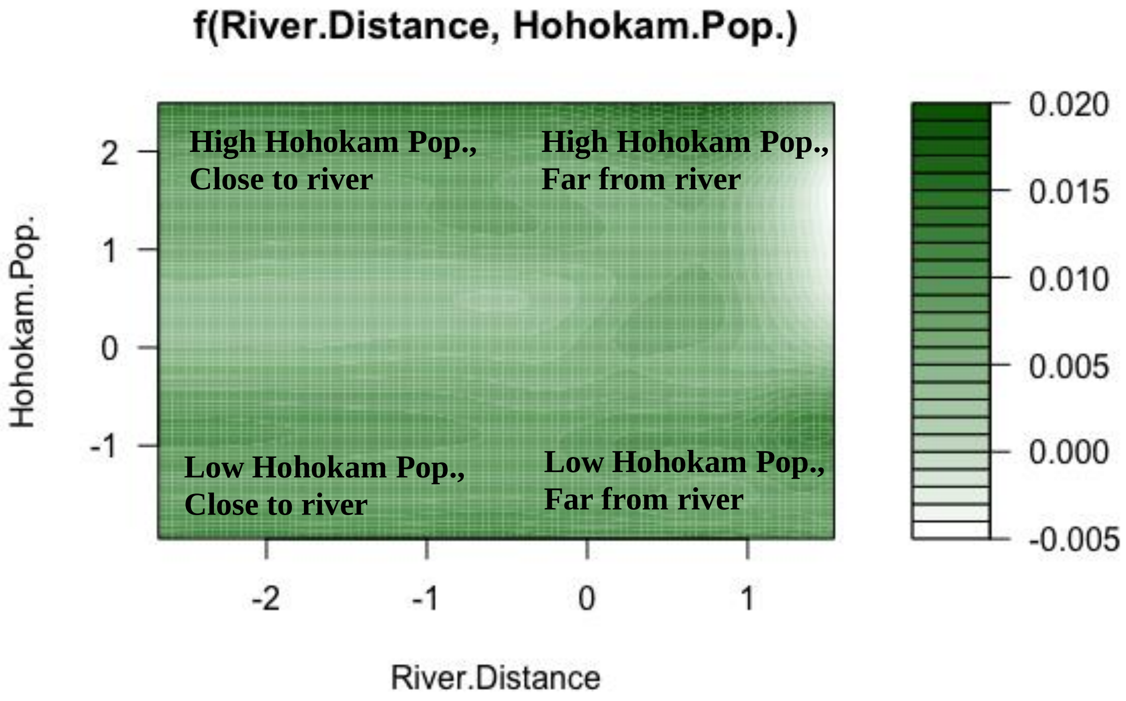


Figure 7 Relative food plant species richness was partially predicted by an interaction between River.Distance and Hohokam.Pop in the GAM using the 36 km buffer distance (GAM: s(Hohokam.Pop, River.Distance) F=31.03, P=<2e-16). The red represents higher relative food plant species richness. There was high relative food plant species richness close and far from the rivers regardless of Hohokam population density.

REFERENCES

Abbott, D.R., Smith, A.M., Gallaga, E. (2007). Ballcourts and ceramics: the case for Hohokam marketplace in the Arizona Desert. *Am. Antiquity*. 72, 461-484.

Abrams, M.D. & Nowacki, G.J. (2008). Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. *The Holocene*. 18, 1123-1137.

Allen, A. P. Gillooly, J.F. & Brown, J.H. (2007). Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. Pages 283-299 in D. Storch, P.A. Marquet, and J.H. Brown, editors. Scaling Biodiversity. Cambridge University Press, Cambridge, U.K.

Ansong, M. & Pickering, C. (2013). Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. *PLoS ONE*. 8(11). 1-11.

Auffret, A.G. Berg, J. & Cousins, S.A.O. (2014). The geography of human-mediated dispersal. *Diversity and Distributions*. 20. 1450-1456.

Bailey, G. (2007). Time perspectives, palimpsests and the archaeology of time. *Journal of Anthropological Archaeology*. 26. 198-223.

Bahn, V. & McGill, B.J. (2007). Can niche-based distribution models outperform spatial interpolation. *Global. Ecology and Biogeography*. 1-10.

Barton, H. & Denham, T. (2011). Prehistoric vegeculture and social life in Island Southeast Asia and Melanesia. *Why cultivate? Anthropogenic and archaeological approaches to foraging-farming transitions in Southeast Asia*. In. G. Barker & M. Janowski (Eds.). McDonald Institute for Archaeological Research, Cambridge, UK. pp. 17-25.

Bayman, J.M. (2001). The Hohokam of Southwest North America. *J. World Prehist*. 15, 257-312.

Bell, W.H. & Castetter, E. F. (1937). The Utilization of Mesquite and Screwbean by the Aborigines in the American Southwest. *Ethnobiological Studies in the American Southwest*. University of New Mexico Bulletin, Biological Series, University of New Mexico Press, Albuquerque, 5.

Bell, W.H. & Castetter, E.F. (1941). The Utilization of Yucca, Sotol, and Beargrass by the Aborigines in the American Southwest. *Ethnobiological Studies in the American Southwest*. The University of New Mexico Bulletin, Biological Series, University of New Mexico Press, Albuquerque, 5.

Bitencourt, A.L.V. & Krauspenhar, P.M. (2006). Possible prehistoric anthropogenic effect on *Araucaria angustifolia* (Bert.) O. Kuntze expansion during the late Holocene. *Rev. Bras. Paleontolog.*, 9, 109-116.

Bohrer, V.L. (1987). Methods of recognizing cultural activity from pollen in archaeological sites. *The Kiva*. 46, 135-142.

Bohrer. V.L. (1991). Recently recognized cultivated and encouraged plants among the Hohokam. *The Kiva*. 56, 227-235.

Bovin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denham, T. et. al. (2016). Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *PNAS*. 113, 6388-6396.

Breheny, P. & Burchett, W. (2017). Visualization of regression models using visreg. *The R Journal*. 9, 56-71.

Briggs, J.M., Spielmann, K.A., Schaafsma, H., Kintigh, K.W., Kruse, M., Morehose, K. et. al. (2006). Why ecology needs archaeologists and archaeology needs ecologists. *Front Ecol. Environ*. 4, 180-188.

Brosius, J.P. (1991). Foraging in tropical rain forests: the case of the Penan of Sarawak, East Malaysia (Borneo). *Hum. Ecol*. 19, 123-150.

Bush, M.B., McMichael, C.H., Piperno, D.R., Silman, M.R., Barlow, J., Peres, C.A. et. al. 2015. Anthropogenic influence on Amazonian forests in pre-history: an ecological perspective. *J. Biogeogr*. 42. 2277-2288.

Castetter E.F. & Bell W. H. (1951). *Yuman Indian Agriculture*. University of New Mexico Press. Albuquerque, New Mexico.

Castetter, E.F. & Underhill, R.M. (1935). The Ethnobiology of the Papago Indians. *Ethnobiological Studies in the American Southwest*. University of New Mexico. Bulletin, Biological Series, 4, 1-84.

Chamberlain, S. (2017). rgif: Interface to the Global 'Biodiversity' Information Facility API. R package version 0.9.8. https://cran.r-project.org/web/packages/rgbif/index.html

CIESIN. (2017). Center for International Earth Science Information Network. Columbia University. NASA Socioeconomic Data and Applications Center (SEDAC). Palisades, N.Y. http://doi.org/10.7927/H40Z716C.

Clement, C.R., Denevan, W.M., Heckenberger, M.J., Junqueira, A.B., Neves, E.G., Teixeira, W.G. et. al. (2015). The domestication of Amazonia before European conquest. *Proc. R. Soc. B*. 282, 1-9.

Clement C.R. & Junqueira A.B. (2010). Between a pristine myth and an impoverished future. *Biotropica*. 42. 534-536.

Coblentz, D.D. & Riitters, K.H. (2004). Special paper: topographic controls on the regional-scale biodiversity of the south-western USA. *J. Biogeogr*. 31(7). 1125-1138.

Crosby, Jr. (1972). The Columbian Exchange: The biological and cultural consequences of 1492. Praeger Publishers. Westport, CT. 1-268.

Crosswhite, F.S. (1981). Desert plants, habitat, and agriculture in relation to the major pattern of cultural differentiation in the O'odham people of the Sonoran Desert. *Desert Plants*. 3, 47-76.

Crown, P.L. (1987). Classic period Hohokam settlement and land use in the Casa Grande Ruins area, Arizona. *J. Field Archaeol*. 14(2). 147-162.

Currie, D.J. (1991). Energy and large-scale patterns of animal and plant species richness. *Am. Nat*. 137(1). 27-49.

Currie, D.J., Francis, A.P. & Kerr, J.T. (1999). Some general propositions about the study of spatial patterns of species richness. *Ecoscience*. 6(3). 392-399.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J. et. al. (2004). Predictors and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett*. 7. 1121-1134.

Danielson, J.J. & Gesch, D.B. (2011). Global multi-resolution terrain elevation data 2010 (GMTED2010). U.S. Geological Survey Open-File Report 2011-1073, 1-26.

Darling, J.A. & Lewis, B.V. (2007). Ancient trails of the arid Southwest. *Archaeology Southwest Magazine*. Archaeology Southwest. Tucson, Arizona.

Denevan, W.M. (1992). The pristine myth: the landscape of the Americans in 1492. *Assoc. Am. Geogr*. 82. 369-385.

Doelle, W. H. (1980). Past adaptive patterns in western Papagueria: an archaeological study of nonriverine resource use. University of Arizona Press. University of Arizona. Tucson, AZ.

Doelle, W.H. (1995). Tonto Basin Demography in a Regional Perspective. *In* The Roosevelt Community Development Study: New Perspectives on Tonto Basin

Prehistory. Mark. D. Elson, Mariam, T. Stark & David A. Gregory eds. 201-226. Anthropological Research Papers No 15. Center for Desert Archaeology. Tucson, Arizona.

Elith, J, Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A. et. al. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*. 29. 129-151.

Elith, J. & Leathwick, J.R. (2009). Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677-697.

Fick, S.E. & Hijmans, R.J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol*. 37, 4302-4315.

Fish, S.K. (1984). Agriculture and subsistence implications of the Salt-Gila Aqueduct pollen analysis. *Hohokam Archaeology along the Salt Gila Aqueduct Central Arizona Project: volume VII: Environment and subsistence.* L.S. Teague & P.L. Crown eds. Archaeological Series, Cultural Resource Management Section, Arizona State Museum, The University of Arizona, Tucson. 150. 111-138.

Fish, S.K. (1993). Agriculture and society in arid lands: a Hohokam case study. Dissertation. The University of Arizona Graduate College.

Fish, S.K. & Fish, P.R. (1992). Prehistoric landscapes of the Sonoran Desert Hohokam. *Popul. Environ*. 13(4). 269-283.

Fish, S.K. & Fish, P.R. (1994). Prehistoric desert farmers of the Southwest. *Annu. Rev. Anthropol.*. 23. 83-108.

Fish, S.K. & Fish, P.R. (2007). The Hohokam millennium. 1-12. Fish, S.K. & Fish, P.R. (Eds.). *The Hohokam Millenium*. School for Advanced Research Press. Santa Fe, New Mexico. 1-151.

Ford, A. & Nigh, R. (2015). *The Maya forest garden: eight millennia of sustainable cultivation of the tropical woodlands*. Routledge. New York, NY. 1-187.

Fritz, G.J., Adams, K.R., Rice, G. E. & Czarzasty, J.L. (2009). Evidence for domesticated amaranth from a sedentary period Hohokam house floor at Las Canopas. *KIVA.* 74, 393-419.

Gasser, R.E. (1981). Hohokam use of desert food plants. *Desert Plants*. 3, 216-234.

Gasser, R.E. & Kwaitkowski, S.M. (1991). Regional signatures of Hohokam plant use. *KIVA*. 56, 207-226.

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*. 405. 220-227.

Gaoue, O.G., Coe, M.A., Bond, M., Hart, G., Seyler, B.C. & McMillen, H. (2017). Theories and major hypotheses in ethnobotany. *Econ. Bot.*. XX(X) 1-19.

Ghalambor, C. K., Huey, R.B., Martin, P.R, Tewksbury, J.J. & Wang. G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol*. 46(1). 5-17.

Goncalves, P.H.S., Albuquerque, U.P. & de Medeiros, P.M. (2016). The most commonly available woody plant species are the most useful for human populations: a meta-analysis. *Ecol. Appl.*. 26(7). 2238-2253.

Greenhouse, R., Gasser, R.E. & Gish, J.W. (1981). Cholla bud roasting pits: an ethnoarchaeological example. *Kiva*. 46(4). 227-242.

Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.*. 8. 993-1009.

Guisan, A. & Zimmerman, N.K. (2000). Predictive habitat distribution models in ecology. *Ecol. Model*. 135. 147-186.

Hall, S.J., Trujillo, J., Nakase, D., Strawhacker, C., Kruse-Peeples, M., Schaafsma, H. et. al. (2013). Legacies of prehistoric agricultural practices within plant and soil properties across an arid ecosystem. *Ecosystems*. 16, 1273-1293.

Halper, E.B., Scott, C.A. & Yool, S.R. (2012). Correlating vegetation, water use, and surface temperature in a semiarid city: a multiscale analysis of the impacts of irrigation by single family residences. *Geogr. Anal*. 44. 235-257. .

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J., Kaufman, D.M. et. al. (2003). Energy, water and broad-scale geographic patterns of species richness. *Ecology*. 84(12). 3105-3117.

Hijmans, R.J, Phillips. S., Leathwick, J. & Elish, J. (2007). dismo: species distribution modeling. R package version 1.1-4.

Hill, B.J. Clark, J.J. Doelle, W. H. & Lyons, P.D. (2004). Prehistoric demography in the Southwest: migration, coalescence, and Hohokam population decline. *Am. Antiq*. 69(4). 689-716.

Hill, B.J. Wilcox, D., Doelle, W. & Robinson, W. (2012). Coalescent Communities Database Version 2.0. Archaeology Southwest. Tucson, Arizona.

Hill, J.B, Peeples, M.A., Huntley, D.L. & Carmack, H. J. (2015). Spatializing Social Network Analysis in the Late Precontact U.S. Southwest. *Advances in Archaeological Practice*. 3(1). 63-77.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat*. 163(2). 192-211.

Hodgson, W.C. (2001). *Food Plants of the Sonoran Desert*. The University Arizona Press. Tucson, Arizona. 1-299.

Hope, D. Gries, C, Casagrande, D., & Redman, C.L. (2006). Drivers of spatial variation in plant diversity across the Central Arizona-Phoenix ecosystem. *Soc. Nat. Resour*. 19. 101-116.

Hope, D., Gries, C., Zhu, W., Fagan, W.F., Redman, C.L., Grimm, N.B. et. al. (2003). Socioeconomics drive urban plant diversity. *PNAS*. 100(15). 8788-8792.

Howard, J.B. n.d. Hohokam legacy: desert canals. Pueblo Grande Museum Profiles. No. 12. Accessible at: http://www.waterhistory.org/histories/hohokam2/

Jablonski, D., Roy, K. & Valentine, J.W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*. 314(5796). 102-106.

Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *Am. Nat.* 101(919). 233-249.

Janzen, D.H. (1986). Chihuahuan desert nopaleras: defaunated big mammal vegetation. *Annu. Rev. Ecol. Syst.*. 17. 595-636.

Jones, K. & Wrigley, N. (1995). Generalized additive models, graphical diagnostics, and logistic regression. *Geogr. Anal*. 21(1). 1-18.

Junqueira. A.B., Levis. C., Bongers, F., Pena-Claros, M., Clement, C.R., Costa, F. et. al. (2017). Response to comment on "persistent effects of pre-Columbian plant domestication on Amazonian forest composition'. *Science*. 358, 1-2.

Kerkhoff, A.J., Moriarty, P.E. & Weiser, M.D. (2014). The latitudinal species richness gradient in new world woody angiosperms is consistent with the tropical conservatism hypothesis. *PNAS*. 11(22). 8125-8130.

Lamanna, C., Blonder, B., Violle, C., Kraft, N.J.B., Sandel, B., Simova, I. et. al. (2014). Functional trait space and the latitudinal diversity gradient. *PNAS*. 1-6.

Levis, C., Costa, F.R.C, Bongers, F., Pena-Claros, M., Clement, C.R., Junqueira, A.B. et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*. 355, 925-931.

Levis, C., Flores, B.M., Moreira, P.A., Luize, B.G., Alves, R.P, Franco-Moraes, J. et al. (2018). How people domesticated Amazonian forests. *Front. Ecol. Evol*. 5, 1-21.

Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue II, J., Duran, S.M. et. al. (2017). The BIEN R package. A tool to access the Botanical Information and Ecological Network (BIEN) database. *Methods Ecol. Evol*. 91, 373-379.

Malhi, Y. (2017). The concept of the Anthropocene. *Annu. Rev. Environ. Resour.*. 42. 77-104.

McKey, D., Rostain, S., Iriarte, J., Bruno, G., Birk, J.J., Holst, I. et. al. (2010). Pre-Columbian agricultural landscapes, ecosystem engineers, and self-organized patchiness in Amazonia. *PNAS*. 107, 7823-7828.

McMichael, C.H., Feeley, K.J., Dick, C.W., Piperno, D.R. & Bush, M.B. (2017). Comment on ‘Persistent effects of pre-Columbian plant domestication on Amazonian forest composition’. *Science*. 358, 1-2.

