PLANT FUNCTIONAL GROUPS AND SUCCESS IN A CHANGING ENVIRONMENT: MODELING PHYSIOLOGICAL NICHOES OF COLORADO PLATEAU PLANTS

by
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Quantifying the environmental and physiological niches of plant species is crucial to predicting their sensitivity to global change, and aggregating plant species by functional type is fundamental both to ecological theory and to the practicality of large-scale efforts to predict the consequences of global change. However, traditional functional types are not always predictive of individual species’ responses to change. Here, an inverse species distribution modeling approach is used to identify functionally similar species based on physiological niche in order to better anticipate the consequences of climate change on the Colorado Plateau, USA. The Colorado Plateau is a semiarid region particularly sensitive to climate change and represents the intersection of several different ecosystems with overlapping plant functional types. While seeing evidence for similarities within traditional functional groups defined by growth form and photosynthetic pathway, we identified revised functional groupings which more precisely reflect differences in tolerance of key environmental variables relevant to climate change sensitivity, including soil moisture, maximum temperature threshold, and minimum temperature threshold. One
group is sensitive to high maximum temperature and can tolerate very low soil moisture conditions. The projected ranges of these low-temperature species are small and often overlap considerably with the Colorado Plateau, but they have recently declined on the Plateau with warming temperatures. Another group includes species which have recently increased on the Colorado Plateau, and is largely unconstrained by maximum temperature and soil moisture. These results support the idea that the historical Colorado Plateau specialist niche may be threatened by warming temperatures.
ACKNOWLEDGEMENTS

I would like to acknowledge Richard Gill for his years of guidance and mentorship, Sam St. Clair and Steven Peck for their assistance in my committee, Matt Larcombe and Steven Higgins for their TTR expertise, and Sarah Spendlove, Caroline Morris, and Evan Long for help in the initial stages of modeling.
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Introduction

As anthropogenic climate change accelerates, a fundamental challenge facing plant species is the reduction or shift of their ecological niches. The concept of a niche, or the set of environmental conditions in which a species has a positive population growth rate, is a basic tenet of ecology and a key lens for understanding and predicting the responses of plant communities to large-scale environmental change (Scheele et al. 2017; Hutchinson 1957). An important way of linking plant niche to sensitivity to change, as well as a paradigm historically central to community ecology, is by identifying the role of functional traits, or the characteristics that define a plant’s strategy of growth, survival, and reproduction (Ehleringer, Cerling, and Helliker 1997; Reich et al. 2003; Suding et al. 2008; Lavorel and Garnier 2002; Noy-Meir 1973; Adler et al. 2014). Because functional traits represent a mechanistic explanation for a plant’s niche, plants with similar traits are often grouped together with the expectation of having similar responses to environmental change (Smith et al. 1997; Ehleringer, Cerling, and Helliker 1997; Noy-Meir 1973). Identifying such groups and their expected responses can be a powerful tool for predicting community and ecosystem dynamics (Lavorel and Garnier 2002; Suding et al. 2008). Not only does this make synthesizing ecological patterns easier in general, but it is also indispensable for methods such as dynamic vegetation modeling which rely on the reduced complexity of functional types, with the assumption that these groups reflect meaningful differences in species’ roles and responses to change in an ecosystem (Díaz and Cabido 1997).

However, due to the prevalence and importance of the functional group paradigm in ecology and conservation, it is important to rigorously examine these assumptions,
especially in the context of specific ecosystems. Do the shared traits typically used to separate broad functional groups, such as C$_3$ and C$_4$ photosynthesis or growth form, always reflect distinct physiological tolerances in a given environmental context? Where these functional groups overlap, and as community dynamics shift due to climate change, the responses of functional groups have not always been consistent (McCarron and Knapp 2001; Pakeman 2004; Dyer et al. 2001). This may be due to dynamic or plastic responses of individual species to different environmental conditions, varying tradeoffs between traits, or inconsistent definitions and measurements of traits (McCarron and Knapp 2001; Pakeman 2004; Dyer et al. 2001; Kraft, Godoy, and Levine 2015). Thus, relying on traditional functional group divisions to predict responses to change in a particular setting without examining the variation within these groups can be problematic.

While empirical studies of plant functional traits and responses to the environment are an important method of discovering and assessing functional groups, large-scale patterns can be more feasibly identified through another form of modeling, species distribution models (SDMs). SDMs have been widely used to incorporate the conditions found throughout a species’ observed range to characterize the breadth of the species’ niche and identify threats to this niche (Evans et al. 2016; Thuiller, Lavorel, and Araújo 2005; Schurr 2012). There are a range of SDM approaches, with the simplest models, such as Bioclim, using correlations between environmental covariates and the spatial occurrence patterns of sample species locations (Booth et al. 2014). On the other end of the spectrum are process-based models which simulate the mechanisms behind plant distributions, such as physiology and demography (Evans et al. 2016). Process-based models have been proposed as a more realistic alternative to correlative models,
but are more complex, often requiring more input data and computational resources, and may lead to overfitting of model parameters (Evans et al. 2016).

The Thornley Transport Resistance SDM (TTR), a relatively simple hybrid process-based and correlative model, provides a compromise between these approaches. TTR uses an inverse modeling approach to fit the parameters of a physiological model of plant growth (the Thornley-transport resistance model) with species distribution data and multiple environmental covariates, and can then simulate growth at a location based on its environmental profile (Higgins et al. 2012). As a result, TTR has the unique advantage of explicitly modeling the parameters of a plant’s physiological niche, or its physiological niche dimensions, in addition to projecting a geographical range. This information is highly valuable for addressing questions about specific environmental tolerances, particularly within or between groups. Higgins and Richardson (2014) used this approach to investigate the niche breadth of invasive species as compared to introduced and naturalized species, addressing the hypothesis that broad tolerance to certain environmental variables can predict invasiveness. Similarly, the projected physiological niches can be compared within functional groups to assess whether these groups truly reflect similar physiological niches and thus predict sensitivity to change. Not only is comparison of *a priori* groups possible, but also the identification of groups *a posteriori* based on niche similarity. This should result in a more accurate assessment of actual functional groupings and environmental sensitivity on a group level.

