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Can the invaded range of a species be predicted sufficiently using only native-range data? Lehmann lovegrass (*Eragrostis lehmanniana*) in the southwestern United States

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Abstract

Predictions of species invasions are often made using information from their native ranges. Acquisition of native-range information can be very costly and time-consuming and in some cases may not reflect conditions in the invaded range. Using information from the invaded range can enable much faster modeling at finer geographic resolutions than using information from a species' native range. We used confirmed presence points from the native range, southern Africa, and the invaded range, the southwestern United States, to predict the potential distribution of the perennial bunchgrass *Eragrostis lehmanniana* Nees, (Lehmann lovegrass), in its invaded range in the United States. The two models showed strong agreement for the area encompassed by the presence points in the invaded range, and offered insight into the overlapping but slightly different ecological niche occupied by the introduced grass in the invaded range. Regions outside of the scope of inference showed less agreement between the two models. *E. lehmanniana* was selected via seeding trials before being planted in the United States and therefore represents an isolated genotype from the native-range population. Models built using confirmed presence points from the invaded range can provide insight into how the selected genotype is expressed on the landscape and considers influences not present in the native range. Models created from locations in both the invaded and native ranges can lead to a more complete understanding of an introduced species' potential for spread, especially in the case of anthropogenic selection.
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Keywords: Genetic algorithm for rule-set prediction; Distribution modeling; *Eragrostis lehmanniana*; Invasive plants; Invaded-range models

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1. Introduction

Non-indigenous invasive species are a major threat to native species diversity and ecosystem function, causing economic impacts estimated at more than US $100 billion annually (Pimentel et al., 1999). Invasive species have been called the "single most formidable natural disaster threat of the 21st century" (Schnase et al., 2002). Hence, early detection of invaders is critical: predictive models can enable early detection by focusing research efforts to areas most likely to be impacted.

Ecological niche modeling and climate-matching has gained momentum recently for predicting potential invasions (Hoffman, 2001; Peterson and Vieglais, 2001; Welk et al., 2002; McKenny et al., 2003; Peterson, 2003; Peterson and Robins, 2003; Peterson et al., 2003; Arriaga et al., 2004; Drake and Bossenbroek, 2004; Iguchi et al., 2004). These methods are based on the assumption that a species' ecological niche can be described as the *n*-dimensional hypervolume of environmental conditions under which it is able to maintain populations without immigration (Grinnell, 1917). Almost exclusively, species' invasions outside of their native ranges have been predicted with this method using locations where it is confirmed to exist, or known presence points, from their native ranges. However, using locations from the native range assumes the same factors determine the distribution of the species in the invaded range. Depending on the species' introduction history, this assumption may not be appropriate. In addition, acquiring data from native ranges is often very expensive and time-consuming, and not always feasible. Finally, the scale at which species' potential invaded-range distributions can be modeled using native-range data is often too coarse for specific management decisions.

Because of the drawbacks associated with making predictions for an invasion using native-range information, the question of whether confirmed presences in a species' invaded range can be used to successfully predict its eventual distribution is fertile ground for research, remaining relatively unexplored (but see Welk, 2004; Hierro et al., 2005). The purpose of the present study was to investigate whether invaded-range models could be used effectively in place of native-range models in the case of a purposely introduced species.

To explore this idea, we selected *Eragrostis lehmanniana*, a perennial bunchgrass with a unique introduction history to the southwestern United States. In the 1930s, several accessions of *E. lehmanniana* were brought from southern Africa to Arizona to counteract low plant cover and highly eroded soils resulting from decades of overgrazing and drought (Crider, 1945). Seed from a single cultivar (A-68) was produced and distributed widely in Arizona and neighboring states from the 1930s through the 1980s (Cox and Ruyle, 1986). Geographic range predictions for *E. lehmanniana* made using invaded-range points may be as effective and potentially more appropriate than those made using native-range points because *E. lehmanniana* populations in the United States represent a subset of genetic variation present in African populations (Schussman, 2002). Further, very little genetic change is expected because the individuals brought to Arizona and used to produce seed for erosion control were apomictic (Burson and Voigt, 1996). Apomictic reproduction allows for the production of seeds that are genetically identical to the maternal plant. Given its introduction history and reproductive biology, we believe that *E. lehmanniana* represents an ideal candidate for investigating the variability in models predicted using native and invaded-range information for species with little genetic variability.