Merriam, C.H. (1890). Results of a biological survey of the San Francisco Mountain region and the desert of the Little Colorado, Arizona. *North. Am. Fauna.*. 3. 1-136.

Merriam, C.H. (1894). Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Nat. Geo.*. 6. 229-238.

Mills, B.J., Clark, J.J., Peeples, M.A., Haas, Jr., W.R., Roberts Jr., J.M., Hill, B., et. al. (2013). Transformation of social networks in the late pre-Hispanic US Southwest. *PNAS*. 110(15). 5785-5790.

Mills, B.J., Peeples, M.A., Haas, Jr., W. R., Borck, L., Clark, J.J. Roberts, J.M. (2015). Multiscalar perspectives on social networks in the late prehispanic Southwest. *Am. Antiq*. 80(1). 3-24.

Nabhan, G.P. (2016). *Gathering the Desert.* University of Arizona Press. Tucson, Arizona. 1-221.

Naimi, B. & Araujo, M.B. (2016). sdm: a reproducible and extensible R platform for species distribution modeling. *Ecography*. 39, 368-375.

Omernik, J.M. (2004). Perspectives on nature and definition of ecological regions. *Environ. Manage*. 34, Suppl. 1, S27-S38.

Parker, K.C. (1991). Topography, substrate, and vegetation patterns in the northern sonoran desert. *J. Biogeogr*. 18(2). 151-163.

Pausas, J. G. & Bond, W.J. (2018). Humboldt and the reinvention of nature. *J. Ecol.* 1-7.

Peeples, M. (2006). Hohokam Population Database. (tDARK id: 1582); doi: 10.6067/XCV8FX780Z

Piperno, D.R., McMichael, C., & Bush, M.B. (2015). Amazonia and the Anthropocene: what was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? *The Holocene*. 25, 1588-1597.

Rea, A.M. (1997). *At the desert's green edge: an ethnobotany of the Gila River Pima*. The University Press. Tucson, Arizona. 1-413.

Ross, N.J. (2011). Modern tree species composition reflects ancient Maya "forest gardens" in northwest Belize. *Ecol. Appl*. 21(1). 75-84.

Sedrez dos Reis, M, Ladio, A. & Peroni, N. (2014). Landscapes with Araucaria in South America: evidence for a cultural dimension. *Ecol. Soc*. 19, 43.

SEINet Portal Network. (2018). http://:swbiodiversity.org/seinet/index.php.

Stevens, G.C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat*. 133(2). 240-256.

Stuart, G., Gries, C. & Hope, D. (2006). The relationship between pollen and extant vegetation across an arid urban ecosystem and surrounding desert in Southwest USA. *J. Biogeogr*. 33. 573-591.

Suarez-Estaban, A., Fahrig, L., Delibes, M. & Fedriani, J. M. (2016). Can anthropogenic linear gaps increase plant abundance and diversity? *Landscape Ecol*. 31. 721-729.

Thiel, J.H. (2010). Historic-era farming. *Archaeology Southwest Magazine*. Archaeology Southwest. Tucson, Arizona.

Thuiller, W., Miguel B., A. & Sandra, L. (2003). Generalized models vs. classification tree analysis: predicting spatial distributions of plant species at different scales. *J. Veg. Sci*. 14, 669-680.

Tomiolo, S. & Ward, D. (2018). Species migrations and range shifts: a synthesis of causes and consequences. *Perspect. Plant Ecol. Syst*. 33. 62-77.

USEPA: United States Environmental Protection Agency. (2016). *Ecoregions of North America*. Available at: https://www.epa.gov/eco-research/ecoregions-north-america. Last accessed 03 August 2018.

U.S. Geological Survey. (2013). USGS Small-scale Dataset - 100-Meter Resolution Grayscale Shaded Relief of the Conterminous United States 201304 GeoTIFF: U.S. Geological Survey.

Walker, J.S., Grimm, N.B., Briggs, J.M., Gries, C. & Dugan, L. (2009). Effects of urbanization on plant species diversity in central Arizona. *Front. Ecol. Environ.* 7(9). 465-470.

Warren II, R.J. (2016). Ghosts of cultivation past- Native American dispersal legacy persists in tree distribution. *PLoS ONE*. 11, 1-16.

Wiens, J.J. & Donoghue, M.J. (2004). Historical biogeography, ecology and species richness. *Trends Ecol. and Evol*. 19(12). 639-644.

Wilcox, D.R., Gregory, D.A. & Hill, B. (2007). Zuni in the Puebloan and Southwestern Worlds. *In* Zuni Origins: Toward a New Synthesis of Southwestern Archaeology. David A. Gregory and David R. Wilcox, eds. 165-209. University of Arizona Press. Tucson, Arizona.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenior, J., Damgaard, C.F. et. al. (2013). The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modeling. *Biol. Rev. Camb. Philos. Soc*. 88, 15-30.

Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B).* 73(1). 3-36.

Wood, S.N. (2017). Generalized additive models.: an introduction with R (wnd edition). Chapman and Hall/CRC.

Yang, X, Barton, H.J, Wan, Z., Li, Q., Ma, Z., Li, M. et. al. (2013). Sago-type palms were an important plant food prior to rice in southern subtropical China. *PLoS ONE*. 8, 1-8.

Van Zonneveld, M. Larranaga, N., Blonder, B., Coradin, L., Hormaza, J.I. & Hunter. D. (2018). Human diets drive range expansion of megafauna-dispersed fruit species. *PNAS*. 10, 1-6.

Varien, M.D. (1999). *Sedentism and Mobility in a Social Landscape: Mesa Verde and Beyond*. University of Arizona Press. Tucson, Arizona.

Zizka, A. (2018). CoordinateCleaner: automated cleaning of occurrence records from biological collections. R. package version 1.0-7. http://CRAN-R-project.org/package=CoordinateCleaner

REFERENCES

Abbott, D.R., Smith, A.M., Gallaga, E. (2007). Ballcourts and ceramics: the case for Hohokam marketplace in the Arizona Desert. *Am. Antiquity*. 72, 461-484.

Abrams, M.D. & Nowacki, G.J. (2008). Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. *The Holocene*. 18, 1123-1137.

Agrawai, A. & Redford, K. (2009). Conservation and displacement: an overview. *Conservat. Soc.* 7, 1-10.

Allen, A. P. Gillooly, J.F. & Brown, J.H. (2007). Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. Pages 283-299 in D. Storch, P.A. Marquet, and J.H. Brown, editors. Scaling Biodiversity. Cambridge University Press, Cambridge, U.K.

Anaya, F.C. & Espírito-Santo, M.M. (2018). Protected areas and territorial exclusion of traditional communities: analyzing the social impacts of environmental compensation strategies in Brazil. *Ecol. Soc*. 8, 1-13.

Ansong, M. & Pickering, C. (2013). Are weeds hitchhiking a ride on your car? A systematic review of seed dispersal on cars. *PLoS ONE*. 8(11). 1-11.

Arakaki, M., Christin, P., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R.M, et. al. (2011). Contemporaneous and recent radiations of the world's major succulent plant lineages. *PNAS*. 108, 8379-8384.

Auffret, A.G. Berg, J. & Cousins, S.A.O. (2014). The geography of human-mediated dispersal. *Divers. Distrib*. 20. 1450-1456.

Bahn, V. & McGill, B.J. (2007). Can niche-based distribution models outperform spatial interpolation. *Glob. Ecol. Biogeogr.*. 1-10.

Barton, H. & Denham, T. (2011). Prehistoric vegeculture and social life in Island Southeast Asia and Melanesia. *Why cultivate? Anthropogenic and archaeological approaches to foraging-farming transitions in Southeast Asia*. In. G. Barker & M. Janowski (Eds.). McDonald Institute for Archaeological Research, Cambridge, UK. pp. 17-25.

Bailey, G. (2007). Time perspectives, palimpsests and the archaeology of time. *J. Anthropol Archaeol.*. 26. 198-223.

Bayman, J.M. (2001). The Hohokam of Southwest North America. *J. World Prehist*. 15, 257-312.

Bell, W.H. & Castetter, E. F. (1937). The Utilization of Mesquite and Screwbean by the Aborigines in the American Southwest. *Ethnobiological Studies in the American Southwest*. University of New Mexico Bulletin, Biological Series, University of New Mexico Press, Albuquerque, 5.

Bell, W.H. & Castetter, E.F. (1941). The Utilization of Yucca, Sotol, and Beargrass by the Aborigines in the American Southwest. *Ethnobiological Studies in the American Southwest*. The University of New Mexico Bulletin, Biological Series, University of New Mexico Press, Albuquerque, 5.

Bettinger, R.L., Barton, L. & Morgan, C. (2010). The origins of food production in North China: a different kind of agricultural revolution. *Evol. Anthropol*. 19. 9-21.

Bitencourt, A.L.V. & Krauspenhar, P.M. (2006). Possible prehistoric anthropogenic effect on *Araucaria angustifolia* (Bert.) O. Kuntze expansion during the late Holocene. *Rev. Bras. Paleontolog.*, 9, 109-116.

Bocherens, H. (2018). The rise of the anthroposphere since 50,000 years: an ecological replacement of megaherbivores by humans in terrestrial ecosystems? *Front Ecol. Evol*. 6, 1-8.

Bohrer, V.L. (1987). Methods of recognizing cultural activity from pollen in archaeological sites. *The Kiva*. 46, 135-142.

Bohrer. V.L. (1991). Recently recognized cultivated and encouraged plants among the Hohokam. *The Kiva*. 56, 227-235.

Bovin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denham, T. et. al. (2016). Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. *PNAS*. 113, 6388-6396.

Breheny, P. & Burchett, W. (2017). Visualization of regression models using visreg. *The R Journal*. 9, 56-71.

Bretting, P.K. (1986). Changes in fruit shape in *Proboscidea parvifora* ssp. *parviflora* (Martyniaceae) with domestication. *Econ. Bot*. 40, 170-176.

Briggs, J.M., Spielmann, K.A., Schaafsma, H., Kintigh, K.W., Kruse, M., Morehose, K. et. al. (2006). Why ecology needs archaeologists and archaeology needs ecologists. *Front Ecol. Environ*. 4, 180-188.

Brockington, D. & Igoe, J. (2006). Eviction for conservation: a global overview. *Conservat. Soc.* 4, 424-470.

Brosius, J.P. (1991). Foraging in tropical rain forests: the case of the Penan of Sarawak, East Malaysia (Borneo). *Hum. Ecol*. 19, 123-150.

Bush, M.B., McMichael, C.H., Piperno, D.R., Silman, M.R., Barlow, J., Peres, C.A. et. al. (2015). Anthropogenic influence on Amazonian forests in pre-history: an ecological perspective. *J. Biogeogr*. 42. 2277-2288.

Castetter, E.F. & Underhill, R.M. (1935). The Ethnobiology of the Papago Indians. *Ethnobiological Studies in the American Southwest*. University of New Mexico. Bulletin, Biological Series, 4, 1-84.

Castetter E.F. & Bell W. H. (1951). *Yuman Indian Agriculture*. University of New Mexico Press. Albuquerque, New Mexico.

Chamberlain, S. (2017). rgif: Interface to the Global 'Biodiversity' Information Facility API. R package version 0.9.8. https://cran.r-project.org/web/packages/rgbif/index.html

CIESIN. (2017). Center for International Earth Science Information Network. Columbia University. NASA Socioeconomic Data and Applications Center (SEDAC). Palisades, N.Y. http://doi.org/10.7927/H40Z716C.

Clement, C.R., Denevan, W.M., Heckenberger, M.J., Junqueira, A.B., Neves, E.G., Teixeira, W.G. et. al. (2015). The domestication of Amazonia before European conquest. *Proc. R. Soc. B*. 282, 1-9.

Clement C.R. & Junqueira A.B. (2010). Between a pristine myth and an impoverished future. *Biotropica*. 42. 534-536.

Coblentz, D.D. & Riitters, K.H. (2004). Special paper: topographic controls on the regional-scale biodiversity of the south-western USA. *J. Biogeogr*. 31(7). 1125-1138.

Crosby, Jr. (1972). The Columbian Exchange: The biological and cultural consequences of 1492. Praeger Publishers. Westport, CT. 1-268

Crosswhite, F.S. (1981). Desert plants, habitat, and agriculture in relation to the major pattern of cultural differentiation in the O'odham people of the Sonoran Desert. *Desert Plants*. 3, 47-76.

Crown, P.L. (1987). Classic period Hohokam settlement and land use in the Casa Grande Ruins area, Arizona. *J. Field Archaeol*. 14(2). 147-162.

Currie, D.J., Francis, A.P. & Kerr, J.T. (1999). Some general propositions about the study of spatial patterns of species richness. *Ecoscience*. 6(3). 392-399.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J. et. al. (2004). Predictors and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett*. 7. 1121-1134.

Danielson, J.J. & Gesch, D.B. (2011). Global multi-resolution terrain elevation data 2010 (GMTED2010). U.S. Geological Survey Open-File Report 2011-1073, 1-26.

Darling, J.A. & Lewis, B.V. (2007). Ancient trails of the arid Southwest. *Archaeology Southwest Magazine*. Archaeology Southwest. Tucson, Arizona.

De Bont, R. (2015). “Primitives” and protected areas: international conservation and the “naturalization” of indigenous people, ca. 1910-1975. *JHI*. 2, 215-236.

del Barco., M. (1981). Ethnology and linguistics of Baja California. F. Tiscareno, trans. Dawson’s Book Shop, Los Angeles, Calif.

Denevan, W.M. (1992). The pristine myth: the landscape of the Americans in 1492. *Ann. Assoc. Am. Geogr*. 82. 369-385.

Doelle, W. H. (1980). Past adaptive patterns in western Papagueria: an archaeological study of nonriverine resource use. University of Arizona Press. University of Arizona. Tucson, AZ.

Doelle, W.H. (1995). Tonto Basin Demography in a Regional Perspective. *In* The Roosevelt Community Development Study: New Perspectives on Tonto Basin Prehistory. Mark. D. Elson, Mariam, T. Stark & David A. Gregory eds. 201-226. Anthropological Research Papers No 15. Center for Desert Archaeology. Tucson, Arizona.

Doughty, C.E. Wolf, A., Morueta-Holme, N., Jorgensen, P.M., Sandel, B., Violle. et. al. (2015). Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography*. 38, 001-010.

Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Jakomulska, A., et. al. (2002). A balanced view of scale in spatial statistical analysis. *Ecography*. 25, 626-640.

eFloras. (2008). Published on the Internet http://www.efloras.org (accessed July 2018). Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA.

Elith, J, Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A. et. al. (2006). Novel methods improve prediction of species’ distributions from occurrence data. *Ecography*. 29. 129-151.

Elith, J. & Leathwick, J.R. (2009). Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40, 677-697.

Ellis, E.C., Kaplan, J.O., Fuller, D. Q., Vavrus, S., Goldwijk, K.K. & Verburg, P.H. (2013). Used planet: a global history. *PNAS*. 110(20). 7978-7985.

Felger, R.S. & Moser, M.B. (1976). Seri Indian food plants: desert subsistence without agriculture. *Ecol. Food Nutr*. 5, 13-27.

Fick, S.E. & Hijmans, R.J. (2017). Worldclim 2: New 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol*. 37, 4302-4315.

Fish, S.K. (1993). Agriculture and society in arid lands: a Hohokam case study. Dessertation. The University of Arizona Graduate College.

Fish, S.K. (1984). Agriculture and subsistence implications of the Salt-Gila Aqueduct pollen analysis. *Hohokam Archaeology along the Salt Gila Aqueduct Central Arizona Project: volume VII: Environment and subsistence.* L.S. Teague & P.L. Crown eds. Archaeological Series, Cultural Resource Management Section, Arizona State Museum, The University of Arizona, Tucson. 150. 111-138.

Fish, S.K. (2000). Hohokam impacts on Sonoran Desert environment. *Imperfect Balance: Landscape Transformations in the Precolumbian Americas.* Ed. David L. Lentz. Columbia University Press. N.Y.

Fish, S.K. & Fish, P.R. (1992). Prehistoric landscapes of the Sonoran Desert Hohokam. *Popul. Environ.*. 13(4). 269-283.

Fish, S.K. & Fish, P.R. (1994). Prehistoric desert farmers of the Southwest. *Annu. Rev. Anthropol.* 23. 83-108.

Fish, S.K. & Fish, P.R. (2007). The Hohokam millennium. 1-12. Fish, S.K. & Fish, P.R. (Eds.). *The Hohokam Millenium*. School for Advanced Research Press. Santa Fe, New Mexico. 1-151.

Ford, A. & Nigh, R. (2015). *The Maya forest garden: eight millennia of sustainable cultivation of the tropical woodlands*. Routledge. New York, NY. 1-187.

Foster, D., Swanson, F., Aber, J., Burke, I., Brokaw, N., Tilman, D. et. al. (2003). The importance of land-use legacies to ecology and conservation. *Bioscience*. 53(1). 77-88.

Fraaije, R.G.A., ter Braak, C.J.F., Verduyn, B, Verhoeven, J.T.A. & Soons, M.B. (2015). Dispersal versus environmental filtering in a dynamic system: drivers of vegetation patterns and diversity along stream riparian gradients. *J. Ecol.* 103, 1634-1646.