The Colorado Plateau represents an ideal study system to use physiological niche modeling to identify plant functional groups with the goal of predicting sensitivity to global change. Located in the southwestern United States, the Colorado Plateau is at the
intersection of several biomes, including the Mojave Desert, a warm desert, and the Great Basin Desert, a cold desert, with influences from the short grass steppe and the Sonoran Desert. It includes both grasslands and shrublands. As a result, the Plateau flora is diverse, and contrasting functional groups overlap considerably in range (Witwicki, Munson, and Thoma 2016). The sensitive semiarid region has also already seen the effects of climate change (Munson 2013; Lauenroth and Bradford 2006). Long-term vegetation monitoring studies have revealed patterns in species-specific responses to recent change (Munson et al. 2011; Munson 2013). A USGS study of Colorado Plateau national parks found that shrubs have expanded with increases in temperature while perennial grasses have decreased over the past two decades, although this depended on site characteristics (Munson et al. 2011). This kind of shift in community distribution leads to major changes in ecosystem function, further altering the water balance (Bradford et al. 2014), reducing plant productivity and forage for livestock and wildlife, and increasing erosion (Munson 2013; Munson, Belnap, and Okin 2011). These changes may be irreversible (Munson 2013). Being able to quantify and predict plant species’ sensitivities to climate change is thus crucial, as is determining if traditional functional groups such as grasses and shrubs will reliably respond in similar ways.

Native desert plants on the Colorado Plateau can be grouped into several broad categories along functional lines relevant to plants’ response to climate change. At the broadest level, the dominant growth forms in the region, shrub and perennial grass, represent a set of traits such as rooting depth, woodiness, longevity, and growth rate that may, as the USGS monitoring study suggests, impact tolerance to elements of climate change such as water stress (Noy-Meir 1973; Munson et al. 2011). Shrubs, typically with
deeper roots and slower growth than grass, have the potential for higher drought tolerance (Noy-Meir 1973). Photosynthetic pathway, either C₃ or C₄, is also highly relevant to changes in temperature, as C₄ photosynthesis is more efficient in higher temperatures and has been shown to have a strong geographic association with temperature (Ehleringer 1997). It is possible to identify other functional groups, but the validity and importance of the shrub-grass and C₃-C₄ distinctions are well-supported (Smith et al. 1997). This study will examine how relevant these traits are to patterns in Colorado Plateau plant niches and sensitivity to climate change.

The goal of this study is to identify functionally similar species based on physiological niche to better anticipate the consequences of climate change on the Colorado Plateau. Using an inverse modeling approach that fits a physiologically based growth model to known distributional data, we can delimit each species’ niche across key climatic parameters relevant to different functional strategies in a semiarid environment. We structure our analysis to capture the key species of the Colorado Plateau in four distinct a priori groups—C₃ shrub, C₃ grass, C₄ shrub, C₄ grass—to assess the validity of these functional groupings. Our modeling approach defines a niche based on the physical environmental space where plant growth is feasible, which also delineates the species’ potential geographical range. Comparing the dimensions of plant niches in environmental and geographical space then allows us to determine whether species within the same functional groups share similar niches, and whether these appear to be driven by expected functional tolerances. These niche dimensions also provide a way to explore a posteriori whether non-traditional physiological groupings exist that may have implications for identifying species with higher sensitivity to global change. Additionally,
we examine the relationship between the size of geographical range projections made by the model and the constraints represented by underlying physiological niches. Finally, we determine the level of endemism of each species relative to the Colorado Plateau based on the overlap of their ranges with the Colorado Plateau.

In order to achieve the broad goal of this study, we identified three objectives:

a) Determine whether the physiological niches of Colorado Plateau species coincide with traditional functional groups, or whether there are previously unrecognized groupings that better describe patterns in species’ environmental tolerances.

b) Identify physiological constraints explaining species’ geographical range sizes and potential sensitivity to climate change.

c) Identify geographical and physiological niche variables indicative of Colorado Plateau endemism.

**Methods**

*Model*

The TTR species distribution model fits the parameters of a mechanistic physiological model of plant growth (the Thornley Transport-Resistance model) via environmental covariates in order to infer the physiological niche of the species. The original TTR model simulates carbon, nitrogen, and biomass allocation between the roots and shoots of a plant over time as a function of root-shoot gradients (Fig. 1, described in Higgins et al. 2012). In their species distribution implementation of the model, Higgins et al. (2012) incorporate environmental forcing into TTR via equations describing the
influence of environmental variables, including light, temperature, soil moisture, and soil nitrogen, on the physiological processes in the plants (Fig 2). The ideal values of the parameters of these functions are inferred from the environmental conditions found at known occurrence locations for a species by maximizing the likelihood that plants will grow in these locations and minimizing their growth in absence locations. In other words, environmental parameters are found which best explain the observed distribution of the species. This process allows the projected geographical species distribution to be constrained by physiological thresholds of the plant such as the optimal temperature window for photosynthesis, providing a more robust prediction of species occurrence, as well as quantifying the physiological niche.

Figure 1. a) The TTR model as modified by Higgins et al. 2012. The top half of the diagram with solid blue boxes represents the core TTR model and the processes influencing carbon and nitrogen allocation in plant roots and shoots, and the open boxes below are the environmental variables added to the model by Higgins et al. b) Illustration of a trapezoidal function linking environmental covariate, maximum temperature, with physiological process, photosynthesis.
Physiological niche is defined by the parameters that TTR fits for the set of environmental covariates coupled with physiological processes. Trapezoidal functions delimit the upper and lower bounds on these processes as a function of a given variable (Fig. 2b). Covariate-process pairs include the effect of average monthly maximum temperature, radiation, soil moisture, and shoot nitrogen on carbon uptake, i.e. photosynthesis; the effect of mean temperature, soil moisture, and soil nitrogen on nitrogen uptake; the effect of minimum temperature on growth; and the effect of mean temperature on respiration (Fig. 1). Several of the pairs, namely maximum temperature-carbon uptake, soil moisture-nitrogen, and minimum temperature-growth, have two free parameters at each of the lower and upper limits of the trapezoidal window, while the rest of the pairs have two free parameters only at the lower limit and are assumed to be unconstrained above the minimum thresholds.