We built two models to predict the range of *E. lehmanniana* to explore differences in distribution predicted using two different sets of input data. The first model predicted the potential distribution of *E. lehmanniana* in the United States using the ecological niche predicted from its native range in South Africa; the second model predicted the potential distribution of *E. lehmanniana* in the United States using the ecological niche predicted from areas already known to be invaded within the United States. The results of these models were then compared to independent test points in the invaded range to test model performance.

2. Materials and methods

2.1. Distribution data

We collected 350 point locations of *E. lehmanniana* within South Africa, Namibia, Botswana and Lesotho from the Southern African Botanical Diversity

Network's PRECIS database, the Natal Herbarium, the C.E. Moss Herbarium, and Kruger National Park. To minimize spatial autocorrelation, we randomly selected a subset of 200 well-distributed points. The native-range study area for predictions and sensitivity analysis was restricted to a rectangular grid containing southern Africa, from 16°S to 36°S and 11°E to 38°E.

We obtained over 1000 localities of species' occurrences within Arizona and New Mexico from several sources including the Santa Rita Experimental Range, Bureau of Land Management, The Nature Conservancy, U.S. Department of Defense, U.S. Fish and Wildlife Service, U.S. Forest Service, U.S. Geological Survey and the U.S. National Park Service. We randomly selected 100 of the 1000 tightly-clustered presence points to minimize spatial autocorrelation. The invaded-range study area was restricted to the United States, from 23°N to 51°N and 66°W to 126°W, then subsetted to the region roughly bounded by the state of Arizona, from 106°W to 115°W and 31°N to 37°N.

2.2. Environmental data

The base environmental data consisted of 19 global geographic coverages. Elevation, slope, aspect, flow direction, flow accumulation and topographic index (U.S. Geological Survey, 2001) were generalized to 0.1° resolution from 0.01° datasets. Data averaged for the period 1961–1990 were resampled from 0.5° datasets to 0.1° datasets; these data included mean annual precipitation; maximum, minimum and mean annual temperatures; wet days; vapor pressure; solar radiation and frost days (IPCC, 2004). We created grids representing seasonal precipitation by summing monthly precipitation averages for the period 1961–1990 (IPCC, 2004). Seasons were defined as winter (DJFM), spring (AMJ), summer (JAS) and autumn (ON) in the United States and winter (JAS), spring (ON), summer (DJFM) and autumn (AMJ) in southern Africa (Cox et al., 1988a). Season definitions differ from the convention of even 3 month seasons to capture the unique seasonality of precipitation and temperature in Arizona and southern Africa. Datasets representing soil texture in the upper soil horizon (top 1-m) were downloaded from the Oak Ridge National Laboratory Distributed Active Archive Center (Post and Zobler, 2000) and resampled from 0.5° to 0.1° datasets.

2.3. Modeling

The genetic algorithm for rule-set prediction (Stockwell and Noble, 1992; Stockwell and Peters, 1999) is a niche-based model receiving wide application. GARP is an iterative artificial intelligence-based approach that includes several inferential tools. This model has proven successful at predicting species' potential distributions under a wide variety of conditions (Peterson and Cohoon, 1999; Peterson et al., 1999, 2001, 2002a,b,c; Godown and Peterson, 2000; Sánchez-Cordero and Martinez-Meyer, 2000; Peterson, 2001; Feria and Peterson, 2002; Stockwell and Peterson, 2002a,b).