Fritz, G.J., Adams, K.R., Rice, G. E. & Czarzasty, J.L. (2009). Evidence for domesticated amaranth from a sedentary period Hohokam house floor at Las Canopas. *KIVA.* 74, 393-419.

Fuller, D.Q., Willcox, G., & Allaby, R.G. (2011). Early agricultural pathways: moving outside the 'core area' hypothesis in Southwest Asia. *J. Exp. Bot*. 63(2). 617-633.

Gasser, R.E. (1981). Hohokam use of desert food plants. *Desert Plants*. 3, 216-234.

Gasser, R.E. & Kwaitkowski, S.M. (1991). Regional signatures of Hohokam plant use. *KIVA*. 56, 207-226.

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature*. 405. 220-227.

Garnett, S.T., Burgess, N.D., Fa, J.E., Fernandez-Llamazares, A., Molnar, Z., Robinson, C.J. et. al. (2018). A spatial overview of the global importance of Indigenous lands for conservation. *Nat. Sustain*. 1. 369-374.

Gaoue, O.G., Coe, M.A., Bond, M., Hart, G., Seyler, B.C. & McMillen, H. (2017). Theories and major hypotheses in ethnobotany. *Econ. Bot.* 20(10) 1-19.

Gavin, M.C., McCarter, J., Mead, A., Berkes, F., Stepp, J.R., Peterson, D. et. al. (2015). Defining biocultural approaches to conservation. *TRENDS Ecol. Evol.* 30(3). 140-145.

Ghalambor, C. K., Huey, R.B., Martin, P.R, Tewksbury, J.J. & Wang. G. (2006). Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.* 46(1). 5-17.

Gill, J.L. (2014). Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytol*. 201, 1163-1169.

Goncalves, P.H.S., Albuquerque, U.P. & de Medeiros, P.M. (2016). The most commonly available woody plant species are the most useful for human populations: a meta-analysis. *Ecol. Appl*. 26(7). 2238-2253.

Greenhouse, R., Gasser, R.E. & Gish, J.W. (1981). Cholla bud roasting pits: an ethnoarchaeological example. *Kiva*. 46(4). 227-242.

Gruca, M., Camara-Leret, R., Macia, M.J. & Balslev, H. (2014). New categories for traditional medicine in the Economic Botany Data Collection Standard. *Journal of Ethnopharmacology*. 155. 1388-1392.

Guisan, A. & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecol. Lett*. 8. 993-1009.

Guisan, A. & Zimmerman, N.K. (2000). Predictive habitat distribution models in ecology. *Ecol.Model.*. 135. 147-186.

Guimaraes Jr., P.R., Galetti, M. & Jordono, P. (2008). Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. *PLoS ONE*. 3, e1745.

Guiterman, C.H., Swetnam, T.W. & Dean, J.S. (2015). Eleventh-century shift in timber procurement areas for the great houses of Chaco Canyon. *PNAS*. 113(5). 1186-1190.

Guo, Q., Taper, M., Schoenberger, M., Brandle, J. (2005). Spatial-temporal population dynamics across species range: from centre to margin. *OIKOS*. 108, 47-57.

Hall, S.J., Trujillo, J., Nakase, D., Strawhacker, C., Kruse-Peeples, M., Schaafsma, H. et. al. (2013). Legacies of prehistoric agricultural practices within plant and soil properties across an arid ecosystem. *Ecosystems*. 16, 1273-1293.

Halper, E.B., Scott, C.A. & Yool, S.R. (2012). Correlating vegetation, water use, and surface temperature in a semiarid city: a multiscale analysis of the impacts of irrigation by single family residences. *Geogr. Anal*. 44. 235-257.

Hansen-Speer, K. (2013). Chapter 5: analysis of plant remains from the Marana mound site. *Power and Economy in Early Classic Period Hohokam Society: An Archaeological Perspective from the Marana Mound Site*. James M. Bayman, Paul R. Fish & Suzanne K. Fish eds. Arizona State Museum Archaeological Series. Arizona State Museum. The University of Arizona. Tucson, Arizona.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J., Kaufman, D.M. et. al. (2003). Energy, water and broad-scale geographic patterns of species richness. *Ecology*. 84(12). 3105-3117.

Hawkins, B.A. (2001). Ecology's oldest pattern? *TRENDS Ecol Evol*. 16(8). 470.

Hijmans, R.J, Phillips. S., Leathwick, J. & Elish, J. (2007). dismo: species distribution modeling. R package version 1.1-4.

Hill, B.J. Clark, J.J. Doelle, W. H. & Lyons, P.D. (2004). Prehistoric demography in the Southwest: migration, coalescence, and Hohokam population decline. *Am. Ant*. 69(4). 689-716.

Hill, B.J. Wilcox, D., Doelle, W. & Robinson, W. (2012.) Coalescent Communities Database Version 2.0. Archaeology Southwest. Tucson, Arizona.

Hill, J.B, Peeples, M.A., Huntley, D.L. & Carmack, H. J. (2015). Spatializing Social Network Analysis in the Late Precontact U.S. Southwest. *Adv. Archaeol. Pract*. 3(1). 63-77.

Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *Am. Nat.* 163(2). 192-211.

Hodgson, W.C. (2001). *Food Plants of the Sonoran Desert*. The University Arizona Press. Tucson, Arizona. 1-299.

Hodgson, W.C. & Salywon, A.M. (2013). Two new *Agave* species (Agavaceae) from central Arizona and their putative pre-Columbian domesticated origins. *Brittonia*. 65, 5-15.

Hodgson, W.C., A.M., Salywon, Doelle, W.H. (2018). Hohokam lost crop found: a new *Agave* (Agaveceae) species only known from large-scale pre-Columbian agricultural fields in southern Arizona. *Syst. Bot*. 43, 734-740.

Holt, R.D., Keitt, T.H, Lewis, M.A., Maurer, B.A., Taper, M.L. (2005). Theoretical models of species' borders: single species approaches. *OIKOS*. 108, 18-27.

Hope, D., Gries, C., Zhu, W., Fagan, W.F., Redman, C.L., Grimm, N.B. et. al. (2003). Socioeconomics drive urban plant diversity. *PNAS*. 100(15). 8788-8792.

Hope, D. Gries, C, Casagrande, D., & Redman, C.L. (2006). Drivers of spatial variation in plant diversity across the Central Arizona-Phoenix ecosystem. *Soc. Nat. Resour*. 19. 101-116.

Howard, J.B. n.d. Hohokam legacy: desert canals. Pueblo Grande Museum Profiles N. 12. Accessible at: http://www.waterhistory.org/histories/hohokam2/

Jablonski, D., Roy, K. & Valentine, J.W. (2006). Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*. 314(5796). 102-106.

Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *Am. Nat*. 101(919). 233-249.

Janzen, D.H. (1986). Chihuahuan desert nopaleras: defaunated big mammal vegetation. *Annu. Rev. Ecol. Evol. Syst*. 17. 595-636.

Jones, K. & Wrigley, N. (1995). Generalized additive models, graphical diagnostics, and logistic regression. *Geogr. Anal.*. 21(1). 1-18.

Junqueira. A.B., Levis. C., Bongers, F., Pena-Claros, M., Clement, C.R., Costa, F. et. al. (2017). Response to comment on "persistent effects of pre-Columbian plant domestication on Amazonian forest composition'. *Science*. 358, 1-2.

Kerkhoff, A.J., Moriarty, P.E. & Weiser, M.D. (2014). The latitudinal species richness gradient in new world woody angiosperms is consistent with the tropical conservatism hypothesis. *PNAS*. 11(22). 8125-8130.

Kodis, M., Galante, P., Sterling, E.J. & Blair, M.E. (2018). Ecological niche modeling for a cultivated plant species: a case study on taro (*Colocasia esculenta*) in Hawaii. *Ecol. Appl*. 28, 967-977.

Kohler, F. & Brondizio, E.S. (2016). Considering the needs of indigenous and local populations in conservation programs. *Conserv. Biol*. 31(2). 245-251.

Lamanna, C., Blonder, B., Violle, C., Kraft, N.J.B., Sandel, B., Simova, I. et. al. (2014). Functional trait space and the latitudinal diversity gradient. *PNAS*. 1-6.

Leitch A.R. & Leitch, I.J. (2008). Genome plasticity and the diversity of polyploid plants. *Science*. 320, 481-483.

Levis, C., Costa, F.R.C, Bongers, F., Pena-Claros, M., Clement, C.R., Junqueira, A.B. et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*. 355, 925-931.

Levis, C., Flores, B.M., Moreira, P.A., Luize, B.G., Alves, R.P, Franco-Moraes, J. et al. (2018). How people domesticated Amazonian forests. *Front. Ecol. Evol*. 5, 1-21.

Loendorf, C.R., Fertelmes, C.M., Lewis, B.V. (2013). Hohokam to Akimel O'odham: obsidian acquisition at the historic period Sacate Site (GR-909), Gila River Indian Community, Arizona. *Am. Antiq*. 78, 266-284.

Loendorf, C. & Lewis, B.V. (2017). Ancestral O'odham: Akimel O'odham cultural traditions and the archaeological record. *Am. Antiq*. 82, 123-139.

MacDougall, A. (2003). Guest editorial: did Native Americans influence the northward migration of plants during the Holocene? *J. Biogeogr*. 30, 633-647.

Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue II, J., Duran, S.M. et. al. (2017). The BIEN R package. A tool to access the Botanical Information and Ecological Network (BIEN) database. *Methods Ecol. Evol*. 91, 373-379.

Majure, L.C. & Ervin, G.N. (2007). The opuntias of Mississippi. *Haseltonia*. 14, 111-126.

Malhi, Y. (2017). The concept of the Anthropocene. *Annu. Rev. Environ. Resour*. 42. 77-104.

McGill, B.J. (2010.) Matters of scale. *Science*. 328. 575-576.

McGuire, R.H. & Howard, A.V. (1987). The structure and organization of Hohokam shell exchange. *Kiva*. 52(2). 113-146.

McKey, D., Rostain, S., Iriarte, J., Bruno, G., Birk, J.J., Holst, I. et. al. (2010). Pre-Columbian agricultural landscapes, ecosystem engineers, and self-organized patchiness in Amazonia. *PNAS*. 107, 7823-7828.

McMichael, C.H., Feeley, K.J., Dick, C.W., Piperno, D.R. & Bush, M.B. (2017). Comment on 'Persistent effects of pre-Columbian plant domestication on Amazonian forest composition'. *Science*. 358, 1-2.

Merriam, C.H. (1890). Results of a biological survey of the San Francisco Mountain region and the desert of the Little Colorado, Arizona. *North Am. Fauna*. 3. 1-136.

Merriam, C.H. (1894). Laws of temperature control of the geographic distribution of terrestrial animals and plants. *Nat. Geo*. 6. 229-238.

Merrill, W.L., Hard, R.J., Mabry, J.B., Fritz, G.J., Adams, K.R., Roney, J.R. et. al. (2009). The diffusion of maize to the southwestern United States and its impact. *PNAS*. 50, 21019-21026.

Meyer, R.S., Duvual, A.E. & Jensen, H.R. (2012). Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops. *New Phytol.* 196, 29-48.

Milla, R., Morente-Lopez, J., Alonso-Rodrigo, Miguel, Martin-Robles, N & Chapin III, F.S. (2014). Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proc. R. Soc. B*. 281, 1-9.

Mills, B.J., Clark, J.J., Peeples, M.A., Haas, Jr., W.R., Roberts Jr., J.M., Hill, B., et. al. (2013). Transformation of social networks in the late pre-Hispanic US Southwest. *PNAS*. 110(15). 5785-5790.

Mills, B.J., Peeples, M.A., Haas, Jr., W. R., Borck, L., Clark, J.J. Roberts, J.M. (2015). Multiscalar perspectives on social networks in the late prehispanic Southwest. *Am. Ant.*. 80(1). 3-24.

Minkov, A. S., Sabath, N. & Mayrose, I. (2016). Whole-genome duplication as a key factor in crop domestication. *Nat. Plants*. 2, 1-4.

Moerman, D. (2003). Native American ethnobotany. A database of plants used as drugs, foods, dyes, fibers and more, by natives of North America. http://naeb.brit.org/about

Nabhan, G.P. (2016). *Gathering the Desert.* University of Arizona Press. Tucson, Arizona. 1-221.

Naimi, B. & Araujo, M.B. (2016). sdm: a reproducible and extensible R platform for species distribution modeling. *Ecography*. 39, 368-375.

Nesheim, I., Halvorsen, R. & Nordal, I. (2010). Plant composition in the Maya Biosphere Reserve: natural and anthropogenic influences. *Plant Ecol.* 208, 93-122.

Normand, S. Hoye, T.T., Forbes, B.C., Bowden, J.J., Davies, A.L., Odgaard, B.V. et. al. (2017). Legacies of historical human activities in arctic woody plant dynamics. *Annu. Rev. Environ. Resour*. 42. 541-567.

Omernik, J.M. (2004). Perspectives on nature and definition of ecological regions. *Environ. Manage*. 34, Suppl. 1, S27-S38.

Parker, K.C., Trapnell, D.W., Hamrick, J.L. & Hodgson, W.C. (2014). Genetic and morphological contrasts between wild and anthropogenic populations of *Agave parryi* var. *huachucensis* in south-eastern Arizona. *Ann. Bot.* 113, 939-952.

Parker, K.C., Hamrick, J.L., Hodgson, W.C., Trapnell, D.W., Parker, A.J. & Kuzoff, R. K. (2007). Genetic consequences of Pre-Columbian cultivation for *Agave murpheyi* and *A. delamateri* (Agavaceae). *Am. J. Bot*. 94, 1479-1490.

Parker, K.C. (1991). Topography, substrate, and vegetation patterns in the northern sonoran desert. *J. Biogeogr*. 18(2). 151-163.

Pausas, J. G. & Bond, W.J. (2018). Humboldt and the reinvention of nature. *J. Ecol.*. 1-7.

Peeples, M. (2006). Hohokam Population Database. (tDARK id: 1582); doi: 10.6067/XCV8FX780Z.

Peterson, A. T. (2011). Ecological niche conservatism: a time-structured review of evidence. *J. Biogeogr*. 38, 817-827.

Piperno, D.R., McMichael, C., & Bush, M.B. (2015). Amazonia and the Anthropocene: what was the spatial extent and intensity of human landscape modification in the Amazon Basin at the end of prehistory? *The Holocene*. 25, 1588-1597.

Rea, A.M. (1997). *At the desert's green edge: an ethnobotany of the Gila River Pima*. The University Press. Tucson, Arizona. 1-413.

Rice, A., Glick, L., Abadi, S., Einhorn, M., Kopelman, N.M, Salman-Minkov, A. et. al. (2014). The chromosome counts database (CCDB)- a community resource of plant chromosome numbers. *New Phytol*. 206, 19-26.

Ross, N.J. (2011). Modern tree species composition reflects ancient Maya “forest gardens” in northwest Belize. *Ecol. Appl.*. 21(1). 75-84.

Sedrez dos Reis, M, Ladio, A. & Peroni, N. (2014). Landscapes with Araucaria in South America: evidence for a cultural dimension. *Ecol. Soc*. 19, 43.

SEINet Portal Network. (2018). http://:swbiodiversity.org/seinet/index.php.

Shepard Jr., G.H. & Ramirez, H. (2011). “Made in Brazil”: human dispersal of the Brazil Nut (*Bertholletia excelsa*, Lecythidaceae) in ancient Amazonia. *Econ. Bot*. 65, 44-65.

Soberon, J. & Peterson, A.T. (2005). Interpretations of models of fundamental ecological niches and species’ distributional areas. *Biodiv. Inf.* 2. 1-10.

Soberon, J. & Nakamura, M. (2009). Niches and distributional areas: concepts, methods, and assumptions. *PNAS*. 106. 19644-19650.

Stahl, U., Reu, B., Wirth, C. (2014). Predicting species’ range limits from functional traits for the tree flora of North America. *PNAS*. 38, 13739-13744

Stevens, G.C. (1989). The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat*. 133(2). 240-256.

Stuart, G., Gries, C. & Hope, D. (2006). The relationship between pollen and extant vegetation across an arid urban ecosystem and surrounding desert in Southwest USA. *J. Biogeogr*. 33. 573-591.

Suarez-Estaban, A., Fahrig, L., Delibes, M. & Fedriani, J. M. (2016). Can anthropogenic linear gaps increase plant abundance and diversity? *Landscape Ecol*. 31. 721-729.

Svenning, J.C. & Skov, F. (2004). Limited filling of the potential range in European tree species. *Ecol. Lett.* 7, 565-573.

Svenning, J.C., Normand, S., Scov, F. (2008). Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. *Ecography*. 31, 316-326.

Thiel, J.H. (2010). Historic-era farming. *Archaeology Southwest Magazine*. Archaeology Southwest. Tucson, Arizona.

Thuiller, W., Miguel B., A. & Sandra, L. (2003). Generalized models vs. classification tree analysis: predicting spatial distributions of plant species at different scales. *J. Veg. Sci*. 14, 669-680.

Tomiolo, S. & Ward, D. (2018). Species migrations and range shifts: a synthesis of causes and consequences. *Perspect. Plant Ecol, Syst*. 33. 62-77.

USDA, NRCS. (2018). The PLANTS Database (http://plants.usda.gov, July 2018). National Plant Data Team, Greensboro, NC 27401-4901 USA.

USEPA: United States Environmental Protection Agency. (2016). *Ecoregions of North America*. Available at: https://www.epa.gov/eco-research/ecoregions-north-america. Last accessed 03 August 2018.