Although the TTR physiological model outputs biomass-based abundance values, in reality, abundance is affected by factors not included in the model such as herbivory. To avoid unrealistic assumptions, Higgins et al. (2012) proposed the transformation of abundance values into probability of presence or absence via the complementary log-log function. Presence or absence is then predicted based on the probability threshold that maximizes the proportions of true positive and true negative predictions.

Model performance was evaluated using false positive and false negative rates. A low false negative rate is more important than a low false positive rate, as a false positive could represent dispersal limitation or survey limitations, while a false negative is a confirmed error. We felt confident in model fit when false negatives fell below a 15% threshold.
Plant species

The plant species included in the study represent the dominant members of the Colorado Plateau and include representative species from all combinations of two major *a priori* functional groupings: shrubs and grasses, and C$_3$ and C$_4$ photosynthesis. The categories are fairly evenly represented except for C$_4$ shrubs because of the uncommonness of this combination.

<table>
<thead>
<tr>
<th>Species</th>
<th>Photosynthesis</th>
<th>Growth form</th>
</tr>
</thead>
<tbody>
<tr>
<td>Achnatherum hymenoides</td>
<td>C$_3$</td>
<td>grass</td>
</tr>
<tr>
<td>Achnatherum lettermanii</td>
<td>C$_3$</td>
<td>grass</td>
</tr>
<tr>
<td>Hesperostipa comata</td>
<td>C$_3$</td>
<td>grass</td>
</tr>
<tr>
<td>Pascopyrum smithii</td>
<td>C$_3$</td>
<td>grass</td>
</tr>
<tr>
<td>Poa fendleriana</td>
<td>C$_3$</td>
<td>grass</td>
</tr>
<tr>
<td>Aristida arizonica</td>
<td>C$_4$</td>
<td>grass</td>
</tr>
<tr>
<td>Chondrosium eriopodum</td>
<td>C$_4$</td>
<td>grass</td>
</tr>
<tr>
<td>Chondrosium gracile</td>
<td>C$_4$</td>
<td>grass</td>
</tr>
<tr>
<td>Hilaria jamesii</td>
<td>C$_4$</td>
<td>grass</td>
</tr>
<tr>
<td>Muhlenbergia pungens</td>
<td>C$_4$</td>
<td>grass</td>
</tr>
<tr>
<td>Sporobolus airoides</td>
<td>C$_4$</td>
<td>grass</td>
</tr>
<tr>
<td>Sporobolus cryptandrus</td>
<td>C$_4$</td>
<td>grass</td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>C$_3$</td>
<td>shrub</td>
</tr>
<tr>
<td>Coleogyne ramosissima</td>
<td>C$_3$</td>
<td>shrub</td>
</tr>
<tr>
<td>Ephedra viridis</td>
<td>C$_3$</td>
<td>shrub</td>
</tr>
<tr>
<td>Ericameria nauseosa</td>
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<td>shrub</td>
</tr>
<tr>
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<td>C$_3$</td>
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</tr>
<tr>
<td>Krascheninnikovia lanata</td>
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<tr>
<td>Sarcobatus vermiculatus</td>
<td>C$_3$</td>
<td>shrub</td>
</tr>
<tr>
<td>Atriplex canescens</td>
<td>C$_4$</td>
<td>shrub</td>
</tr>
<tr>
<td>Atriplex confertifolia</td>
<td>C$_4$</td>
<td>shrub</td>
</tr>
</tbody>
</table>

Table 1. Colorado Plateau plant species included in study and functional groupings.
Data

Species occurrence data for each species were obtained from the Geographic Biodiversity Information Facility (GBIF), which is an aggregation of georeferenced herbaria records, and were cleaned to remove points with inaccurate coordinates. The number of valid georeferenced occurrence points per species varied from 200 to over 3000. TTR requires pseudo-absence or background points randomly sampled from the region surrounding known occurrence points if verified absence data is lacking. For each species, 2000 background points were sampled within 5 degrees of the outermost presence points from 0.5-degree grid cells not containing a presence point. Because the false positive to false negative ratio is used in the fitting of the model, TTR is sensitive to the density of background point distribution. When 2000 points were selected from within 1 degree of outermost points, the model would not converge in many cases, and when selected from the extent of North America, the projected ranges were unrealistically broad, likely due to the coarser resolution of background conditions represented by these points. A 5-degree radius allowed successful model fitting without inflating most ranges significantly.

Environmental forcing data included 30-year normal minimum, maximum and mean monthly temperatures from the WorldClim gridded climate dataset (Hijmans et al. 2005); soil moisture and solar radiation from Trabucco and Zomer’s (2010) global soil water balance geospatial database; and soil nitrogen data from the Global Soils Data Task Group (2000) Global Gridded Surfaces of Selected Soil Characteristics.
Analysis

Physiological niche. Our first objective was to assess the similarity of TTR physiological niche output within functional groups and to identify other potential groupings. Physiological niche is defined for each covariate-process pair by trapezoidal functions which can be compared in terms of midpoint, breadth, or the individual parameters which define the points in the trapezoid. Niche midpoint was compared across functional groups for each covariate-process pair via Welch’s ANOVA for unbalanced variances due to the unevenness in the group sizes, using the car package in R. Significant tests were followed by the Games-Howell post-hoc test. Physiological niche values will be reported on a normalized scale.

Physiological niche breadth for each variable was estimated by finding the difference between the average of the trapezoidal boundaries on either side. Niche breadth was also compared between groups via Welch’s ANOVA.