The GARP model predicts species' environmental niches by identifying non-random relationships between environmental characteristics of known presence localities in comparison with the entire study region. Known presence points are divided into training and test data sets. GARP works in an iterative process of rule selection, evaluation, testing and incorporation or rejection to create a rule-set that best represents the environmental conditions under which the species is found (Peterson et al., 1999). First, GARP chooses a method from a set of possibilities (e.g., logistic regression, bioclimatic rules), and applies it to the data. Then, a rule is generated and its accuracy is evaluated via test points intrinsically re-sampled from both the known study region and from the study region as a whole. The change in predictive accuracy from one iteration to the next is used to select among rules for the final model. Rules may change in ways similar to the ways DNA mutates, hence, the name "genetic algorithm". As implemented here, the algorithm runs either for 1000 iterations or until convergence. The final rule-set, or ecological niche model, is then projected onto a digital map as the species' potential geographic distribution and imported into ArcView 3.2 (ESRI 1999) using the Spatial Analyst extension for visualization.

2.4. Native and invaded range modeling

The general steps for the modeling were:

1. Build models using native-range (southern African) datasets, select subset of 10 best models.

2. Project rules onto native range (southern Africa) and invaded range (southwestern United States).
3. Build models using invaded-range (southwestern United States) datasets, select subset of 10 best models.
4. Project rules onto invaded range (southwestern United States) and native range (southern Africa).

Specifically, we produced 300 replicate models of *E. lehmanniana*'s ecological niche using the subset of training points for southern Africa (native range). For each model, points were randomly split into two equally sized training and testing datasets of available occurrence points. To choose the best subset of the 300 native-range models, we adopted a best-subsets selection procedure (Anderson et al., 2003; Peterson et al., 2003). Following this method, we selected the best subset of models by eliminating all models that had non-zero omission error based on independent test points, calculated the median area predicted present among these zero omission points, and then identified the 10 models closest to the overall median area predicted. These 10 models were summed to create a final output grid of model agreement, ranging from 0 (areas not predicted present by any of the 10 models) to 10 (areas predicted present by all 10 models). The rule sets from these 10 models were projected onto the same environmental grids for the United States (invaded range) to generate predictions of *E. lehmanniana* distribution. This procedure was repeated using the environmental base layers and unique presence points collected within the southwestern United States and then projected onto both the South African and United States environmental grids to determine how well GARP could predict *E. lehmanniana*'s ecological niche within southern Africa and the southwestern United States and Mexico.

2.5. Model testing and visualization

We tested the predictive power of the models by overlaying extrinsic test data and tallying observed correct predictions. The proportion of the total study extent predicted as present (occupied by the species) multiplied by the number of extrinsic test data points is used as a random expectation of successful prediction points if no non-random association existed between prediction and test points (Peterson and Shaw, 2003). Following Peterson and Shaw (2003), we implemented a Chi-squared test (1 d.f.) to test the significance of the departure from random expectations. We used 147 randomly selected extrinsic points to test the native-range models, and 183 randomly selected extrinsic points to test the invaded-range models.

To identify environmental dimensions important for defining *E. lehmanniana*'s geographic potential, we used a series of sequential jackknife manipulations in which all possible combinations of a reduced set (e.g., $N-1$) of N environmental coverages were used to generate native-range models. We assessed model quality by exploring correlation between variable inclusion and omission error (Peterson and Cohoon, 1999). Variables that were positively correlated with improvement in avoiding omission error were considered to be most important in defining *E. lehmanniana*'s environmental niche.

Using the subsets of known presence points in Arizona and South Africa selected for the models, a correlation-based principal components analysis (PCA) was performed on the environmental variables associated with the points using PRIMER v5 (PRIMER-E Ltd. 2001). Prior to analysis, skewed variables were transformed using the log or square-root transformation.

3. Results

3.1. Model predictivity and influential variables

Ecological niche models developed in this study were highly predictive of the distribution of *E. lehmanniana* based on random subsets. All of the best-subsets models were highly statistically significant when compared with random expectations (χ^2 tests, d.f. = 1, all best-subsets models $P < 0.001$).

