

# EXPANSION AND CONTRACTION TENSION ZONES IN WESTERN U.S. PINON-JUNIPER WOODLANDS UNDER PROJECTED CLIMATE CHANGE

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## EXTENDED ABSTRACT

Populations of piñons and junipers across the interior west have been highly dynamic over the last two centuries, undergoing an overall expansion but punctuated with regional mortality. Accumulating demographic studies across the interior west indicate the drivers of expansion and contraction of populations are compounded by regional land use legacies, but have an underlying climatic component. The key implication is that piñon and juniper distributions respond to climatic variation across spatial and temporal scales by expansion from, and contraction to, areas of long-term persistence relative to their centurial (piñons) and millennial (junipers) life spans. Individualistic climatic tolerances among piñon and juniper species lead to temporally dynamic assemblages in the landscape that vary regionally. Failure to recognize species-specific zones of contraction, expansion, and persistence across the landscape and across regions has led to controversial management practices developed for certain species under certain conditions but extrapolated to different species under disparate conditions (Romme et al. 2009). Contrasting demographics between expanding, contracting, and persisting populations of piñons and junipers enables localized field classifications of these species-specific zones and their emergent woodland types. However, differential mortality rates among piñons and junipers during the last decade indicate distribution-wide shifts in co-occurrence have already begun in response to contemporary climate change (Breshears et al. 2009). Needed, therefore, is a similar classification of woodlands at a scale relevant to global climate change (e.g., Wiens et al. 2009) to aid in identifying regional conservation priorities and provide context for extrapolating management practices, such as regeneration prescriptions.

The response of woody plant distributions to climate can be elucidated in a variety of ways, and both piñons and junipers have provided model systems for empirical and experimental investigations. Yet the physiological mechanisms underlying mortality are far from integrated at the whole-tree level (e.g., Plaut et al. 2012). Although mechanistically linking individual trees to global climate change forecasts is infeasible in this regard (Sala et al.), strong empirical relationships between growth rates and climate over the last century have been found across the greater geographic breadth of several western conifer species, including *P. edulis*, and have been extrapolated to forecast climates (Williams et al. 2010). A similar technique is to empirically relate the probability of the current presence/absence of a species to current climatic conditions often referred to as species distribution models (SDMs, Guisan and Zimmermann 2000). Such models may then be extrapolated to forecast climate change scenarios (Iverson et al. 2008, Refheldt et al. 2008).

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There are many interwoven technical and conceptual challenges to the process of creating SDMs that have received legitimate criticism. Technically, the development of SDMs relies on statistical techniques challenged by the availability of presence/absence observations and by the availability of relevant predictor variables at an appropriate scale (e.g., Weins et al. 2009). This situation is complicated further by the degree to which the potential distribution is realized. Although a species current distribution may be modeled with perfect statistical accuracies, such a static SDM may not be amenable to the application of climate change scenarios that may introduce no-analog climate conditions for which no empirical relationships currently exist for modeling purposes. A statistically accurate SDM that is built with appropriate variables will be indicative of geographic shifts in the climatic conditions in which a species is currently most competitive, but introduces the added complexity of the processes by which species track this shift with respect to biotic, topographic, and edaphic interactions. Because sessile species must track climate through completion of the life cycle, it is necessary to consider the nested nature of life stage-specific niche dimensions (i.e., the regeneration niche, Jackson et al. 2009). To address these interwoven challenges, we develop a nested scale, life history-based framework for organizing the vast and varied research addressing the life history of piñons and junipers to guide an empirical approach to build, parameterize, and interpret species-specific distribution models. Biotic interactions modify the overarching influence of climate on piñon and juniper distributions, leading to lagged or accelerated responses of individuals, landscape populations, and continental distributions. Discordance between climatic suitability and spatial distribution generates zones under pressure of expansion or contraction but held in tension by spatial constraints and biotic interactions. We delineate these tension zones under forecast climate change scenarios of the 21st century.

Technical challenges surrounding this process are minimized by using presence/absence observations from the Forest Inventory and Analysis Program (FIA) (McRoberts et al. 2005) that maintains a systematic inventory of forests across the U.S with an underlying probabilistic design. We investigated numerous environmental predictor variables hypothesized as related to the species distributions and chose the simplest expressions of seasonal temperature and moisture to avoid problems associated with forecast climatic conditions having no contemporary analog. We used Random Forests (RF) (Breiman 2001; Cutler et al. 2007), a commonly employed statistical tool for distribution forecasting.

Conceptual challenges are minimized by working with presence observations from across the entirety of each species distribution, thereby sampling the breadth of the realized distribution (Pearman et al. 2008). Absences are drawn from a biologically meaningful, spatially defined sample frame (e.g., Zarnetske et al. 2007). This sample frame addresses the implication of geographic disequilibrium between species distributions and the current climate by limiting model development to areas where the species has actually had a likely opportunity to grow and excludes areas where the species has likely never had an opportunity to grow. This constraint in absence selection avoids overfitting models, which typically leads to higher decay rates in forecast probabilities. Initial modeled distributions are limited to this model-building domain and are evaluated in their ability to describe the current, observed distribution. The initial distribution models are applied to forecast climate change scenarios through life stage-specific thresholds within spatial constraints. The modeling domain and spatial constraint are based on a review of quaternary distribution dynamics in conjunction with current demographic and dispersal studies. The life stage thresholds are empirically estimated by relating FIA plot measures of seedlings and mortality with modeled climatic suitability within the context of reviewed life history studies.

These species-specific models were applied to two climate change scenarios, following the Intergovernmental Panel on Climate Change (IPCC) storylines A2a and B2a, representing extreme and moderate global change at the time of publication (Hijmans et al. 2005). We use the Hadley Center Coupled Atmosphere-Ocean Global Circulation Model (HadCM3 GCM) as the basis of the climate projections. Climate change scenarios were applied at three 30-year time steps over the 21st century. After the initial distribution is set for each species, the life stage thresholds and spatial constraints determine the ability for distributions to track forecasted climate change. The emergent distribution is composed of a sequence of possible local extinction, recruitment, and sustained populations expected from a nested-niche model (Jackson et al. 2009). The variety of possible states across the forecast climate probabilities of each species are collapsed into classes of contraction, persistence, and expansion. With a spatial resolution of 1 km, these classes designate spatial zones reflective of distribution behavior at both a landscape/ multi-decadal scale and at a continent/ centurial scale. Shifts in the landscape are measured as changes in modeled elevation bands and correspond to shifts in the altitudinal zonation of life zones. Continental shifts in distribution are measured as changes in modeled latitudinal and longitudinal distribution and correspond to regional zones of expansion, contraction, or persistence. We present the modeled expansion and contraction as indicative of pressures corresponding to the leading and trailing edge dynamics of these distributions. The assemblage of these species distribution models, in turn, is classified into zones of species increase, decrease, or turnover.

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