To identify alternative a posteriori functional groups based on physiological similarity, we performed the k-means clustering algorithm, using as input the 24 parameters which define the total niche dimensions for each species. The algorithm works by calculating the total distance between instances in all the provided attributes (the 24 parameters in this case), grouping instances with the closest of \( k \) random centroids (or means), and iteratively updating the centroids and regrouping until the clusters no longer change. As \( k \) is arbitrary, there are multiple methods for identifying an optimal \( k \) which maximizes between-group diversity and minimizes within-group diversity. We used the Bayesian Information Criterion for model selection, a lower value of which typically designates a better division (Jombart and Collins 2015).
The k-means clustering algorithm is also a precursor to the discriminant analysis of principal components (DAPC). DAPC is similar to principal component analysis (PCA), but it is performed on pre-determined groups in order to identify discriminant functions (similar to principal components) which maximize variation between groups and minimize variation within groups, rather than maximizing the total variance as PCA does (Jombart, Devillard, and Balloux 2010). These discriminant functions can be interpreted based on their loadings, or the original variables which contribute the most to the makeup of the function. We performed DAPC using the R package adegenet to quantify the separation of the *a posteriori* clusters resulting from k-means and identified the loading variables of the first two discriminant functions to determine the most important niche variables separating the *a posteriori* groups. The niche midpoints and breadths of *a posteriori* groups were also compared via Welch’s ANOVA.

*Geographical niche.* Our second objective was to synthesize physiological niche and projected geographical range characteristics to identify variables contributing to functional groups’ sensitivity. In addition to plotting the projected range, the geographical niche size can also be described quantitatively as the proportion of 0.5-degree grid cells in a fixed subset of North America that were included in the range. Another measure is the north-south spread, or the distance in degrees latitude between the northernmost and southernmost points of the range. A large overall potential range size indicates environmental generalists and a higher chance of having inhabitable range as climate change progresses, with a high north-south spread and high northernmost point particularly indicative of migratory potential.
Our third objective was to identify ranges and niches measuring the degree of endemism to the Colorado Plateau. Toward this objective, we calculated the proportion of grid cells in a species’ projected range which overlapped with the Colorado Plateau. The Colorado Plateau boundary was defined by the Nature Conservancy ecoregions.

Results

Model performance

The model performed well overall when pseudo-absence points were selected from the area within five degrees of outer presence points. The average false negative rate was 0.069 and the average false positive rate was 0.231 (Table 2). One species, *Coleogyne ramosissima*, did not converge at a 5-degree radius for background points; the model output using continental-scale background points is included. One species originally included in the input was excluded from the analysis, *Ephedra torreyana*, because the model could not converge (likely because of too few presence data). *Chondrosom gracile* was the only species whose false negative rate was above our threshold of 0.15, indicating a relatively poor model fit.
<table>
<thead>
<tr>
<th>Species</th>
<th>True Positive</th>
<th>False Negative</th>
<th>True Negative</th>
<th>False Positive</th>
<th>Range Size</th>
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</thead>
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<tr>
<td><em>Achnatherum hymenoides</em></td>
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Table 2. False positive, true negative, false negative, and true positive rates and range sizes (proportion of grid cells of fixed subset of North America) of TTR range projections for each species.

**Physiological niches**

**Patterns in a priori functional groups.** Our first objective was to assess the alignment of physiological niches with *a priori* functional groups (Fig. 2). We expected that C₃ and C₄ groups would separate on temperature, soil and leaf nitrogen, and soil water axes because of fundamental differences in sensitivity to high-temperature photorespiration, nitrogen use efficiency, and water use efficiency (Ehleringer, Cerling, and Helliker 1997). We anticipated that grasses and shrubs would separate on soil moisture axes (Noy-Meir 1973). While there was no statistically significant difference
between the four groups in niche midpoints and breadths for any variable, soil moisture-nitrogen uptake was significantly lower in shrubs, with an average normalized midpoint of 0.176, than in grasses, which had an average midpoint of 0.331 (p= 0.02), consistent with predictions (Fig 3a).

The maximum temperature-carbon uptake niche showed tendencies that were consistent with expectations, as shown by the median values, but included individual species which disrupted these patterns (Fig 2). Consequently, there were no significant differences between C₃ and C₄ groups (Fig 3a,b). C₃ grasses generally had wider maximum temperatures niches than C₄ grasses, with a normalized median midpoint of 0.70 and a median breadth of 0.45 (Fig 2). *Hesperostipa comata* was very different from typical C₃ grasses with maximum temperature ranges exceptionally low and narrow, with a midpoint of 0.32 and a breadth of 0.39. All but two C₄ grasses were restricted to the upper half of the temperature window, between 0.5 and 1 on the normalized temperature scale, with a median maximum temperature midpoint of 0.82 and median breadth of 0.29; *Hilaria jamesii* and *Muleberghia pungens* were instead between 0.2 and 0.65 (Fig 2). C₃ shrubs were generally restricted to the lower half or middle of the maximum temperature window, carbon uptake becoming limited by 0.7; one exception, the gymnosperm *Ephedra viridis*, had a maximum temperature niche beginning at 0.57 and unconstrained on the upper end. For the effect of soil moisture on nitrogen uptake, C₃ and C₄ groups did not differentiate (Fig 3b). However, several grasses in both the C₃ and C₄ categories had notably low soil moisture-N requirements, including *Hesperostipa comata, Hilaria jamesii, Chondrosom eripodium*, and *Muleberghia pungens*, which had midpoints between 0.15 and 0.19 and breadths between 0.17 and 0.26 (Fig. 2). One C₃ grass,
*Achnatherum lettermanii*, had a significantly higher midpoint than any other species at 0.70. Other variables showed considerable variation and no distinctive pattern separating the functional groups.