Jackknife manipulations of the different environmental coverages (Peterson and Cohoon, 1999) suggested that the following variables were critical in constituting the ecological niche of *E. lehmanniana* in its native range: spring, summer and fall precipitation; radiation; silt; annual minimum temperature; annual number of freezing days and elevation. In the invaded range, slope, aspect, fall precipitation and elevation appeared to be influential in defining the plant's niche.

3.2. Model output comparison and visualization

The two approaches used to predict the geographic distribution of *E. lehmanniana* in the United States produced results with rather dissimilar patterns, except for the region surrounding the known presence points (Fig. 1). The results of the two methods had strongest agreement for the region surrounding the known presence points in the United States, centered on Arizona. The strongest disagreements occurred in Texas and California, regions not represented by invaded-range points. Models generated from native-range points predict much greater distributions for these areas than models created using invaded-range points. Areas in the northeastern and southwestern portions of the state are more strongly predicted by the native-range model (i.e., possessing higher values on the final model output grid), and the central portion of the state is more strongly predicted by the invaded-range model. The two models also show strong disagreement for portions of Mexico.

Using the invaded range rules to predict *E. lehmanniana*'s distribution in its native range provides insight into the different rules being formulated in the two regions. When rules generated from invaded range points are projected onto the native range, a very small set of the known distribution is predicted. Fig. 2 displays the area predicted occupied by *E. lehmanniana* using points from the native range (top) and from the invaded range (bottom).

The first four components from the PCA of environmental variables for confirmed presence points in the native and invaded ranges accounted for 80.9% of the variance (36.4, 20.7, 15.4 and 8.5%, respectively;