Violle, C., Reich, P.B., Pacala, S.W., Enquist. B.J., Kattge, J. (2014). The emergence and promise of functional biogeography. *PNAS*. 38, 13690-13696.

U.S. Geological Survey. (2013). USGS Small-scale Dataset - 100-Meter Resolution Grayscale Shaded Relief of the Conterminous United States 201304 GeoTIFF: U.S. Geological Survey.

Walker, J.S., Grimm, N.B., Briggs, J.M., Gries, C. & Dugan, L. (2009). Effects of urbanization on plant species diversity in central Arizona. *Front. Ecol. Environ.* 7(9). 465-470.

Warren II, R.J. (2016). Ghosts of cultivation past- Native American dispersal legacy persists in tree distribution. *PLoS ONE*. 11, 1-16.

Whitehead, S.R., Turcotte, M.M., Poveda, K. (2016). Domestication impacts on pant-herbivore interactions: a meta-analysis. *Phil. Trans. R. Soc. B.* 272, 1-9.

Wiens, J.J. & Donoghue, M.J. (2004). Historical biogeography, ecology and species richness. *Trends Ecol. Evol*. 19(12). 639-644.

Wiens, J.J. & Graham, C.H. (2005). Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Syst*. 26, 519-529.

Wiken, E., Nava, F.J. & Griffith, G. (2011). North American terrestrial ecoregions-level III. Commission for Environmental Cooperation, Montreal, Canada. 1-145.

Wilcox, D.R., Gregory, D.A. & Hill, B. (2007). Zuni in the Puebloan and Southwestern Worlds. *In* Zuni Origins: Toward a New Synthesis of Southwestern Archaeology. David A. Gregory and David R. Wilcox, eds. 165-209. University of Arizona Press. Tucson, Arizona.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.*. 34. 273-309.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenior, J., Damgaard, C.F. et. al. (2013). The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modeling. *Biol. Rev. Camb. Philos. Soc.* 88, 15-30.

Wood, S.N. (2017). Generalized additive models.: an introduction with R (wnd edition). Chapman and Hall/CRC.

Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. Royal Stat. Soc. (B).* 73(1). 3-36.

Yang, X, Barton, H.J, Wan, Z., Li, Q., Ma, Z., Li, M. et. al. (2013). Sago-type palms were an important plant food prior to rice in southern subtropical China. *PLoS ONE*. 8, 1-8.

Van Zonneveld, M. Larranaga, N., Blonder, B., Coradin, L., Hormaza, J.I. & Hunter. D. (2018). Human diets drive range expansion of megafauna-dispersed fruit species. *PNAS*. 10, 1-6.

Varien, M.D. (1999). *Sedentism and Mobility in a Social Landscape: Mesa Verde and Beyond.* University of Arizona Press. Tucson, Arizona.

Zizka, A. (2018). CoordinateCleaner: automated cleaning of occurrence records from biological collections. R. package version 1.0-7. http://CRAN-R-project.org/package=CoordinateCleaner

APPENDIX A

LIST OF FOOD PLANTS AND CONGENERS EXCEL SPREADSHEET

APPENDIX B

PHYLOGENETIC LITERATURE REVIEW

Alexander, P.J., Windham, M.D., Govindarajulu, R., Al-Shehbaz, I.A. & Bailey, C.D. (2010). Molecular phylogenetics and taxonomy of the genus *Thysanocarpus* (Brassicaceae). *Syst. Bot*. 35, 559-577.

Andreason, K. (2012). Phylogeny, hybridization, and evolution of habit and breeding system in *Sidalcea* and *Eremalche* (Malvaceae). *Int. J. Plant. Sci*. 173, 532-548.

Andres-Hernandez, A.R., Terrazaz, T., Salazar, G. & Ochoterena, H. (2014). Phylogenetic analysis based on structural and combined analyses of *Rhus* s.s. (Anacardiaceae). *Bot. J. Linn. Soc*. 176, 452-468.

Aradhya, M.K., Potter, D., Gao, F. & Simon, C.J. (2007). Molecular phylogeny of *Juglans* (Juglandaceae): a biogeographic perspective. *Tree Genet. Genomes*. 3, 363-378.

Archibald, J.K., Kephart, S.R., Theiss, K.e., Petrosky, A.L. & Culley, T.M. (2015). Multilocus phylogenetic inference in subfamily Chlorogaloideae and related genera of Agavaceae-informing questions in taxonomy and multiple ranks. *Mol. Phylogenet. Evol*. 84, 266-283.

Arias, S., Terrazas, T. & Cameron, K. (2003). Phylogenetic analysis of *Pachycereus* (Cactaceae, Pachycereeae) based on chloroplast and nuclear DNA sequences. *Syst. Bot*. 28, 547-557.

Ashworth, W.E.T.M. (2000). Phylogenetic relationships in Phoradendreae (Viscaceae) inferred from three regions of the nuclear ribosomal Cistron. I. Major lineages and paraphyly of *Phoradendron*. *Syst. Bot*. 25, 349-370.

Baldwin, B.G. (2005). Origin of the serpentine-endemic herb *Layia discoidea* from the widespread *L. glandulosa* (Compositae). *Evolution*. 59, 2473-2479.

Barcenas, R.T. (2015). A molecular phylogenetic approach to the systematics of Cylindropuntieae (Opuntioideae, Cactaceae). *Cladistics*. 0, 1-9.

Biral, L., Simmons, M.P., Smidt, E.C., Tembrock, L.R., Bolson, M., Archer, R.H. et. al. (2017). Systematics of New World *Maytenus* (Celastraceae) and a new delimitation of the genus. *Syst. Bot*. 42, 680-693.

Bogler, D.J & Simpson, B.B. (1996). Phylogeny of Agavaceae based on ITS rDNA sequence variation. *Am. J. Bot*. 83, 1225-1235.

Bringel, Jr., J.B., Pastore, J.F.B. & Cavalcanti, T.B. (2017). An unusual new species of *Bidens* (Asteraceae, Coreopsideae) with its phylogenetic position and taxonomic notes. *Syst. Bot.* 42, 301-312.

Burns, J.H., Faden, R.B. & Steppan, S.J. (2011). Phylogenetic studies in the Commelinaceae subfamily Commelinoideae inferred from nuclear ribosomal and chloroplast DNA sequences. *Syst. Bot*. 36, 268-276.

Butterworth, C.A. & Wallace, R.S. (2004). Phylogenetic studies of *Mammillaria* (Cactaceae): insights from chloroplast sequence variation and hypothesis testing using the parametric bootstrap. *Am. J. Bot*. 91, 1086-1098.

Cappa, J.J., Yetter, C., Fakra, S., Cappa, P.J., Detar, R., Landes, C. et. al. (2015). Evolution of selenium hyperaccumulation in *Stanleya* (Brassicaceae) as inferred from phylogeny, physiology and X-ray microprobe analysis. *New Phytol*. 205, 583-595.

Carvalho-Sobrinho, J.G., Alverson, W.S., Alcantara, S., Queiroz, L.P., Mota, A.C. & Baum, D.A. (2016). Revisiting the phylogeny of Bombacoideae (Malvaceae): novel relationships, morphologically cohesive clades, and a new tribal classification based on multilocus phylogenetic analyses. *Mol. Phylogenet. Evol*. 101, 56-74.

Catalano, S.A., Vilardi, J.C, Tosto, D. & Saidman, B. O. (2008). Molecular phylogeny and diversification history of *Prosopis*. *Biol. J. Linn. Soc*. 93, 621-640.

Chan, R., Baldwin, B.G. & Ornduff, R. (2001). Goldfields revisited: a molecular phylogenetic perspective on the evolution of *Lasthenia* (Compositae: Heliantheae *Sensu Lato*). *Int. J. Plant. Sci.* 162, 1347-1360.

Chin, S., Shaw, J., Haberle, R., Wen, J. & Potter, D. (2013). Diversification of almonds, peaches, plums and cherries-molecular systematics and biogeographic history of *Prunus* (Rosaceae). *Mol. Phylogenet. Evol*. 76, 34-48.

Cota-Sanchez, J.H. (1997). A phylogenetic study of *Ferocactus* Britton and Rose (Cactaceae: Cactoideae). Doctoral dissertation. Iowa State University. 1-176.

Davis, C.C. & Anderson, W.R. (2010). A complete generic phylogeny of Malpighiaceae inferred from nucleotide sequence data and morphology. *Am. J. Bot.* 97, 2031-2048.

De-Nova, J.A., Medina, R., Montero, J.C., Weeks, A., Rosell, J.A., Olson, M.E. et. al. (2012). Insights into the historical construction of species-rich Mesoamerican seasonally dry tropical forests: the diversification of *Bursera* (Burseraceae, Sapindales). *New Phytol*. 193, 276-287.

Delgado-Salinas, A., Bibler, R. & Lavin, M. (2006). Phylogeny of the genus *Phaseolus* (Leguminosae): a recent diversification in an ancient landscape. *Syst. Bot*. 31, 779-791.

Douglas, N.A. & Manos, P.S. (2007). Molecular phylogeny of Nyctaginaceae: taxonomy, biogeography, and characters associated with a radiation of xerophytic genera in North America. *Am. J. Bot*. 94, 856-872.

Feodorova, T.A., Voznesenskaya, E.V., Edwards, G.E. & Roalson, E. H. (2010). Biogeographic patterns of diversification and the origins of C4 in *Cleome* (Cleomaceae). *Syst. Bot*. 35, 811-826.

Fishbein, M., Chuba, D., Ellison, C., Mason-Gamer, R.J. & Lynch, S.P. (2011). Phylogenetic relationships of *Asclepias* (Apocynaceae) inferred from non-coding Chloroplast DNA sequences. *Syst. Bot*. 36, 1008-1023.

Fuentes-Bazan, S., Uotila, P. & Borsch, T. (2012). A novel phylogeny-based generic classification for *Chenopodium* senu lato, and a tribal rearrangement of Chenopodioideae (Chenopodiaceae). *Willdenowia*. 42, 5-24.

Gagnon, E., Lewis, G.P., Sotuyo, J.S., Hughes, C.E. & Bruneau, A. (2013). A molecular phylogeny of *Caesalpinia* sensu lato: increased sampling reveals new insights and more genea than expected. *S. Afr. J. Bot*. 89, 111-127.

Garcia, C.C., Barfuss, M.H.J., Sehr, E.M., Barboza, G.E., Samuel, R., Moscone, E.A. et. al. (2016). Phylogenetic relationships, diversification, and expansion of chili peppers (*Capsicum*, Solanaceae). *Ann. Bot*. 118, 35-51.

Garcia, S., McArthur, E.D., Pellicer, J., Sanderson, S.C., Valles, J. & Garnatje, T. (2011). A molecular phylogenetic approach to western North America endemic *Artemisia* and allies (Asteraceae) untangling the sagebrushes. *Am. J. Bot*. 98, 638-653.

Giussani, L.M., Cota-Sanchez, J.H., Zuloaga, F.O. & Kellog, E.A. (2001). Panicoideae (Poaceae) shows multiple origins of C4 photosynthesis. *Am. J. Bot.* 88, 1993-2012.

Goodson, B.E., Rehman, S.K. & Jansen, R.K. (2011). Molecular systematics and biogeography of *Descurainia* (Brassicaceae) based on nuclear ITS and non-coding chloroplast DNA. *Syst. Bot*. 36, 957-980.

Gustafsson, C. & Persson, C. (2002). Phylogenetic relationships among species of the neotropical genus *Randia* (Rubiaceae, Gardenieae) inferred from molecular and morphological data. *Taxon*. 51, 661-674.

Gutierrez, R. (2011). A phylogenetic study of the plant family Martyniaceae (Order Lamiales). PhD Disseration, Arizona State University. ProQuest LLC.

Hansen, A.K., Gilbert, L.E., Simpson, B.B., Downie, S.R., Cervie, A.C. & Jansen, R.K. (2006). Phylogenetic relationships and chromosome number evolution in *Passiflora*. *Syst. Bot*. 31, 138-150.

Hansen, D.R. (2012). The molecular phylogeny of *Pectis* L. (Tageteae, Asteraceae), with implications for taxonomy, biogeography, and the evolution of C4 photosynthesis. Doctoral Dissertation. The University of Texas at Austin. 1-153.

Hasenstab-Lehman, K.E. & Simpson, M.G. (2012). Cat's eyes and popcorn flowers: phylogenetic systematics of the genus *Cryptantha* s.l. (Boraginaceae). *Syst. Bot.* 37, 738-757.

Hauenschild, F., Matuszak, S., Muellner-Riehl, A.N. & Favre, A. (2016). Phylogenetic relationships within the cosmopolitan buckthorn family (Rhamnaceae) support the resurrection of *Sarcomphalus* and the description of *Pseudoziziphus* gen. nov. *Taxon*. 65, 47-64.

Hawkins, J.A., Boutaoui, N., Cheung, K.Y., van Klinkan, R.D. & Hughes, C.E. (2007). Intercontinental dispersal prior to human translocation revealed in a cryptogenic invasive tree. *New Phytol*. 175, 575-587.

Hipp, A.L., Manos, P.S., Gonzales-Rodriguez, A., Hahn, M., Kaproth, M., McVay, J.D. et. al. (2017). Sympatric parallel diversification of major oak clades in the Americas and the origins of Mexican species diversity. *New Phytol.* 217, 439-452.

Hufford, L., McMahon, M.M, Sherwood, A.M, Reeves, G. & Chase, M.W. (2003). The major clades of Loasaceae: phylogenetic analysis using the plastid *mat*K and *trn*L-*trn*F regions. *Am. J. Bot*. 90, 1215-1228.

Ibanez, M.S. & Camadro, E.L. (2015). Reproductive behavior of the wild carrots *Daucus pusillus* and *Daucus montanus* from Argentina. *Botany*. 93, 179-286.

Ickert-Bond, S.M. & Wojciechowksi, M.F. (2004). Phylogenetic relationships in *Ephedra* (Gnetales): evidence from nuclear and chloroplast DNA sequence data. *Syst. Bot.* 29, 834-849.

Islam, M.B. & Simmons, M.P. (2006). A thorny dilemma: testing alternative intrageneric classifications within *Ziziphus* (Rhamnaceae). *Syst. Bot*. 31, 826-842.

Johnson-Fulton, S.B. & Watson, L.E. (2017). Phylogenetic systematics of Cochlospermaceae (Malvales) based on molecular and morphological evidence. *Syst. Bot*. 42, 271-282.

Kadereit, G., Mavrodiev, E.V., Zacharias, E.H. & Sukhorukov, A.P. (2010). Molecular phylogeny of Atripliceae (Chenopodioideae, Chenopodiaceae): implications for systematics, biogeography, flower, and fruit evolution, and the origin of C4 photosynthesis. *Am. J. Bot.* 97, 1664-1687.

Kapralov, M.V., Akhani, H., Voznesenskaya, E.V., Edwards, G., Franceschi, V. & Roalson, E.H. (2006). Phylogenetic relationships in the Salicornioideae/Suaedoideae/Salsoloideae s.l. (Chenopodiaceae) clade and a clarification of the phylogenetic position of *Bienertia* and *Alexandra* using multiple DNA sequence datasets. *Syst. Bot*. 31, 571-585.

Kelch, D.G. & Baldwin, B.G. (2003). Phylogenery and ecological radiation of New World thistles (*Cirsium*, Cardueae – Compositae) based on ITS and ETS rDNA sequence data. *Mol. Ecol.* 12, 141-151.

Kellogg, E.A., Aliscioni, S.S., Morrone, O., Pensiero, J. & Zuloaga, F. (2009). A Phylogeny of *Setaria* (Poaceae, Panicoideae, Paniceae) and related genera based on the chloroplast gene *ndh*F. *Int. J. Plant Sci*. 170, 117-131.

Kempton, E.A. (2012). Systematics of Eriogonoideae s.s. (Polygonaceae). *Syst. Bot.* 37, 723-737.

Kim, Y., Kim, S. & Landrum. L.R. (2004). Taxonomic and phytogeographic implications from ITS phylogeny in *Berberis* (Berberidaceae). *J. Plant Res*. 117, 175-182.

Kimball, R.T. & Crawford, D.J. (2004). Phylogeny of Coreopsideae (Asteraceae) using ITS sequence suggests lability in reproductive characters. *Mol. Phylogenet. Evol*. 33, 127-139.

Lavin, M., Wojciechowski, M.F., Gasson, P., Hughes, C. & Wheeler, E. (2003). Phylogeny of Robinioid legumes (Fabaceae) revisited: *Coursetia* and *Gliricidia* recircumscribed, and a biogeographical appraisal of the Caribbean endemics. *Syst. Bot*. 28, 387-409.

Lee, J., Baldwin, B.G. & Gottlieb L.D. (2003). Phylogenetic relationship among the primarily North American genera of Cichorieae (Compositae) based on analysis of 18S-26S nuclear rDNA ITS and ETS sequences. *Syst. Bot.* 28, 616-626.

Lee, J., Mummenhoff, K. & Bowman, J.L. (2002). Allopolyploidization and evolution of species with reduced floral structures in *Lepidium* L. (Brassicaceae). *PNAS*. 99, 16835-16840.
Lehtonen, S. (2009). Systematics of the Alismataceae-a morphological evaluation. *Aquat. Bot.* 91, 279-290.