Figure 2a. The physiological niche dimensions for carbon uptake inferred by TTR from species distribution for 21 Colorado Plateau species. Environmental covariates are grouped by physiological process, labelled at the bottom of each group of columns. For each trapezoidal plot, covariates are on the x-axis with marked ranges and the process response variable is on the y-axis, from 0 (completely inhibited) to 1 (not limited). Temperatures are in degrees C, soil moisture is volumetric (0-100), radiation is in mm per day, shoot nitrogen (Nshoot) is a concentration. Species are labelled by 4-letter code with the first two letters from the genus and second two from the species. Functional groups are indicated by color.
Figure 2b. Additional physiological niche dimensions inferred by TTR from species distribution for 21 Colorado Plateau species. Environmental covariates are grouped by physiological process, labelled at the bottom of each group of columns. For each trapezoidal plot, covariates are on the x-axis with marked ranges and the process response variable is on the y-axis, from 0 (completely inhibited) to 1 (not limited). Temperatures are in degrees C, soil moisture is volumetric (0-100), nitrogen (Nsoil) is %N in topsoil. Species are labelled by 4-letter code with the first two letters from the genus and second two from the species. Functional groups are indicated by color.
Fig 3. Midpoint means and confidence intervals for normalized a) soil moisture-nitrogen uptake for grasses and shrubs (p = .02), b) soil moisture for all four groups (non-significant), c) maximum temperature-carbon uptake for C3 and C4 groups (non-significant), d) maximum temperature-carbon uptake for all four a priori groups (non-significant).

A posteriori functional groups

To identify a grouping which would better separate the physiological variation found within a priori functional groups, we performed the k-means clustering algorithm using the 24 parameters defining the niche dimensions for each species to determine the overall similarity between species. We used the Bayesian Information Criterion to check for an optimal cluster number (k), and while the lowest (best) score occurred at the maximum k, or one less than the number of species, the initial downward slope in score from k = 1 began to level off around k = 4 and k = 5 (Fig. 4). Because we began with
four *a priori* functional groups, we chose to proceed with $k = 4$, with which the algorithm identified the clusters listed in Table 3.

Fig 4. Bayesian Information Criterion for each number of possible clusters for the species based on niche parameters. A lower BIC indicates better fit.

<table>
<thead>
<tr>
<th>Species</th>
<th>Functional group</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Group 1: Shrub-like</strong></td>
<td></td>
</tr>
<tr>
<td><em>Achnatherum hymenoides</em></td>
<td>C$_3$ grass</td>
</tr>
<tr>
<td><em>Sporobolus airoides</em></td>
<td>C$_4$ grass</td>
</tr>
<tr>
<td><em>Artemisia tridentata</em></td>
<td>C$_3$ shrub</td>
</tr>
<tr>
<td><em>Ericameria nauseosa</em></td>
<td>C$_3$ shrub</td>
</tr>
<tr>
<td><em>Gutierrezia sarothrae</em></td>
<td>C$_3$ shrub</td>
</tr>
<tr>
<td><em>Krascheninnikovia lanata</em></td>
<td>C$_3$ shrub</td>
</tr>
<tr>
<td><em>Sarcobatus vermiculatus</em></td>
<td>C$_3$ shrub</td>
</tr>
<tr>
<td><em>Atriplex canescens</em></td>
<td>C$_4$ shrub</td>
</tr>
<tr>
<td><em>Atriplex confertifolia</em></td>
<td>C$_4$ shrub</td>
</tr>
<tr>
<td>Species</td>
<td>Functional group</td>
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<tr>
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<tr>
<td><strong>Group 2: Low-Temperature</strong></td>
<td></td>
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<tr>
<td><em>Hesperostipa comata</em></td>
<td>C₃ grass</td>
</tr>
<tr>
<td><em>Hilaria jamesii</em></td>
<td>C₄ grass</td>
</tr>
<tr>
<td><em>Muhlenbergia pungens</em></td>
<td>C₄ grass</td>
</tr>
<tr>
<td><em>Coleogyne ramosissima</em></td>
<td>C₃ shrub</td>
</tr>
<tr>
<td><strong>Group 3: High Temperature Grass</strong></td>
<td></td>
</tr>
<tr>
<td><em>Pascopyrum smithii</em></td>
<td>C₃ grass</td>
</tr>
<tr>
<td><em>Poa fendleriana</em></td>
<td>C₃ grass</td>
</tr>
<tr>
<td><em>Aristida arizonica</em></td>
<td>C₄ grass</td>
</tr>
<tr>
<td><em>Chondrosum eriopodium</em></td>
<td>C₄ grass</td>
</tr>
<tr>
<td><em>Chondrosum gracile</em></td>
<td>C₄ grass</td>
</tr>
<tr>
<td><em>Sporobolus cryptandrus</em></td>
<td>C₄ grass</td>
</tr>
<tr>
<td><em>Ephedra viridis</em></td>
<td>C₃ shrub</td>
</tr>
<tr>
<td><strong>Group 4: Achnatherum lettermanii</strong></td>
<td></td>
</tr>
<tr>
<td><em>Achnatherum lettermanii</em></td>
<td>C₃ grass</td>
</tr>
</tbody>
</table>

Table 3. Species grouped by cluster as determined *a posteriori* by the k-means clustering algorithm. *A priori* functional group based on growth form and photosynthetic pathway is also listed. Group numbering is arbitrary.

*A posteriori* cluster 1 captures the shrub functional group plus additional grasses, and cluster 3 captures high thermal tolerant grasses and a single shrub (EPVI). The shrub cluster also includes a C₃ grass (*Achnatherum hymenoides*) and C₄ grass (*Sporobolus airoides*). C₃ grasses are distributed throughout the clusters. Cluster 2 has an eclectic mix of *a priori* functional types, but all four species are dominants in the Colorado Plateau community. Cluster 4 consists of a single C₃ grass, *Achnatherum lettermanii*. 
Discriminant analysis of principal components allowed us to quantify the separation of these \textit{a posteriori} groups along discriminant function axes and to identify the loading variables which contributed the most variance to these principal components (Fig. 5). Axis 1 corresponds primarily to the lower limit of the effect of soil moisture on nitrogen uptake, and all four groups are distinct on this axis. Axis 2 corresponds to the second point in the lower limit of soil moisture-nitrogen uptake, the upper limit of maximum temperature-carbon uptake, and the lower limit of the effect of minimum temperature on growth. Clusters 1 and 3 did not separate along this axis, but clusters 2 and 4 were distinct. The third axis corresponds to the upper limit of soil moisture on nitrogen and the upper limit of mean temperature-nitrogen uptake.