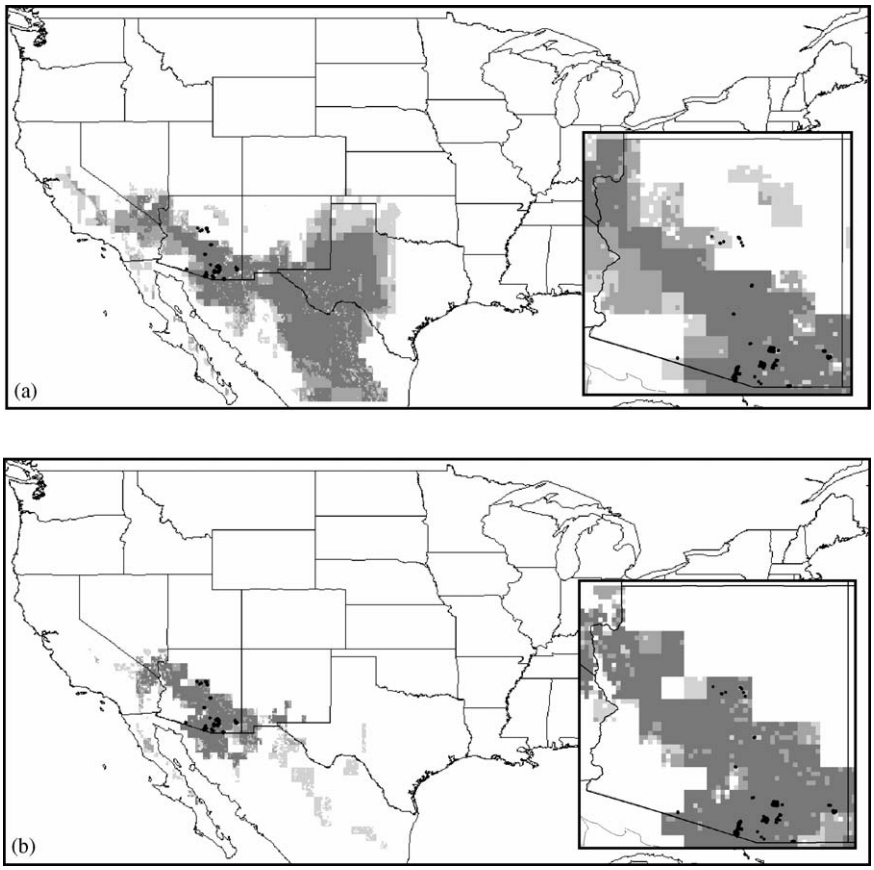

Fig. 1. *Eragrostis lehmanniana* potential distribution using native-range data (a) and introduced-range data (b). Known presence points are black dots. Increasingly dark shades of gray indicate greater model agreement.

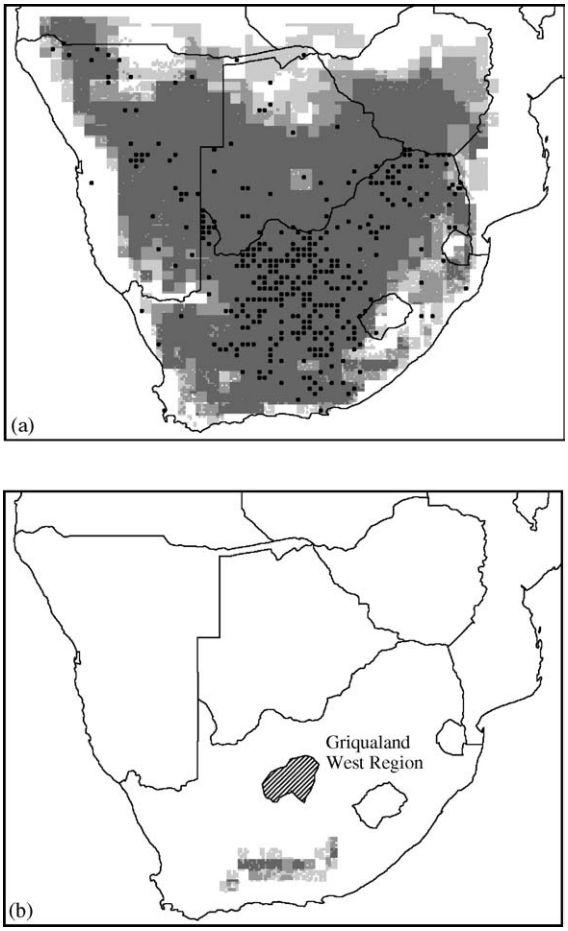

Fig. 2. *Eragrostis lehmanniana* potential distribution using native-range data (a) and introduced-range data (b). Known presence points are black dots. Increasingly dark shades of gray indicate greater model agreement. Hatched region in (b) represents the origin of the A-68 accession.

Table 1). Component 1 loads most highly on temperature variables. Precipitation variables contribute the highest loadings to Component 2. Components 3 and 4 are a mix of soil variables, radiation and precipitation variables. Separation of known presence points in Arizona from known presence points in southern Africa occur primarily along the second axis (Fig. 3).

4. Discussion

Species invasions are often predicted using information from their native ranges (Hoffman, 2001; Peterson and Vieglais, 2001; Welk et al., 2002; Peterson et al., 2003, 2004). However, building models using data from the invaded range is also a common practice (e.g., Zalba et al., 2000; Higgins et al., 2001; Underwood et al., 2004). Acquisition of native-range

Table 1
Four-component solution generated by principal components analysis for predicting distribution of *Eragrostis lehmanniana* in Arizona, USA