Levin, R.A., Wagner, W.L., Hoch, P.C., Hahn, W.J., Rodriguez, A., Baum, D.A. et. al. (2004). Paraphyly in tribe Onagreae: insights into phylogenetic relationships of Onagraceae based on nuclear and chloroplast sequence data. *Syst. Bot*. 29, 147-164.

Liede, S. & Tauber, A. (2000). *Sarcostemma* R.Br. (Apocynaceae-Asclepiadoideae)- a controversial generic circumscription reconsidered: evidence from *trn*L-F spacers. *Plant. Syst. Evol.* 225, 133-140.

Liu, X., Ickert-Bond, S.M., Nie, Z., Zhou, Z., Chen, L. & Wen, J. (2016). Phylogeny of the *Ampelocissus-Vitis* clade in Vitaceae supports the New World origin of the grape genus. *Mol. Phylogenet. Evol*. 95, 217-228.

Liu, X., Wang, Z., Wang, D. & Zhang, J. (2016). Phylogeny of *Populus-Salix* (Salicaceae) and their relative genera using molecular datasets. *Biochem. Syst. Ecol*. 68, 210-215.

Loockerman, D.J., Turner, B.L. & Jansen, R.K. (2003). Phylogenetic relationships within the Tageteae (Asteraceae) based on nuclear ribosomal ITS and chloroplast *ndh*F gene sequences. *Syst.Bot.* 281, 191-207.

Lu-Irving, P. & Olmstead, R.G. (2013). Investigating the evolution of Lantaneae (Verbenaceae) using multiple loci. *Bot. J. Linn. Soc.* 171, 103-119.

Majure, L.C., Puente, R., Griffith, M.P., Judd, W.S., Soltis, P.S., & Soltis, D.E. (2012). Phylogeney of *Opuntia* s.s. (Cactaceae): clade delineation, geographic origins, and reticulate evolution. *Am. J. Bot*. 99, 847-864.

Manos, P.S. & Miller, R.E. (2001). Phylogenetic analysis of *Ipomoea*, *Argyreia*, *Stictocardia*, and *Turbina* suggests a generalized model of morphological evolution in morning glories. *Syst. Bot*. 26, 585-602.

Manos, P.S., Doyle, J.J. & Nixon, K.C. (1999). Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* Subgenus *Quercus* (Fagaceae). *Mol. Phylogenet. Evol*. 12, 333-349.

Marlowe, K. & Hufford, L. (2007). Taxonomy and biogeography of *Gaillardia* (Asteraceae): a phylogenetic analysis. *Syst. Bot*. 32, 208-226.

Martin, M.D., Quiroz-Claros, E., Brush, G.S. & Zimmer, E.A. (2018). Herbarium collection-based phylogenetics of the ragweeds (*Ambrosia*, Asteraceae). *Mol. Phylogenet. Evol.* 120, 335-341.

Mason-Gamer, R.J., Orme, N.L. & Anderson, C.M. (2002). Phylogenetic analysis of North American *Elymus* and the monogenomic Triticeae (Poaceae) using three chloroplast DNA data sets. *Genome*. 45, 991-1002.

McDonnell, A., Parks, M. & Fishbein, M. (2018). Multilocus phylogenetics of new world milkweed vines (Apocynaceae, Asclepiadoideae, Gonolobinae). *Syst. Bot*. 43, 77-96.

Miao, B., Turner, B.L. & Mabry, T.J. (1995). Chloroplast DNA variations in Sect. *Cyclachaena* of *Iva* (Asteraceae). *Am. J. Bot*. 82, 919-923.

Miller, J.M. & Chambers, K.L. (2006). Systematics of *Claytonia* (Portulacaceae). *Syst. Bot. Monogr*. 78, 1-236.

Miller, J.S. (2002). Phylogenetic relationships and the evolution of gender dimorphism in *Lycium* (Solanaceae). *Syst. Bot*. 27, 416-428.

Miller, J.T. & Bayer, R.J. (2003). Molecular phylogenetics of *Acacia* subgenera *Acacia* and *Aculeiferum* (Fabaceae: Mimosoideae), based on the chloroplast matK coding sequence and flanking trnK intron spacer regions. Austalian *Syst. Bot*. 16, 27-33.

Miller, R.E. & Rausher, M.D. (1999). Phylogenetics systematics of *Ipomoea* (Convolvulaceae) based on ITS and waxy sequences. *Syst. Bot*. 24, 209-227.

Moody, M.L. & Rieseberg, L.H. (2011). Sorting through the chaff, nDNA gene trees for phylogenetic inference and hybrid identification of annual sunflowers (*Helianthus* sect. *Helianthus*). *Mol. Phylogenet. Evol*. 64, 145-155.

Morgan D.R. (2003). nrDNA external transcribed spacer (ETS) sequence data, reticulate, evolution, and the systematics of *Machaeranthera* (Asteraceae). *Syst. Bot.* 28, 179-190.

Morrone, O., Aegesen, L., Scataglini, M.A., Salariato, D.L., Denham, S.S., Chemisquy, M.A. et al. (2012). Phylogeny of the Paniceae (Poaceae: Panicoideae): integrating plastid DNA sequences and morphology into a new classification. Cladistics. 333-356.

Mummenhoff, K., Bruggemann, H. & Bowman, J.L. (2001). Chloroplast DNA phylogeny and biogeography of *Lepidium* (Brassicaeae). *Am. J. Bot*. 88, 2051-2063.

Nesom, G.L. (2009). Notes on the taxonomy of *Maytenus phyllanthroides* (Celastraceae). *Phytologia*. 91, 64-68.

Nguyen, N.H., Driscoll, H.E. & Specht, C.D. (2007). A molecular phylogeny of wild onions (*Allium*; Alliaceae) with a focus on the western North American center of diversity. *Mol. Phylogenet. Evol*. 47, 1157-1172.

Nishikawa, T., Salomon, B., Komatsuda, T., von Bothmer, R. & Kadowaki, K. (2002). Molecular phylogeny of the genus *Hordeum* using three chloroplast DNA sequences. *Genome*. 45, 1157-1166.

O’Leary, N., Denham, S.S., Salimena, F. & Mulgura, M.E. (2012). Species delimitation in *Lippia* section Goniostachyum (Verbenaceae) using the phylogenetic species concept. *Bot. J. Linn. Soc*. 170, 197-219.

Ocampo, G. & Columbus, J.T. (2012). Molecular phylogenetics, historical biogeography, and chromosome number evolution of *Portulaca* (Portulacaeae). *Mol. Phylogenet. Evol.* 63, 97-112.

Olmstead, R.G., Bohs, L., Migid, H.A., Santiago-Valentin, E., Garcia, V.F. & Collier, S.M. (2008). A molecular phylogeny of the Solanceae. *Taxon*. 57, 1159-1181.

Pastore, J.F.B., Harley, R.M., Forest, F., Paton, A. & van den Berg, C. (2011). Phylogeny of the subtribe Hyptidinae (Lamiaceae tribe Ocimeae) as inferred from nuclear and plastid DNA. *Taxon*. 60, 1317-1329.

Patchell, M.J. Roalson, E.H. & Hall, J.C. (2014). Resolved phylogeny of Cleomaceae on all three genomes. *Taxon*. 63, 315-328.

Patterson, T.B. & Givnish, T.J. (2003). Geographic cohesion, chromosomal evolution, parallel adaptive radiations, and consequent floral adaptations in *Calochortus* (Calochortaceae): evidence from cpDNA phylogeny. *New Phytol*. 161, 253-264.

Pellmyr, O., Segraves, K.A., AlthoV, D.M., Balcazar-Lara, M. & Leebens-Mack, J. (2007). The phylogeny of yuccas. *Mol. Phylogenet. Evol*. 43, 493-501.

Perez-Diaz, A.J., Sharifi-Tehrani, M., Inda, L.A. & Catalan, P. (2014). Polyphyly, gene-duplication and extensive allopolyploidy framed the evolution of the ephemeral *Vulpia* grasses and other fine-leaved Loliinae (Poaceae). *Mol. Phylogenet. Evol.* 79, 92-105.

Petersen, G. & Seberg, O. (2003). Phylogenetic analyses of the diploid species of *Hordeum* (Poaceae) and a revised clarification of the genus. *Syst. Bot*. 28, 293-306.

Peterson, P.M, Arrieta, Y.H. & Romaschenko, K. (2018). Phylogeny of *Muhlenbergia* subg. *Pseudosprobolus*, including *M. spatha* (Poaceae, Chloridoideae, Cynodonteae, Muhlenbergiinae), now found in Zacatecas, Mexico. *PhytoKeys*. 103, 83-94.

Peterson, P.M, Romaschenko, K., Snow, N. & Johnson, G. (2011). A molecular phylogeny and classification of *Leptochloa* (Poaceae: Chloridoideae: Chlorideae) sensu lato and related genera. *Ann. Bot*. 109, 1317-1329.

Peterson, P.M, Romaschenko, K., Arrieta, Y.H. & Saarela, J.M. (2014). A molecular phylogeny and new subgeneric classification of *Sporobolus* (Poaceae: Chloridoideae: Sprobolinae). *Taxon*. 63, 1212-1243.

Peterson, P.M., Romaschenko, K. & Arrieta, Y.H. (2016). A molecular phylogeny and classification of the Cynodonteae (Poaceae: Chloridoideae) with four new genera: *Orthacanthus*, *Triplasiella*, *Tripogonella*, and *Zaqiqah*; three new subtribes: Dactylocteniinae, Orininae, and Zaqiqahinae; and a subgeneric classification of *Distichlis*. *Taxon*. 65, 1263-1287.

Peterson, P.M., Romaschenko, K. & Johnson, G. (2010). A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic tree. *Mol.Phylogenet. Evol.* 55, 580-598.

Rahn, K. (1996). A phylogenetic study of the Plantaginaceae. *Bot. J. Linn. Soc.* 120, 145-198.

Reid, C.S., Carter, R. & Urbatsch, L.E. (2014). Phylogenetic insights into new world *Cyperus* (Cyperaceae) using nuclear ITS sequences. *Brittonia*. 66, 292-305.

Riser II, J.P., Cardinal-McTeague, W.M., Hall, J.C., Hahn, W.J., Sytsma, K.J. & Roalson, E.H. (2013). Phylogenetic relationships among the North American cleomoids (Cleomaceae): a test of Iltis's reduction series. *Am. J. Bot.* 100, 2102-2111.

Rockinger, A., Flores, A.S. & Renner, S.S. (2017). Clock-dated phylogeny for 48% of the 700 species of *Crotalaria* (Fabaceae-Papilionoideae) resolves sections worldwide and implies conserved flower and leaf traits throughout its pantropical range. *BMC Evol. Biol*. 61, 1-13.

Sanchez, D., Terrazas, T., Grego-Valencia, D. & Arias, S. (2017). Phylogeny in *Echinocereus* (Cactaceae) based on combined morphological and molecular evidence: taxonomic implications. *Syst. Biodivers* 16, 28-44.

Schaferhoff, B., Muller, K.F. & Borsch, T. (2009). *Caryophyllales* phylogenetics: disentangling Phytolaccaceae and Molluginaceae and description of Microteaceae as a new isolated family. *Willdenowia*. 39, 209-228.

Schenk, J.J. & Hufford, L. (2011). Phylogeny and taxonomy of *Mentzelia* Section *Bartonia* (Loasaceae). *Syst. Bot*. 36, 711-720.

Schneider, A.C., Colwell, A.E.L., Schneeweiss, G.M. & Baldwin, B.G. (2016). Cryptic host-specific diversity among western hemisphere broomrapes (*Orobanche* s.l., Orobanchaceae). *Ann Bot*. 118, 1101-1111.

Schultheis, L.M. & Baldwin, B.G. (1999). Molecular phylogenetics of Fouquieriaceae: evidence from nuclear rDNA ITS studies. *Am. J. Bot*. 86, 578-589.

SEINet Portal Network. 2018. http://:swbiodiversity.org/seinet/index.php.

Sha, L., Fan, X., Zhang, H., Kang, H., Wang, Y., Wang, X. et. al. (2016). Phylogeny and molecular evolution of the DMC1 gene in the polyploid genus *Leymus* (Triticeae: Poaceae) and its diploid relatives. *J.Syst. Evol*. 54, 250-265.

Shiels, D.R., Hurlbut, D.L., Lichtenwald, S.K. & Monfils, A.K. (2014). Monophyly and phylogeny of *Schoenoplectus* and *Schoenoplectiella* (Cyperaceae): evidence from chloroplast and nuclear DNA sequences. *Syst. Bot*. 39, 132-144.

Simpson, B.B., Tate, J.A. & Weeks, A. (2004). Phylogeny and character evolution of *Hoffmannseggia* (Caesalpinieae: Caesalpinioideae: Leguminosae). *Syst. Bot*. 29, 933-946.

Stetter, M.G. & Schmid, K.J. (2017). Analysis of phylogenetic relationships and genome size evolution of the *Amaranthus* genus using GBS indicates the ancestors of an ancient crop. *Mol. Phylogenet. Evol*. 109, 80-92.

Stride, G., Nylinder. S. & Swenson, U. (2014). Revisiting the biogeography of *Sideroxylin* (Sapotaceae) and an evaluation of the taxonomic status of *Argania* and *Spiniluma*. *Aust. Syst. Bot*. 27, 104-118.

Vaezi, J. & Brouillet, L. (2008). Phylogenetic relationships among diploid species of *Symphyotrichum* (Asteraceae: Astereae) based on two nuclear markers, ITS and GAPDH. *Mol. Phylogenet. Evol*. 51, 540-553.

Vaio, M., Gardner, A., Emshwiller, E. & Guerra, M. (2013). Molecular phylogeny and chromosome evolution among the creeping herbaceous *Oxalis* species of section Corniculatae and Ripariae (Oxalidaceae). *Mol. Phylogenet. Evol*. 68, 199-211.

Voshell, S.M., Baldini, R.M., Kumar, R., Tatalovich, N. & Hilu, K.W. (2011). Canary grasses (Phalaris, Poaceae): molecular phyogenetics, polyploidy and floret evolution. *Taxon*. 60, 1306-1316.

Wagner, W.L., Hoch, P.C. & Raven, P.H. (2007). Revised classification of Onagraceae. *Syst. Bot. Monogr*. 83, 1-240.

Walker, J.B., Drew, B.T. & Systma, K.J. (2015). Unraveling species relationships and diversification within the iconic California Floristic Province sages (*Salvia* subgenus *Audibertia*, Lamiaceae). *Syst. Bot*. 40, 826-844.

Walker, J.B., Systma, K.J., Treutlein, J. & Wink, M. (2004). *Salvia* (Lamiaceae) is not monophyletic: implications for the systematics, radiation, and ecological specializations of *Salvia* and tribe Mentheae. *Am. J. Bot.* 9, 1115-1125.

Wan, Y., Schwaniger, H.R., Baldo, A.M., Labate, J.A., Zhong, G. & Simon, C.J. (2013). A phylogenetic analysis of the grape genus (Vitis L.) reveals broad reticulation and concurrent diversification during neogene and quaternary climate change. *BMC Evol. Biol*. 13, 1-20.

Wang, H., Sun, D. & Sun, G. (2011). Molecular phylogeny of diploid *Hordeum* species and incongruence between chloroplast and nuclear datasets. *Genome*. 986-992.

Watson, L.E., Bates, P.L., Evans, T.M., Unwin, M.M. & Estes, J.R. (2002). Molecular phylogeny of subtribe Artemisinnae (Asteraceae) including Artemisia and its allied and segregate genera. *BMC Evol. Biol*. 2,1-12.

Weese, T.L. & Bohs, L. (2007). A three-gene phylogeny of the genus *Solanum* (Solanaceae). *Systematic Botany*. 32, 445-463.

Wen, J., Berggren, S.T., Lee, C., Ickert-Bond, S., Yi, T., Yoo, K. et. al. (2008). Phylogenetic inferences in *Prunus* (Rosaceae) using chloroplast ndhF and nuclear ribosomal ITS sequences. *J. Syst. Evol.* 46, 322-332.

Wheeler, E.J., Mashayekhi, S., McNeal, D.W., Columbus, J.T. & Pires, J.C. (2013). Molecular systematics of *Allium* subgenus Amerallium (Amaryllidaceae) in North America. *Am. J. Bot.* 100, 701-711.

Whitson, M. & Manos, P.S. (2005). Untangling *Physalis* (Solanaceae) from the Physaloids: a two-gene phylogeny of the Physaline. *Syst. Bot*. 30, 216-230.

Wojciechowski, M.F., Sanderson, M.J. & Hu, J. (1999). Evidence on the monophyly of *Astragalus* (Fabaceae) and its major subgroups based on nuclear ribosomal DNA ITS and chloroplast DNA *trn*L intron data. *Syst. Bot*. 24, 409-437.

Xu, L., Harrison, R.D., Yang, P. & Yang, D. (2011). New insight into the phylogenetic and biogeographic history of genus *Ficus*: vicariance played a relatively minor role compared with ecological opportunity and dispersal. *J. Syst. Evol*. 00, 1-12.

Yi, T., Miller. A.J. & Wen, J. (2007). Phylogeny of *Rhus* (Anacardiaceae) based on sequences of nuclear *nia-i3* intron and chloroplast *trn*C-*trn*D. *Syst. Bot*. 32, 379-391.

Yost, J.M., Bontrager, M., McCabe, S.W., Burton, D., Simpson, M.G., Kay, K.M. et. al. (2013). Phylogenetic relationships and evolution in *Dudleya* (Crassulaceae). *Syst. Bot.* 38, 1096-1104.