![Figure 5. Separation of \textit{a posteriori} groups along the first two discriminant function axes.](image)

These variables provide the physiological basis for the differences between the clusters. Welch’s ANOVA for the first three \textit{a posteriori} functional groups (excluding group 4, with only one member) confirmed significant differences in niche midpoint between at least two of the groups in each of these variables (Fig. 6). Based on Welch’s
ANOVA and the Games-Howell test, there is a significant difference between all three of the groups with multiple members for the effect of maximum temperature on carbon uptake (p<.0001; Fig. 6a) and the effect of minimum temperature on growth (p < .0001; Fig. 6b). Soil moisture required for nitrogen uptake is significantly lower for group 2 than group 3, (p = .019; Fig. 6c) and radiation for photosynthesis is lower in group 2 than both 1 and 3 (p < .0001; Fig. 6d).

Overall, cluster 1, with a core of shrubs, is characterized by medium average maximum and minimum temperature midpoints—0.67 for maximum temperature and 0.7 for minimum temperature—and a low average midpoint of soil moisture for nitrogen uptake, 0.19 (although the niche breadth of this variable is fairly wide). Subsequently, cluster 1 will be called the shrub-like group. Cluster 2 is characterized by a low average maximum temperature of 0.45, low average soil moisture at 0.16, and relatively high minimum temperature at 0.85. Cluster 2 will be called the low temperature group. Cluster 3 is characterized by high or unconstrained maximum temperature with a midpoint of 0.84, a relatively high average soil moisture midpoint of 0.35, and relatively low minimum temperature midpoint at 0.54. Cluster 3 will be called the high temperature grass group. The single member of cluster 4 is distinguished by its high soil moisture midpoint, 0.7 as well as low minimum temperature, 0.4, and will be referred to by its species name, *Achnatherum lettermanii*. 
Figure 6. Means and 95% confidence intervals for the normalized midpoint of a) maximum temperature-carbon uptake, b) minimum temperature-growth, c) soil moisture-nitrogen uptake, d) radiation-carbon uptake, for *a posteriori* functional groups.

*Niche breadth*

Our second objective was to identify patterns in functional groups’ physiological tolerances indicative of sensitivity to climate change. Because a wider niche breadth indicates tolerance of a wider range of conditions in a species, narrow niche breadth is associated with sensitivity. Niche breadth was not significantly different across *a priori* functional groups in any variable. For the first three *a posteriori* functional groups, two variables showed a significant difference in breadth: the effect of soil moisture on nitrogen uptake (p = .014; Fig. 7a) and the effect of radiation on carbon uptake (p < .0001; Fig. 7b). A Games-Howell post hoc test showed the low temperature group, with
an average normalized soil moisture-nitrogen uptake niche breadth of 0.198, to be significantly lower than the high temperature grass group, with an average normalized breadth of 0.579. The shrub-like group’s average normalized soil moisture breadth was 0.335 and *Achnatherum lettermanii*’s was 0.596.

The low temperature group was significantly higher in radiation niche breadth, at 0.7, than either the low temperature group, at 0.39, and the high temperature grass group, at 0.23 (Fig. 7b).

![Figure 7](image_url)

**Figure 7.** Means and 95% confidence intervals for the normalized niche breadth of a) soil moisture’s effect on nitrogen uptake and b) radiation on carbon uptake in the *a posteriori* functional groups.
Figure 8. Boxplots of normalized niche breadths found in *a posteriori* groups for each physiological niche variable.

**Geographical niche**

In addition to identifying potential sensitivity based on physiological niche, we examined the differences between the groups’ geographical range sizes, small ranges being another indication of sensitivity (Fig. 9, Table 2). Geographical range size, reported by proportion of 0.5-degree grid cells in a fixed subset of North America, did not differ significantly between *a priori* functional groups. However, range size did differ significantly between the first three *a posteriori* groups (p = .007; Fig. 10). A Games-Howell test showed that the shrub-like group, with an average range size of 0.15, was
significantly different than the low temperature group, with an average of 0.059, while the high temperature grass group, average 0.12, varied widely and was not significantly different from either group. *Achnatherum lettermanii*, has a range size of 0.045.

Mean latitudinal spread was not significantly different between the groups due to high variance, but showed a trend toward higher spread in the shrub-like group, which had an average spread of 36.2 degrees latitude compared to 16.4 degrees for the low temperature group, 24.4 degrees for the high temperature grass group, and 12.9 degrees for *Achnatherum lettermanii*.

The relationship between physiological niche breadth and geographical range size was not significant in any variable.

![Group 1: Shrub-like](image)

**Fig. 9a.** TTR projected ranges for *a posteriori* group 1. Color corresponds to *a priori* functional group. Black outline is Colorado Plateau boundary.
Group 2: Low temperature

Group 3: High temperature grass

Group 4: *Achnatherum lettermanii*

Fig. 9b. TTR projected ranges for *a posteriori* groups 2-4. Color corresponds to *a priori* functional group. Black outline is Colorado Plateau boundary.
Colorado Plateau niche

Our final objective was to identify the relative importance of the Colorado Plateau to the ranges of the functional groups, informing both their level of endemism to the Colorado Plateau niche and the most important variables determining Colorado Plateau specialism. Mean overlap of projected range with the Colorado Plateau, in the form of percent of total range made up by the Colorado Plateau, did not differ significantly among a priori or a posteriori groups. Although the low temperature group had a higher mean percent overlap than the other a posteriori groups, variance was high (Fig. 11).

There was a significant negative relationship between soil moisture-nitrogen uptake niche breadth and Colorado Plateau overlap, however; a linear regression had a slope of -0.137 with a p-value of 0.017 (Fig. 12a). The midpoint of minimum temperature for growth was also significantly related to Plateau overlap, with a slope of 1.202 (p = .031; Fig 12b).