Variable	PC1	PC2	PC3	PC4
Max annual temperature	0.351	−0.086	0.131	−0.175
Annual temperature	0.332	−0.205	0.214	−0.101
Min annual temperature	0.272	−0.298	0.269	−0.014
Summer precipitation	−0.145	−0.469	−0.112	−0.011
Frost days	−0.211	0.266	−0.354	0.047
Fall precipitation	−0.213	−0.256	−0.227	0.365
Elevation	−0.173	0.126	−0.321	−0.023
Aspect	−0.006	−0.025	−0.012	0.042
Winter precipitation	−0.252	0.236	0.150	−0.371
Wet days	−0.314	−0.272	−0.031	−0.124
Spring precipitation	−0.246	−0.384	−0.002	−0.166
Slope	−0.214	0.162	0.208	−0.132
Silt	−0.229	0.209	0.393	0.121
Sand	0.241	−0.094	−0.417	−0.280
Radiation	0.259	0.005	−0.310	0.364
Annual precipitation	−0.276	−0.327	−0.023	−0.277
Clay	−0.170	−0.163	0.283	0.566
Eigenvalue	6.19	3.51	2.62	1.44
Explained variance (%)	36.4	20.7	15.4	8.5
Cumulative variance explained (%)	36.4	57.1	72.5	80.9

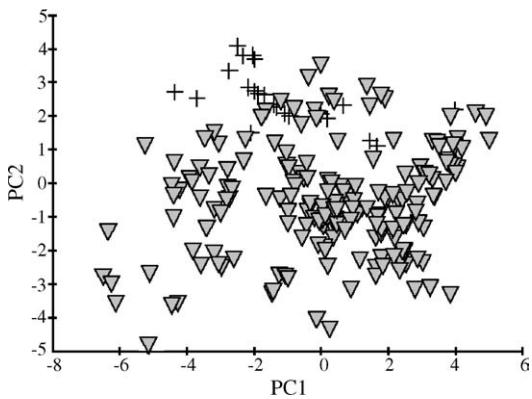

Fig. 3. Principal components analysis plot of environmental conditions associated with known *Eragrostis lehmanniana* presence points in Arizona, USA and southern Africa. Triangles represent known points in Africa, crosses represent known points in Arizona.

information can be very costly and time-consuming, and in some cases infeasible, involving extensive literature searches of sources in different languages. Records must be geographically referenced, which is rare for many herbaria. Peterson et al. (2003) reported spending 2 months obtaining native-range records, versus 1 h obtaining invaded-range records for a study similar to this one. For this study, obtaining native-range data took over double the time to obtain invaded-range points (approximately 3 months), with the advantages that many of the native-range records were already entered into databases and that they were in English.

Another advantage of invaded-range models is that they usually can be built using finer-scale input data layers. To build models in the native range and project the resulting rules onto the invaded range requires the same environmental layers for the two regions. Currently, most environmental layers available on a global scale are coarse, on the order of 0.1° to 1° cells. Limiting models to only one continent enables finer-scale datasets specific to that region to be included in the models.

Few studies have explored the performance of invaded-range versus native-range datasets for predicting invaded-range distributions. A handful of studies have suggested that species will occupy an overlapping but different set of environmental conditions in an invaded range than in their native range (Malanson et al., 1992; Kriticos and Randall, 2001). Kriticos and Randall (2001) suggested that a species' invaded range is predicted best using information from a second invaded range; they reasoned that in invaded ranges the fundamental niche may be more fully realized than in the native range, where the species is constrained by competition and dispersal barriers. Welk (2004) tested the use of invaded-range points to predict the distribution of the invasive *Lythrum salicaria* in North America and suggested a method combining the use of invaded and native-range information would be most insightful.

E. lehmanniana constitutes a special case for invasion prediction, given its unusual introduction scenario. Seed traceable to a limited number of apomictic individuals was widely distributed and planted in the southwestern United States, leading to an invading population with low genetic variability and few mechanisms to evolve. For these reasons, it seems logical to build predictive models using both native and invaded-range points to explore the potential distribution of *E. lehmanniana*. Building models from the species' introduced range, or a combination of both native and introduced ranges, may be the most appropriate approach for purposely introduced plants. This is especially suitable when specific traits were selected for during the introduction, for plants with limited genetic variation due to asexual reproduction, or for plants where a limited number of individuals were introduced.