Zhang, X., Tapia, M., Webb, J.B., Huang, Y. & Miao, S. (2008). Molecular signatures of two cattail species, *Typha domingensis* and *Typha latifolia* (Typhaceae), in South Florida. *Mol. Phylogenet.Evol*.

Zheng, Y., Alverson, A.J., Wang, Q. & Palmer, J.D. (2013). Chloroplast phylogeny of *Cucurbita*: evolution of the domesticated and wild species. *J. Syst. Evol.* 51, 326-334.

APPENDIX C

G.L.MODEL

The first multiple linear regression analysis (G.L.Model) focused exclusively on growth form and life form as these traits had the most data (*n*=534 total species) available for my species list.

$$G.L.Model = \ R/P \sim Food.Usage * (Growth\ Form + Life\ Form)$$

I identified trait predictors of food use and R/P. G.L.Model was statistically significant overall (Adjusted R^2=0.19, F-statistic=14.44, P<2.2e-16). Similar to G.L.P.Model, G.L.Model revealed that the un-used congeners has significantly lower R/P ratios than the Sonoran Desert food plants (Un-used Congener coefficient= -0.08, SE= 0.01, t= -5.45, P=6.0e-08, ANOVA Food.Usage: P < 6.0e-08). Succulent and perennial species had significantly lower R/P ratios within North America (Succulent coefficient = -0.05, SE=0.01, t statistic=-3.12, P=1.87e-03; ANOVA Form: P=2.4e-03; Perennial coefficient = -0.03, SE=0.01, t statistic=-2.22, P=2.7e-02; ANOVA Life Cycle: P=2.7e-02).

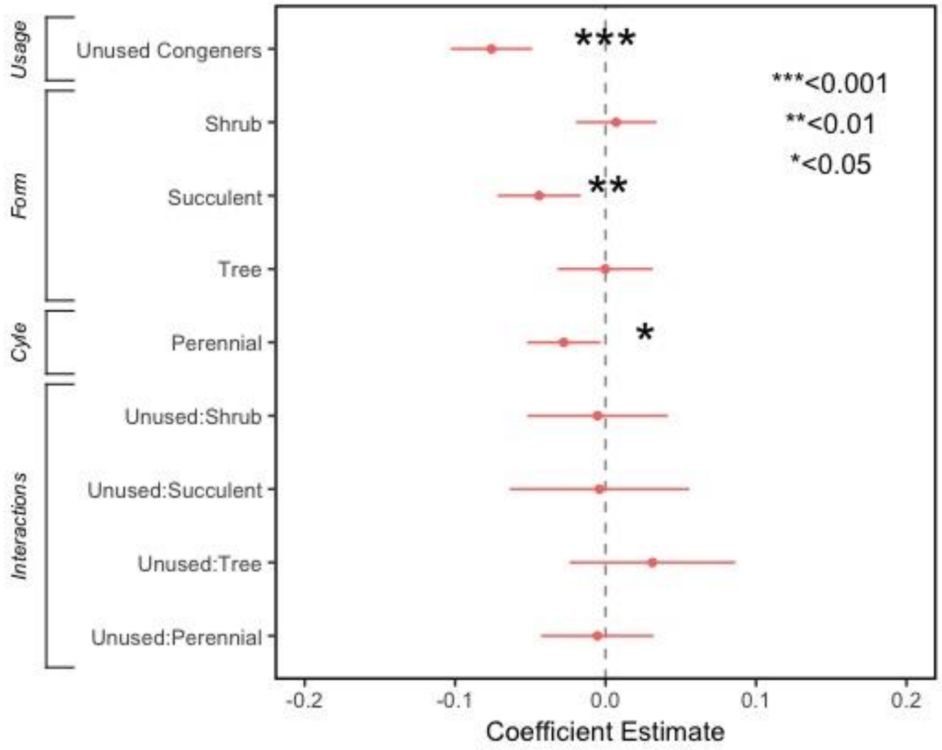


Figure S1 Coefficient estimates for the predictors of R/P in North America (G.L.Model). Data included species for all traits except ploidy (*n* =534). (*), P <0.05; (**) P <0.01; (***), P<0.001). Succulence and perenniality were statistically significant and correlated with R/P. Food use was also statistically significant and correlated with R/P.

APPENDIX D

MEDIAN AND MEAN R/P RATIOS FOR POLYPLOIDY

Polyploidy (un-used congeners)	**Median R/P North America (G.L.P.Model)**	**Mean R/P North America (G.L.P.Model)**
0	0.11	0.12
1	0.18	0.19
Polyploidy (food plants)	**Median R/P North America (G.L.P.Model)**	**Mean R/P North America (G.L.P.Model)**
0	0.19	0.20
1	0.23	0.23

Table S1 The mean and median R/P ratios for polyploid un-used congeners and the food plants using the R/P ratios for North America (1=polyploid, 0=not polyploid).

APPENDIX E

MEDIAN AND MEAN R/P RATIOS FOR SUCCULENTS

Form	**Median R/P North America**	**Median R/P Sonoran Desert**	**Mean R/P North America**	**Mean R/P Sonoran Desert**
Succulent	0.14	0.19	0.15	0.22

Table S2 The median and mean R/P ratios for succulents for both the Sonoran Desert analysis than the North America analysis.

APPENDIX F

HOHOKAM FOOD PLANT USE

The Hohokam occupation of the Sonoran Desert region is characterized by large and long-lasting agricultural communities and, along the major water ways, they created one of the largest irrigation canal systems in the Americas. The Hohokam developed risk management strategies, adapting to the wide range of topographic complexity and environmental variability that characterizes the Sonoran Desert (Fish & Fish 1992). They cultivated crops such as *Zea mays* L. (maize), *Phaseolus acutifolius var. acutifolius* A. Gray (tepary beans), *Curcurbita pepo* L. (pepo squash), and *Amaranthus hybridus* L. (grain amaranth). They also are thought to have encouraged native, wild species using hundreds of miles of irrigation canals along the Salt, San Pedro, Verde, and Gila Rivers, as well as dryland runoff techniques such as rock alignments, terraces and check dams to slow water runoff and capture sediment. (Bayman 2001, Fish & Fish 2007, Abbott et. al. 2007, Hodgson et. al. 2018).

However, the Hohokam also interacted with many non-cultivated species. The Hohokam were direct gatherers and consumers of a wide variety of desert vegetation (Fish & Fish 1992). The Hohokam engaged in both intentional manipulation and unintentional enhancement of plant species for food use (Fish 1993 Other succulents besides agave were perhaps transplanted to a lesser scale throughout Hohokam settlements such as *Opuntia* spp. (prickly-pear) and *Cylindropuntia* spp. (cholla) (Fish 1993). The Hohokam likely encouraged certain weeds as valuable food sources, allowing the weeds to grow amongst crops and sometimes scattering the seeds to ensure their supply (Bohrer 1970, Gasser & Kwiatkowski 1991, Fish & Fish 1992, Fish 1993). The Hohokam applied a “continuum of use” framework which ranged from extensive cultivation of crops to wild-harvesting and dispersal of other native plant species. These native plant species include *Prosopis* spp, (mesquite), *Lycium* spp. (wolfberry), and weedy species such as *Boerhavia* spp. (spiderlings), *Descurainia* spp. (tansy mustard), *Hordeum pusillum* Nutt. (little barley grass), *Trianthema portulacastrum* L. (desert horse purslane), *Panicum* grasses, *Amaranthus* spp. (amaranth) and *Chenopodium* spp. (goosefoot) (Gasser & Kwiatkowski 1991, Bohrer 1970, Fish 2000). Preserved small-seeded wild grasses such as *Sporobolus* sp. (dropseed) and *Eragrastis* sp. (Lovegrass) were found in abundance at the Marana Mound site in Tucson (Hansen-Speer 2013). This small-seeded wild grass had an even higher percentage presence (56%) than corn (46%, suggesting their use as a food source. *Sporobolus* sp. in particular is easily gathered and processed because it has a naked grain (i.e. the seed is easily freed from the glumes and bracts) and more contemporary ethnographic accounts continue to document them as a food source (Castetter & Bell 1951, Hansen-Speer 2013).

The impacts of Hohokam food use have generally been analyzed for individual species at fine spatial scales, i.e., at particular archaeological site complexes. Research on the Cave Creek archaeological complex has showed that agricultural practices have had a discernable impact on plant community dynamics (Hall et. al. 2013). Traces of Hohokam food dispersal can be found at certain archaeological sites. Another study at the Cave Creek archaeological complex used pollen records to show that plants identified as partially domesticated (e.g., plants in the *Chenopodium* and *Amaranthus* genera) by the Hohokam increased during the cultivation time period (Briggs et. al. 2006). High concentrations of herbaceous annuals and perennials as well as moisture-dependent lichens and mosses continue to demonstrate how rock pile features provide beneficial microenvironments compared to areas relatively rock-free (Fish 2000)

APPENDIX G

HOHOKAM FOOD PRODUCTION AND CULTIVATION

The climate of the Salt-Gila Basin (i.e. Phoenix Basin) is generally characterized by long, hot summers, and short, mild winters. Both humidity and rainfall are low, and the rate of evaporation is high (Crown 1987). Average annual precipitation is 241 mm/year with most rainfall occurring in midwinter and the heavy but abrupt monsoon rains in midsummer (Crown 1987). The geological environment of the Basin is a mixture of floodplain, terraces and bajadas (Crown 1987). Along the Gila and Salt Rivers of the Basin, Hohokam constructed the largest irrigation systems in pre-Columbian North America to support large populations in this semi-arid environment (Fish & Fish 2007). Archaeological evidence suggests that there were 14 irrigation networks with an estimated aggregate length of 300 miles in the city of Phoenix (i.e., lower Salt River valley) (Fish & Fish 2007). Research also suggests that in response to this environmental variability and topographic complexity, Hohokam communities integrated different agricultural practices for different environmental zones (Crown 1987, Fish 1993, Fish & Fish 1994).

Zonally differentiated land-use was implemented in conjunction with the Salt and Gila Rivers canal network. Along the Gila River, habitation sites are found within 1km of the canals located in the floodplain with some of the large sites extending outward (Crown 1987). However, the Hohokam would travel further for wild-plant harvesting and trading, creating an extensive socio-economic network (Fish & Fish 1992). Habitation in the Tucson Bain was concentrated within river and mountain flank bands, in proximity to the Santa Cruz River and the Tucson Mountains and Tortolita Mountains. Both the canal irrigation networks that characterizes the Salt-Gila Basin and the Tucson Basin also integrated floodwater diversion on alluvial fans, rockpile complexes, checkdams, contour terraces on upper slopes, and hillside masonry terraces (Fish & Fish 1994). The Tucson Basin can be organized into zones of occupation and food production as well. The particular topography and environment of the zones made some more appropriate for agriculture while others for wild plant harvesting. For example, within the Upper Valley Slope of the Tortolita Mountains, unique and specialized sites have been discovered coinciding with large densities of saguaro. This suggests that this may have been an area where *Carnegiea gigantea* (Engelm.) Briton & Rose saguaro camps were created for the procurement and trading of saguaro fruits (Fish & Fish 1992).

Shells were also used as a currency in exchange for agricultural products in some of the most arid Hohokam habitations. The shells helped facilitate an exchange network of food productions throughout the Hohokam region (McGuire & Howard 1987). The Papagueria is one of the most arid areas within the Sonoran Desert, characterized by high temperatures and low rainfall (i.e., average annual precipitation is less than 15 cm) (Doelle 1980). There is also an absence of permanent streams in the region, and the Hohokam most likely faced relatively low resource predictability from year to year (Doelle 1980). It has been hypothesized that Hohokam in the western Papagueria gathered shells from the Gulf of California and would return to the Papagueria to manufacture shell ornaments (*Glycymeris* bracelets). The Papaguerians would trade both the shells and the jewelry into the Gila Bend and the Phoenix basin in exchange for agricultural products (McGuire & Howard 1987).

APPENDIX H

HOHOKAM 7 KM BUFFER DISTANCE

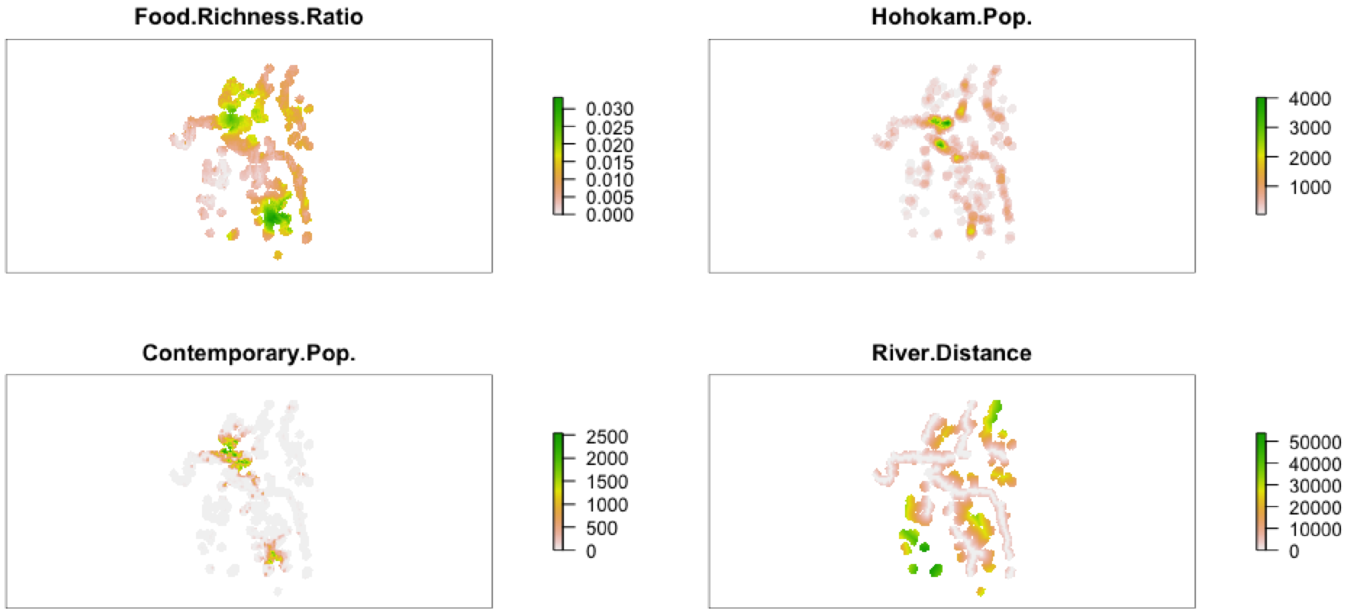


Figure S2 Response variable (i.e. Food.Richness.Ratio) and explanatory variables (i.e. Hohokam.Pop., Contemporary.Pop., and River.Distance) that were used in the GAM at the 7 km buffer distance, consistent with the distance Hohokam would travel for farming. Green represents the highest food plant richness, the highest human populations, and the farthest distance from rivers.

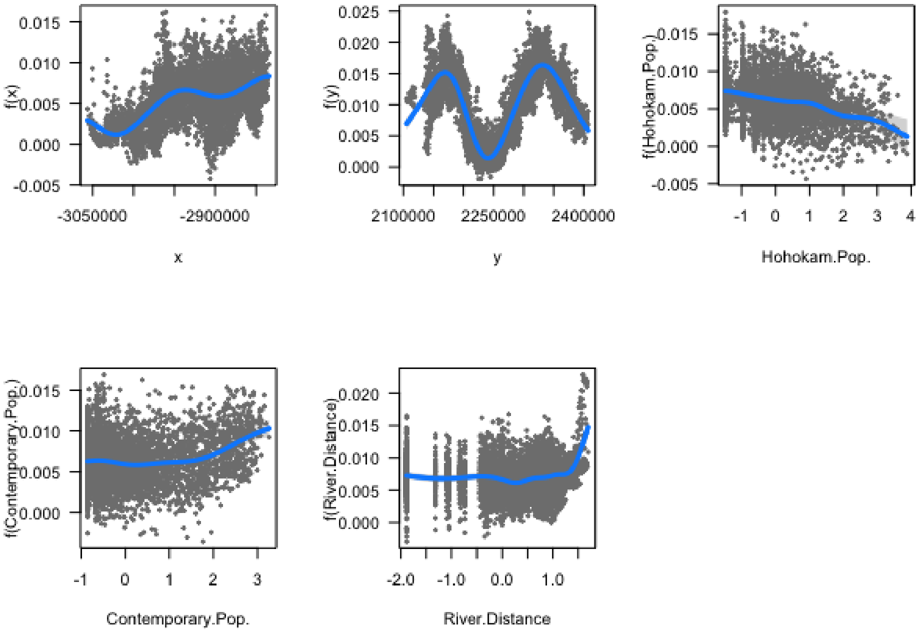


Figure S3 Partial residuals for each explanatory variable used in the GAM for the 7 km buffer distance (Adjusted R^2=0.852, -REML=-2618 with a deviance explained at 85.4%.). Partial residual plots show the relationship between each predictor variable and the response variable given that the other predictor variables are in the model. This is useful for understanding the relative importance of each predictor variable. Contemporary population increase correlates with higher relative food plant richness.