Figure 10. Means and 95% confidence intervals of range size (proportion of North America grid cells) by a posteriori group.
Figure 11. Means and 95% confidence intervals of percent of species total range made up by Colorado Plateau for *a posteriori* groups

Figure 12. a) Relationship between niche breadth in the effect of soil moisture on nitrogen uptake and the percent of species’ range made up by Colorado Plateau. b) Relationship between normalized midpoint of minimum temperature for growth and the percent of species’ range made up by Colorado Plateau.
Discussion

The purpose of this study was to predict the potential sensitivity of key Colorado Plateau species to climate change by determining the physiological patterns underlying plants’ physiological and geographical niches. We identified revised functional groupings which reflect differences in tolerance of key environmental variables relevant to climate change sensitivity, including soil moisture, maximum temperature threshold, and minimum temperature threshold. These novel functional groupings also vary significantly in physiological niche breadth and in geographical range size. A shrub-dominated group with medium maximum temperature thresholds and low soil moisture requirements for nitrogen uptake has consistently large range size, while a group that is sensitive to high maximum temperature and can tolerate very low soil moisture conditions has small average range size. The projected ranges of the low-temperature species often overlap considerably with the Colorado Plateau, and these species, including the grassland dominants *Hilaria jamesii* and *Hesperostipa comata*, have recently declined on the Plateau with warming that has already occurred (Munson et al. 2011). On the other hand, a third group, which is dominated by C₄ grasses, is largely unconstrained by maximum temperature, and has a wide soil moisture niche breadth, includes species which have recently increased on the Colorado Plateau (Munson et al. 2011). These results indicate that while multiple physiological niche dimensions can promote geographic generalism, the historical Colorado Plateau specialist niche may be threatened by warming temperatures.

Our first objective in examining physiological niche was to determine whether traditional functional groups reflect actual physiological tolerances. Our results have
mixed implications for the utility of broad functional traits in delimiting groups that reflect similar physiological tolerances. The fact that a majority of C₃ shrubs grouped together in *a posteriori* clustering, as did C₄ grasses, indicates that these traits do often confer physiological similarity. Notably, shrubs had statistically significantly lower soil moisture-nitrogen uptake niches than grasses, supporting the traditional assumption that shrubs have better tolerance of low soil moisture (Noy-Meir 1973). Although the effect of soil moisture on carbon uptake was not significantly different, soil moisture-nitrogen uptake as modelled by TTR may be a better proxy for soil moisture’s constraint on plant distributions because it is a four-parameter variable in TTR, while soil moisture-carbon uptake has only two parameters, and because nitrogen uptake is tied to biomass addition in the model, indicating conditions conducive to growth. This difference in soil moisture thresholds between grasses and shrubs is thus a meaningful indicator of functional differences.

At the same time, however, these categories obscure other meaningful differences in species such as *Ephedra viridis*, which has a much higher maximum temperature threshold than the rest of the C₃ shrubs, making it more similar to most C₄ grasses. Two C₄ grasses, *Hilaria jamesii* and *Muhlenbergia pungens*, were set apart from other C₄ grasses by low maximum temperature thresholds, while retaining drought tolerance. Meanwhile, C₃ grasses did not sort together in *a posteriori* clustering, and C₄ shrubs clustered with C₃ shrubs. *Achnatherum lettermanii*, a C₃ grass, occupies a niche not shared by any other of these Colorado Plateau species in its high soil moisture requirements and low minimum temperature threshold. The lack of full correspondence between inferred physiological niche and traditional functional groups implies that there
are other criteria than these broad trait categories which are mediating environmental
tolerances and may be more useful in grouping species.

The variation within grass and shrub groups is not entirely surprising, because
although they have very different trait-based strategies, they coexist on a regular basis in
mixed grass- and shrublands. Based on the extent to which distributions of species in
these categories overlap, it is intuitive that their physiological tolerances would sort based
on other factors. Perhaps more surprising is the failure of C₃ and C₄ species to sort clearly
along the maximum temperature niche. While several C₄ grasses are the core of the high-
temperature group, there were also several C₃ plants in this group and, as mentioned, C₄
plants in the lower range. Like shrubs and grasses, C₃ and C₄ plants occur together on the
Colorado Plateau, but tend to be phenologically separated by season (Witwicki, Munson,
and Thoma 2016). Specifically, C₄ grasses tend to grow later in the summer when
temperatures are warmer but when their higher water use efficiency allows them to take
advantage of soil moisture, while C₃ grasses take advantage of cool, wet springs
(Witwicki, Munson, and Thoma 2016). TTR uses monthly climate data and a daily
timestep for plant growth, so this seasonality should be captured (Higgins et al. 2012).
Thus, our results indicate that some C₄ grasses (*Hilaria jamesii* and *Muhlenbergia
pungens*) have adapted to a cooler temperature niche on the Colorado Plateau, perhaps
through other traits that make them competitive with C₃ grasses at cooler temperatures,
allowing them to grow during the spring and fall when there is sufficient soil moisture.
The C₄ shrubs may be constrained by other variables such as soil salinity, as they are
halophytes. Although C₃ plants are traditionally assumed to have a wider physiological
tolerance and potential range than C₄ plants, the variation in both categories in niche
breadth and range size of these species shows that this is a simplistic assumption, especially in the context of the semiarid Southwest.

The anomalies in traditional functional groups we identified on the Colorado Plateau support the importance of defining sensitivities of physiologically defined groups in addition to traditional functional types. This was the focus of our remaining objectives, both in the context of physiological niche and Colorado Plateau endemism. Synthesizing physiological niche characteristics with geographical patterns revealed a compelling connection between geographical occurrence and niche-driven sensitivity on the Colorado Plateau. The shrub-like group, with a low, but fairly broad, soil moisture niche, also has significantly larger projected range sizes than the low temperature group, which has low maximum temperature and soil moisture thresholds and high minimum temperature threshold. The low temperature group has a higher degree of endemism on the Colorado Plateau and its species are known to be historically dominant Plateau species. Taken together, this suggests that the shrub-like group is made up of generalists while the low temperature group species are Colorado Plateau specialists. It also suggests that Colorado Plateau specialists are historically characterized by high drought tolerance, lower maximum temperature thresholds and higher minimum temperature thresholds. This is supported by the significant negative relationship between soil moisture niche breadth and percent of range overlap with the Colorado Plateau. CP dominants are tightly adapted to low soil moisture.