Four classes of factors determine a species' distribution: abiotic conditions, biotic interactions, regions accessible through dispersal and the capacity of the species to adapt to new conditions (Pearson and Dawson, 2003; Soberón and Peterson, 2005). A species' fundamental niche is defined as the region where the abiotic conditions are favorable; a species' realized niche is often the more restricted region where both abiotic and biotic conditions are favorable (Soberón and Peterson, 2005). This region can be yet further minimized when dispersal is considered. In coarse-scale studies, such as the present study, dispersal is proposed to play an important role in describing a species' distribution, and that biotic interactions play a weak role (Soberón and Peterson, 2005). In this case, models can be interpreted in a rather straightforward manner, as the fundamental niche and realized niche is essentially the same region.

4.1. Model visualization and interpretation

Predictions made of the distribution of *E. lehmanniana* in the United States show similar patterns for Arizona and the region surrounding known presence points in the United States; the largest differences occur in Texas, California and New Mexico as well as Mexico. Models created using native-range points predict much greater distributions for these areas than models created using invaded-range points. Spatial coverage of known presence points used in this study come from sites in Arizona, where confirmed presence points are most readily available. Because of the extent of the known presence points used to build and test the models, inference is approximately limited to the state of Arizona. Currently, Arizona is the state in the United States most heavily impacted by *E. lehmanniana*. Within the state of Arizona, areas in the northeastern and southwestern portions of the state are more strongly predicted (i.e., possessing higher values on the final model output grid)

by the native-range model and the central portion of the state is more strongly predicted by the invaded-range model.

The disagreement in the two models' output could be due to a paucity of points in the invaded range, as known presence points used in this study represent only Arizona, where confirmed presence points are most readily available. The invaded range is believed not to be at equilibrium yet as the species is still spreading to new areas. Therefore, building a prediction using these points is likely to represent a smaller set of environmental conditions, resulting in a smaller area being predicted. However, the disagreement in the two models' output also could be due to differences in the ecological niches realized by the native-range populations and United States populations of *E. lehmanniana*. The results of the PCA depict the range of environmental conditions occupied by *E. lehmanniana* in both its native and invaded ranges. Points in Arizona occupy an overlapping but slightly different location in multivariate space than those in *E. lehmanniana*'s native range (Fig. 3), which coincides with the slight disagreement in the two models for Arizona. These results suggest that the niche occupied by *E. lehmanniana* in Arizona is narrower and slightly different than that occupied in its native range. The invaded-range model predicts occupation under conditions of higher temperature and lower total precipitation as well as lower precipitation in all seasons than the native-range model.

The conclusion that the niche occupied by *E. lehmanniana* in Arizona is narrower and slightly different than that occupied in its native range is supported by the projection of invaded range niche rules onto the native range. Using invaded-range rules, only a small portion of the entire distribution is represented, presumably representing only a portion of the ecological niche available in its native range (Fig. 2). The A-68 accession brought to the United States in 1932 was obtained from the Griqualand West Region of South Africa (Cox et al., 1988b), located approximately 300 km north of the region predicted present by the invaded-range model (Fig. 2). The two areas are climatically similar, but the Griqualand region exhibits slightly higher average temperatures than the area predicted by the invaded-range model. If the niche realized in Arizona were merely a subset of that occurring within Africa, the invaded-range model should predict the Griqualand West Region as present. Instead, the invaded-range model predicted a region that exhibited *lower* temperatures than the accession's origin.

The inconsistencies in environmental variables selected through the jackknifing procedure provides support to the differences in the native and invaded-range populations, suggesting that the *E. lehmanniana* population in the invaded range is limited by different variables than those which limit its distribution in its native range. However, an equally plausible explanation could be that the variables found to be influential in the invaded-range model may represent the conditions around the species' present range, but not the conditions that will eventually represent the limiting factors around the whole invaded range of the species. As the species continues to spread in its invaded range, it will be possible to more fully answer this outstanding question. Ultimately, it seems from the results of this modeling effort that different abiotic variables define the native and invaded-range environmental niches of *E. lehmanniana*.