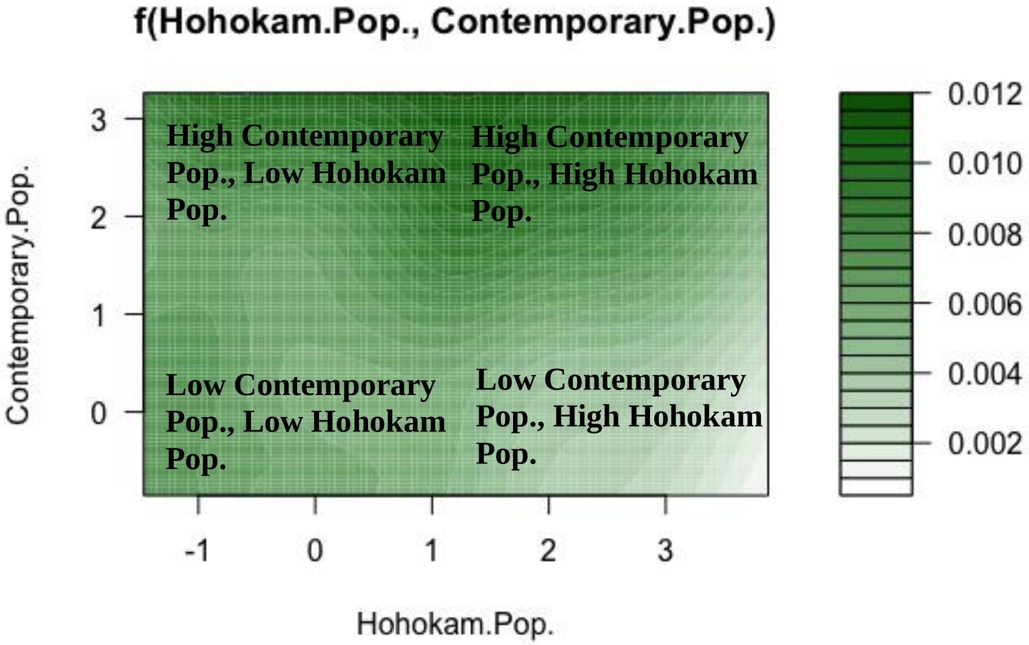


Figure S4 Relative food plant species richness was partially predicted by an interaction between Hohokam.Pop. and Contemporary.Pop in the GAM using the 7 km buffer distance (GAM: s(Hohokam.Pop., Contemporary. Pop. F=13.650, P=<2e-16). The red represents higher relative food plant species richness. There is higher relative food plant species richness with instances of higher contemporary and Hohokam populations, as well as high contemporary populations and low Hohokam populations. There is no instances of high relative food plant species richness with low contemporary population and high Hohokam population, in contrast to the 36 km distance analysis.

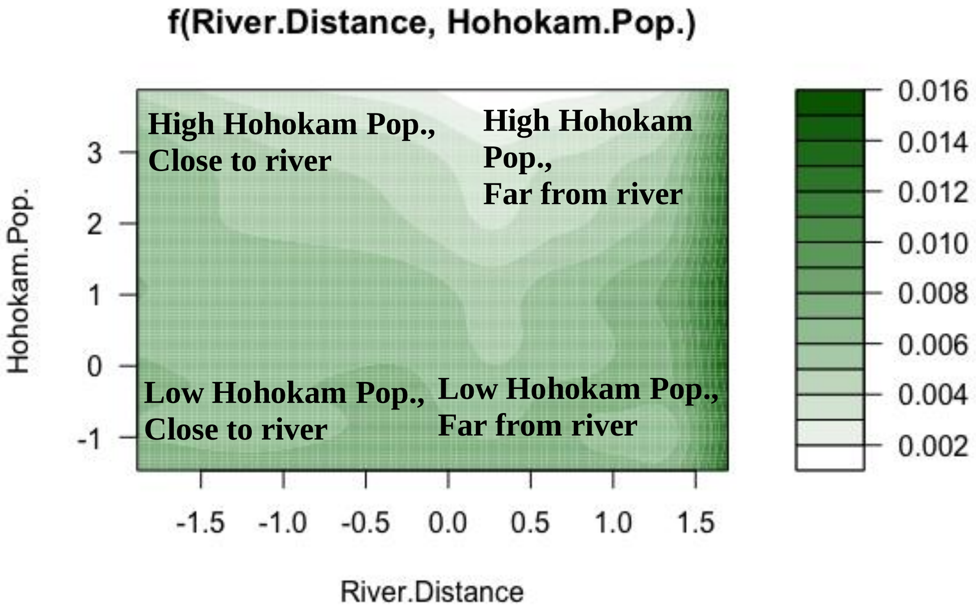


Figure S5 Relative food plant species richness was partially predicted by an interaction between River.Distance and Hohokam.Pop in the GAM using the 7 km buffer distance (GAM: s(Hohokam.Pop., River.Distance) F=3.982, P=<2e-16) . The red represents higher relative food plant species richness. There was only high relative food plant species richness farthest from the rivers, regardless of Hohokam population density.

APPENDIX I

HOHOKAM 36 KM BUFFER DISTANCE WITH CLIMATE VARIABLES

Despite the addition of the climate variables to the model, high relative food plant species richness was partially predicted by high pre-Columbian populations. The GAM regression analysis was statistically significant overall (Adjusted R^2=0.97, -REML = -93690) with a deviance explained of 97%. There was higher relative food plant richness in areas that had the highest pre-Columbian populations (see **Supplementary Information I:** Hohokam 36 km Buffer Distance with Climate Variables **Figs S6 & S7**, GAM: s(Hohokam.Pop.) F=20.193, P=<2e-16). In contrast to the 36 km distance GAM without climate variables, contemporary population remains relatively constant except for a slight decrease at the highest contemporary population densities (see **Supplementary Information I:** Hohokam 36 km Buffer Distance with Climate Variables **Fig. S7**, GAM: s(Contemporary.Pop.) F=6.271, P=<1.65e-08). This suggests that perhaps the climate variables offset some of the influence of contemporary population on relative food plant species richness. This also suggests that perhaps there are persistent legacies of pre-Columbian populations in conjunction with contemporary population and climate.

In addition to the population variables, spatial dependence of the values remained significant for the enrichment of food plant species richness. Just like in the 36 km distance without climate variables and the 7km distance models, modeling the spatial dependence in the systematic part of the model did account for spatial autocorrelation. The spatial term was statistically significant (see **Supplementary Information I:** Hohokam 36 km Buffer Distance with Climate Variables **Fig. S7**, GAM: s(x,y) F=399.145, P=<2.e-16). Relative food plant species richness was not influenced by distance from river except for a decrease in food plant richness at the furthest distance from rivers similar to the 36 km distance without climate variables (see **Supplementary**

Information I: Hohokam 36 km Buffer Distance with Climate Variables **Fig. S7**, GAM: s(River.Distance) F=13.1, P=<2e-16).

I again found that relative food plant species richness was also partially predicted by two interactions. Very similar to the 36 km distance model without climate variables, the highest centers of contemporary population density (i.e., Phoenix and Tucson) and the areas of highest pre-Columbian populations tended to also have some of the highest instances of relative food plant species richness. The interaction between Hohokam population and contemporary population were statistically significant (see **Supplementary Information I:** Hohokam 36 km Buffer Distance with Climate Variables, **Fig. S7**, GAM: s(Hohokam.Pop., Contemporary. Pop.) F=19.046, P=<2e-16; **Fig. S8**). It is again important to note that there were also instances of high relative food plant species richness in areas of solely high contemporary population and solely high Hohokam population estimates (**Fig. S8**). I also found that the interaction between Hohokam population and distance from river was statistically significant (see **Supplementary Information I:** Hohokam 36 km Buffer Distance with Climate, **Fig. S7** GAM: s(Hohokam.Pop, River.Distance) F=21.433, P=<2e-16; **Fig. S9**). The 36 km buffer distance with climate variables model also reflects that, perhaps in certain cases, the Hohokam would inhabit areas close to rivers and then expand their settlements outward.

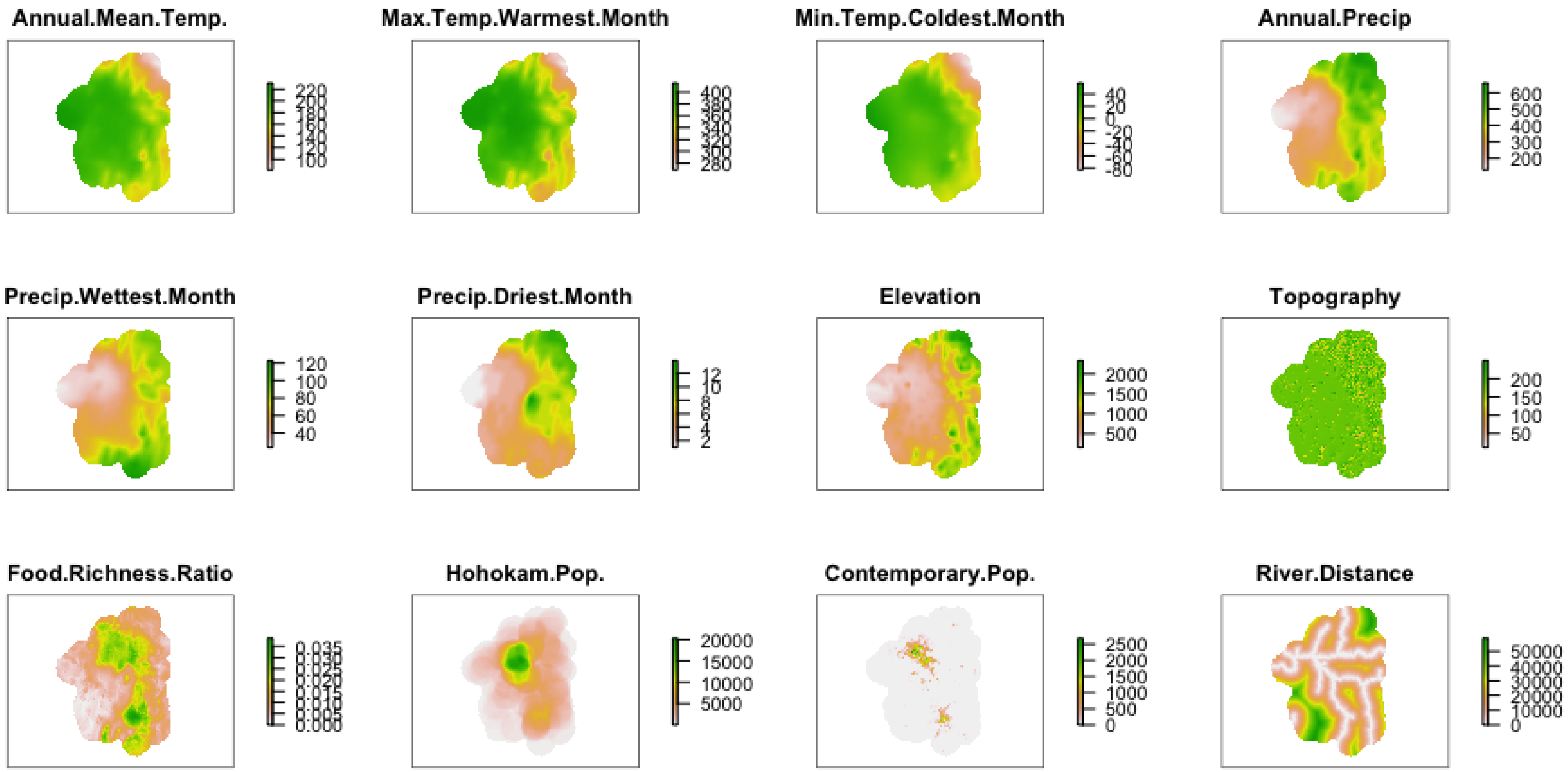
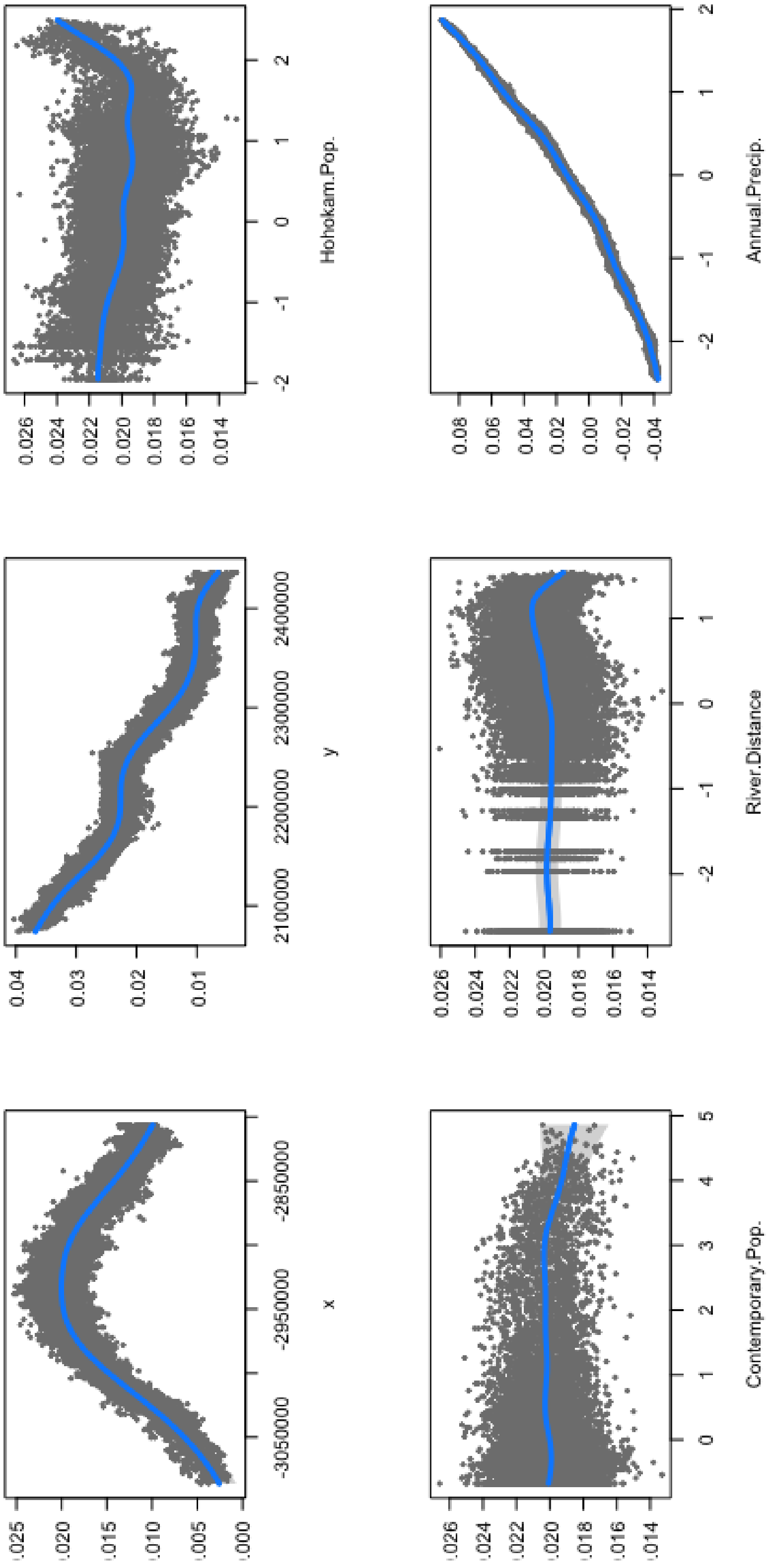
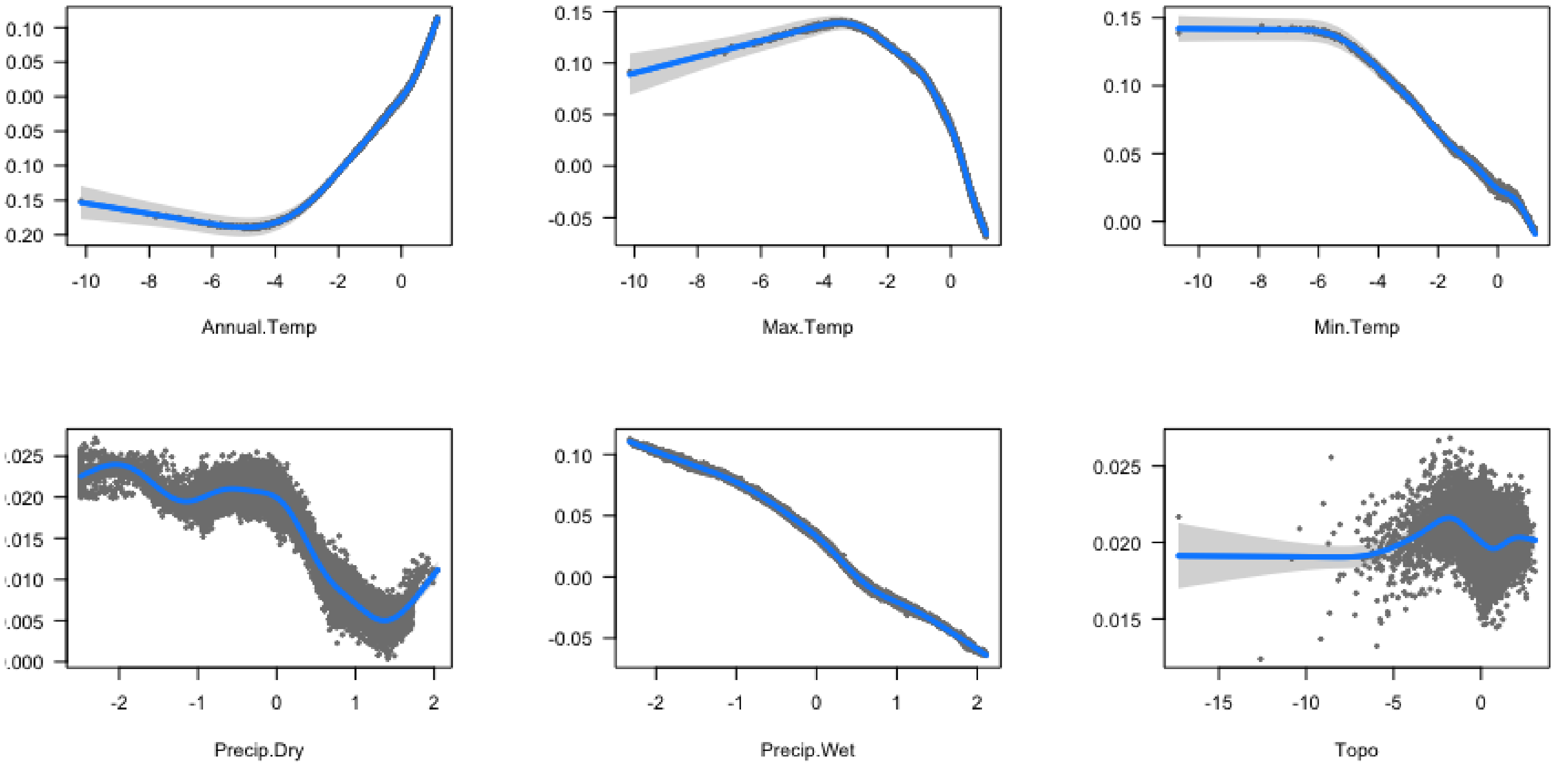