However, several of the species in this specialist group have been shown to be on the decline with increasing temperature on the Colorado Plateau in recent years (Munson et al. 2011). On the other hand, the high temperature grass group, which varies
considerably in range size and has low average Colorado Plateau overlap, but which is clearly distinguished by its high maximum temperature threshold and broad soil moisture niche, includes species which have been increasing in population on the Colorado Plateau with increasing temperature (Munson et al. 2011). This is consistent with the clear differentiation in maximum temperature niche between these groups, with the high temperature grass group tolerating much higher maximum temperatures than the low temperature group. This correspondence between physiologically defined group and observed sensitivity to climate change is a striking example of the power of defining functional groups by physiological tolerances and the potential of this approach to provide predictive information about sensitivity to environmental change.

Although predicting future sensitivity would require projected climate scenarios rather than the historical normals used in this analysis, quantifying species’ physiological niches and identifying variables that differentiate these niches between groups can help generate hypotheses about the most limiting factors of species’ ranges which may be subjected to change. For example, species with higher maximum temperature thresholds such as those in the high temperature grass group are less likely to be physiologically constrained by warming than species with lower temperature niches such as those in the low temperature group. Soil moisture is another variable empirically important in a semiarid environment and also important in separating these groups, particularly by niche breadth. Although a narrow niche is generally indicative of higher sensitivity (Thuiller, Lavorel, and Araújo 2005), if the niche is centered in a part of the range of conditions forecast to become more prevalent, as it is for the soil moisture conditions typically found in the low temperature group, species with these tolerances may experience an increase in
geographical range where they are competitive. On the other hand, groups with a broader
niche that includes low soil moisture, which is true for most of both the medium and low
temperature groups, may still be competitive in handling drought while also gaining or
maintaining favorable niches in other variables.

If growth form and photosynthetic pathway do not broadly predict physiological
tolerances, what physiological traits are responsible for the physiological patterns
inferred from occurrence data? Physiological tolerances are still likely to be mediated by
physiological functional traits which may be shared by species with similar niches. For
example, *Ephedra viridis*, in addition to being a C₃ shrub, is a gymnosperm with vessel
cell vasculature, and also has photosynthetic stems and scale-like leaves. Although the
grasses which *E. viridis* groups with in this analysis are not gymnosperms with
photosynthetic secondary growth, there may be similarities between their architecture.
Traits could also be less discrete and more plastic, such as stomatal closure rate. Shared
physiological niches could also be the result of unrelated traits leading to similar general
tolerance, such as C₄ photosynthesis in one plant and leaf pubescence in another plant
both contributing to heat tolerance.

Another factor to consider in interpreting modeled niches is the effect of range
disequilibrium, which occurs when observed occurrences of a species do not fully align
with existing optimal habitat, violating model assumptions of equilibrium. This is a
common problem in all species distribution models that rely on correlation between
occurrence and environmental conditions. By explicitly modeling physiological
processes in inferring niche, TTR is more robust than correlative models in addressing
this problem, but TTR is still constrained by the environmental conditions of the species’
observed range, or realized niche. As a result, other ecological factors which affect the realized niche of a species, such as competition and dispersal limitation, are likely influencing the modeled niches. For TTR as well as for SDMs in general, there have recently been proposals to incorporate demographics and range dynamics into the models in order to address the above weaknesses (Schurr et al. 2012), which would further improve the power of TTR to infer true physiological niches.

It is also likely that the subset of environmental tolerances included in TTR do not capture the full range of traits influencing species’ niches. For example, if soil salinity had been included, the halophyte *Atriplex* shrubs likely would have separated from the C$_3$ shrubs. However, the explicit physiological processes incorporated into TTR’s inferences makes this a more robust approach than non-process-based species distribution models, which cannot provide information about the inferred parameters of species’ physiological niches. As Higgins et al. (2012) point out, a strength of the TTR SDM is the fact that the parameters of this niche are explicit, which allows clearer detection of error based on empirical or theoretical expectations for a species’ niche. Further analysis of the sensitivity of individual species’ niches to the variables in this study could help to determine where the model potentially may have failed, as could a literature meta-analysis or empirical studies of the expected tolerances of the species. Multi-model comparison could provide context for TTR’s performance in the broader context of SDMs.

TTR is powerful in its quantification of physiological niche dimensions informed by the best available occurrence data and a mechanistic representation of general plant physiological processes (Higgins et al. 2012). This approach provides a framework with
which to compare species’ niches, differentiate physiologically based functional groups, and identify variables which may contribute to global change sensitivity. The model was able to distinguish between generalist and specialist Colorado Plateau species and reflected observed physiological differences between these groups, including differences in temperature tolerance that are correlated to the decline of historically dominant grasses and the increase in species such as *E. viridis*. Particularly with further development, an inverse modeling approach to defining functional groups based on physiological tolerance has potential in uncovering previously overlooked patterns in plant niches and their resulting sensitivity to global change. More broadly, these results illustrate the insight which defining functional groups based on physiological tolerance can provide for species sensitivity to climate change. By identifying groups which share limited tolerance to high temperatures or low soil moisture rather than relying on broad traits to predict these tolerances, sensitivity can be more reliably predicted for groups of species. Quantifying physiological niches can also generate hypotheses about niche formation.

On the Colorado Plateau, both empirical observations and our modeled results make it clear that a physiological niche which historically allowed C₄ grasses to specialize alongside C₃ grasses and shrubs in cooler temperatures with tolerance of low soil moisture is quickly becoming less competitive with warming temperatures, allowing species with tolerance of high maximum temperature to expand their geographical niche. Conservation planning should take into account functional group sensitivity to climate change in both traditional traits and physiologically specific groupings.
References