Figure S6 Response variable (i.e. Food.Richness.Ratio) and explanatory variables (i.e. Hohokam.Pop., Contemporary.Pop., and River.Distance) with the addition of climate variables that were used in the GAM at the 36 km buffer distance, consistent with the distance Hohokam would travel in the Sonoran Desert for wild-harvesting.


x
-3050000
-2950000
-2850000
0.000
0.005
0.010
0.015
0.020
0.025
y
2100000
2200000
2300000
2400000
0.01
0.02
0.03
0.04
Hohokam.Pop.
-2
-1
0
1
2
0.014
0.016
0.018
0.020
0.022
0.024
0.026
Contemporary.Pop.
0
1
2
3
4
5
0.014
0.016
0.018
0.020
0.022
0.024
0.026
River.Distance
-2
-1
0
1
0.014
0.016
0.018
0.020
0.022
0.024
0.026
Annual.Precip.
-2
-1
0
1
2
-0.04
-0.02
0.00
0.02
0.04
0.06
0.08


0.10
0.05
0.00
0.05
0.10
0.15
0.20
-10
-8
-6
-4
-2
0
Annual.Temp
0.15
0.10
0.05
0.00
-0.05
-10
-8
-6
-4
-2
0
Max.Temp
0.15
0.10
0.05
0.00
-10
-8
-6
-4
-2
0
Min.Temp
.025
.020
.015
.010
.005
.000
-2
-1
0
1
2
Precip.Dry
0.10
0.05
0.00
-0.05
-2
-1
0
1
2
Precip.Wet
0.025
0.020
0.015
-15
-10
-5
0
Topo

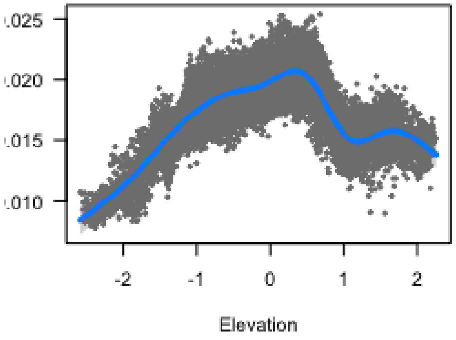


Figure S7 Partial residuals for each explanatory variable used in the GAM for the 36 km buffer distance with climate variables (Adjusted R^2=0.97, -REML=-93690 with a deviance explained at 97%.). Partial residual plots show the relationship between each predictor variable and the response variable given that the other predictor variables are in the model. This is useful for understanding the relative importance of each predictor variable. Similar to the model without the climate variables, Hohokam population increase correlates with higher relative food plant species richness.

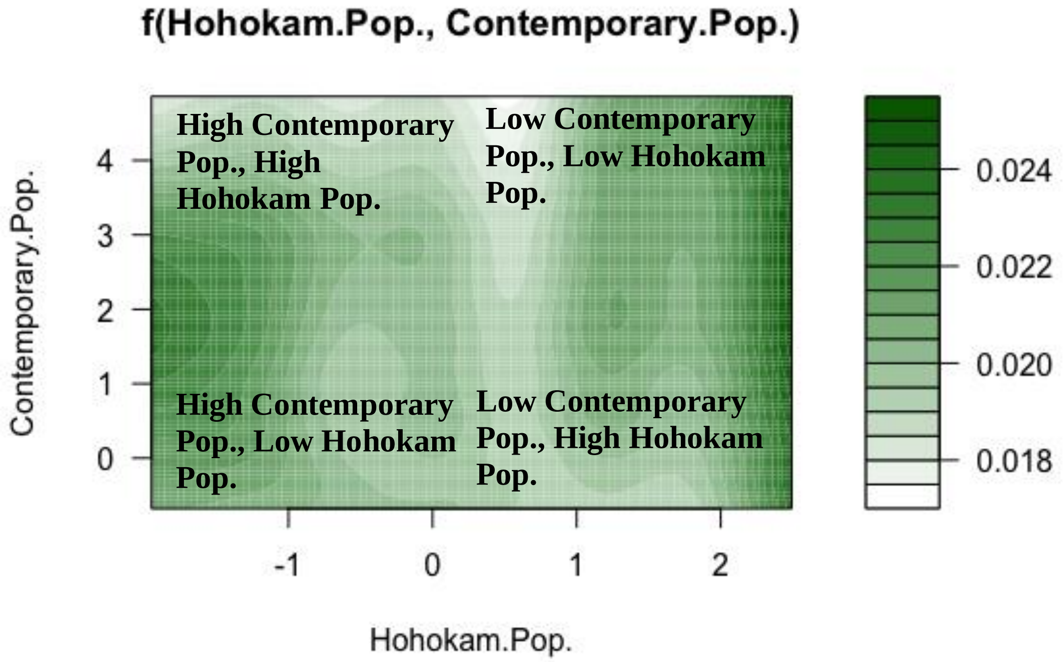


Figure S8 Relative food plant species richness was partially predicted by an interaction between Hohokam.Pop. and Contemporary.Pop in the GAM using the 36 km buffer distance with climate variables (GAM: s(Hohokam.Pop., Contemporary. Pop.) F=19.046, P=<2e-16). The red represents higher relative food plant species richness. There is higher relative food plant species richness with instances of higher contemporary Hohokam populations, high Hohokam populations and low contemporary populations, as well as higher contemporary population and low Hohokam population. There are also instances of higher food plant species richness with both low contemporary and Hohokam population.

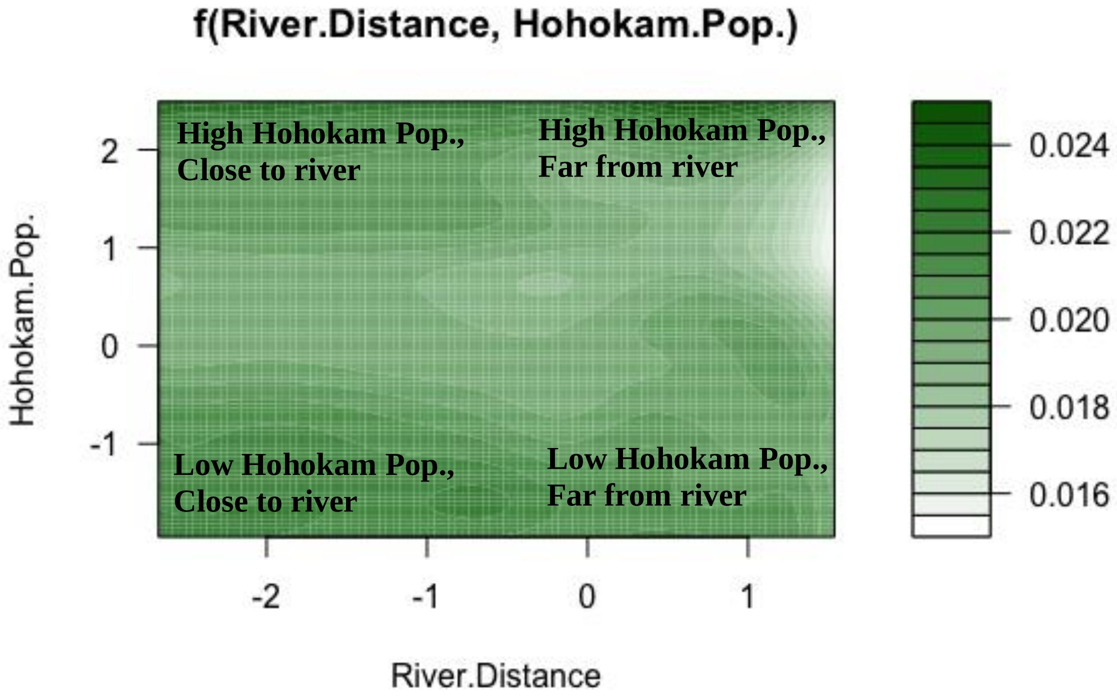


Figure S9 Relative food plant species richness was partially predicted by an interaction between River.Distance and Hohokam.Pop in the GAM using the 36 km buffer distance with climate variables (GAM: s(Hohokam.Pop., River.Distance) F=21.433 P=<2e-16). The red represents higher relative food plant species richness. Similar to the other 36 km model, there was high relative food plant species richness close and far from the rivers regardless of Hohokam population density.

APPENDIX J

MAP OF HOHOKAM STUDY AREA POPULATION ESTIMATES

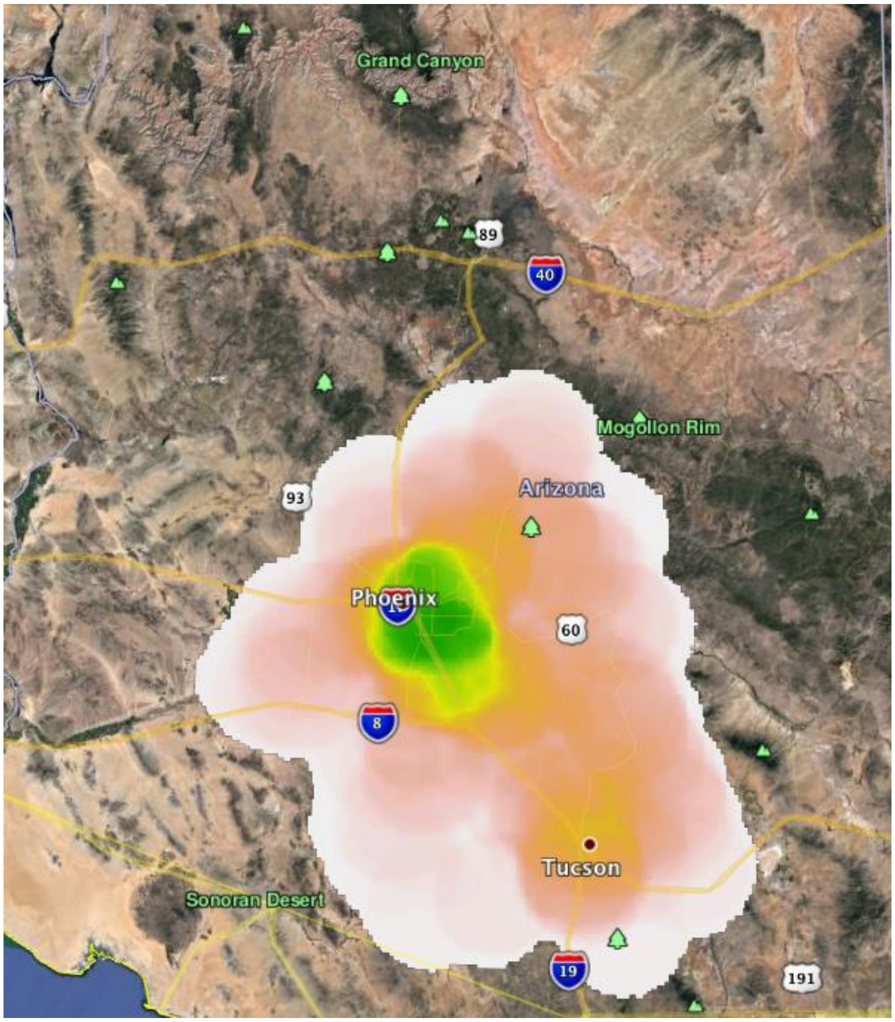


Figure S10. 36 km buffer distance overlaid by the contemporary locations of the Phoenix and Tucson metropolitan areas in Arizona, U.S (combined population approximately 8 million).

APPENDIX K

HOHOKAM DEFINED REGION

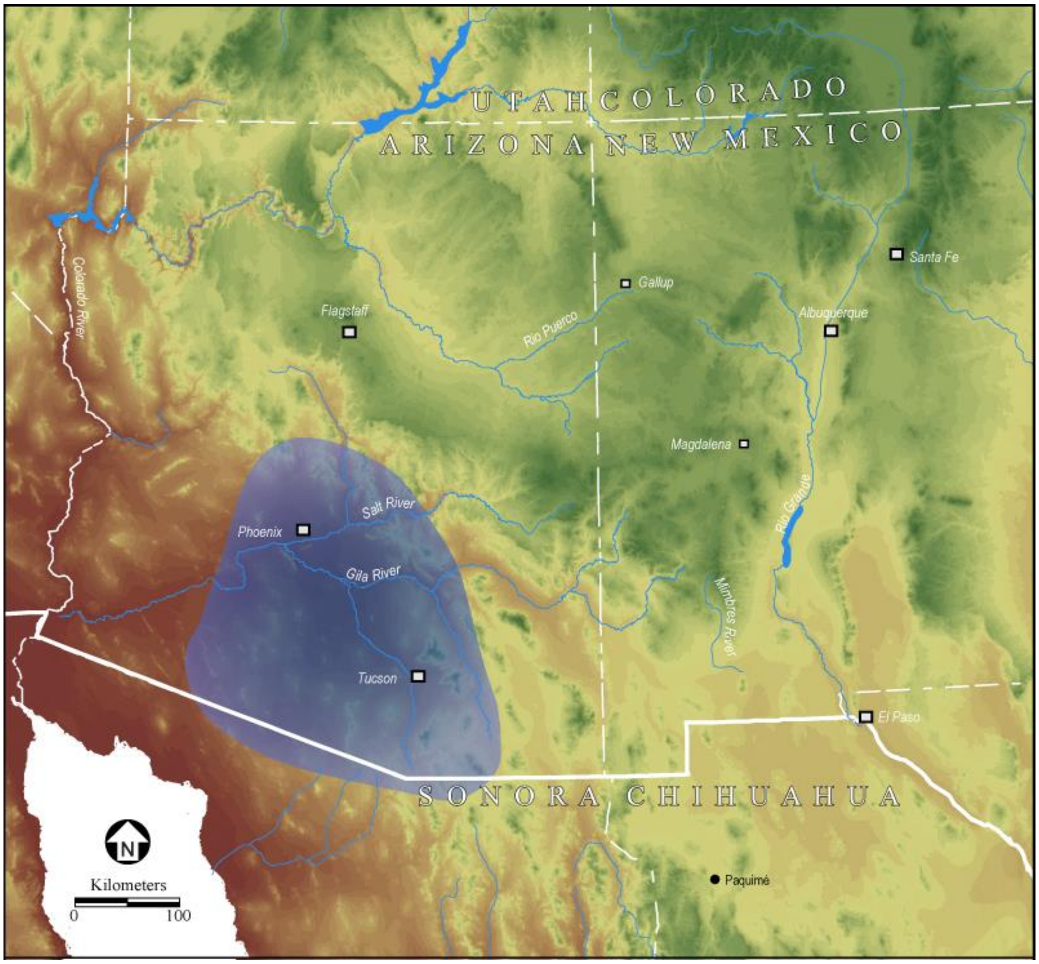


Figure S11 The Hohokam inhabited approximately 80,000 km2 in the southern half Arizona which includes both Phoenix and Tucson. The Hohokam created an extensive canal network that has inspired the modern canal networks in contemporary times.

APPENDIX L

EXAMPLES OF HOHOKAM PLANTS USED FOR FOOD

Figure S12 Several plants that were used by the Hohokam for food. The Hohokam used a wide variety of plant functional types. (a) *Hordeum pusillum* Nutt. Little Barley. (b) *Chenopodium berlandieri* Moq. Pit-Seed Goosefoot. (c) *Prosopis glandulosa* Torr. Honey Mesquite. (d) *Opuntia engelmannii* Salm-Dyck. Engelmann prickly pear. SEINet Portal Network 2018.

APPENDIX M

METADATA FOR 36 KM AND 7 KM RASTERSTACKS

APPENDIX N

METADATA FOR R/P RATIO CSV FILES