The invaded-range model prediction of occupation under conditions of higher temperature and lower total precipitation argues against *E. lehmanniana*'s occupation of Texas and California. Field experiments and expert observations have repeatedly supported this notion (Cox and Ruyle, 1986; Barkworth and Capels, 2004; B. Carr, B. Rice, F. Miller, J. DiTomaso, personal communications). These observations suggest that northern New Mexico, California, and Texas are on the edge of the ecological niche that the A-68 *E. lehmanniana* accession occupies, and that the potential distribution map created using the invaded-range model is most plausible.

Because the A-68 accession was selected to be especially drought-tolerant, the United States *E. lehmanniana* may not compete as well under more mesic conditions, as in western Texas and California. The second axis of the PCA is dominated by precipitation variables all decreasing up the axis. Based on the partial overlap for the two sets of points along the second axis, it appears that precipitation, particularly seasonality of precipitation, is a key variable in determining the distribution of United States *E. lehmanniana* populations. However, the potential for *E. lehmanniana* to dominate grasslands in these areas may still exist. Specifically, if the conditions in Texas and California grasslands were to become much drier, *E. lehmanniana* may be able to better compete and could become more dominant.

Based on field observations by experts, it seems the model predicted using invaded-range points may more accurately represent the potential distribution for *E. lehmanniana*. In addition, building two separate models revealed the difference in environmental niches occupied by the same species in the two locations, demonstrating that different abiotic factors define the niche in the native and the invaded ranges. The results of this study suggest that models built using both native- and invaded-range points can provide insight into how the selected genotype is expressed on the landscape. In addition, this study demonstrates that invaded-range models may work as effectively and can possibly provide more information than native-range models, especially in the case of a purposely introduced species. Therefore, species with little genetic variation and well-known introduction histories may be best modeled with invaded-range points, minimizing the costs and time involved, as well as increasing model accuracy.

4.2. The role of ecotype in invaded range predictions

The specific geographic origin of an invading species is often unknown, as is the mechanism for introduction. However, if an invader is introduced from only a portion of its native range, only the portion of the invaded range representing the set of environmental conditions tolerated by that introduced ecotype may become invaded. This appears to be the case with *E. lehmanniana*, where the invaded range already affected and the region expected to be at risk for invasion based on the ecotype introduced to the United States is smaller than that predicted from the entire niche realized in its native range. The practice of using the entire native range to predict a species' invaded range is inappropriate when only a portion of the genetic variability of the native population is introduced, and can lead to overprediction of the species' invaded range. Yet, when the origin of the invader is unknown, conservative estimates may be desired, and using the entire native range can yield "worst case" scenarios from which to make management decisions.

Experiments are the best way to test predictions made by models. Predictive models can offer insight into the potential spread of invasive species, but do not consider factors affecting species distributions such as biotic interactions. Mechanistic studies addressing these factors are necessary to augment the predictions made by correlative models. In addition, incorporation of predictive model output with invasibility models (Shea and Chesson, 2002) could offer insight into areas within the predicted habitat that are most threatened by invasion.

5. Conclusions

The results of this study demonstrate that geographic distributions of invading species built on points occupied in the invaded range may perform as effectively and can possibly provide more information than those developed from the native range, at least for the region encompassed by confirmed presence points in the invaded range. In addition, predictions made using invaded-range points can offer insight into the environmental conditions tolerated by the invader and inconsistencies in the ecological niche between native to invaded ranges. The sole use of invaded-range points to make invaded-range predictions may be the most appropriate method for modeling distributions of intentionally introduced plants, especially when the introduction involved intense selection of the plant, as in the case of *E. lehmanniana*. Intense selection, asexual reproduction and limited introduction numbers all function to create a non-native population with an environmental niche that represents a subset of the native range niche. Since not all invaders can be predicted to represent a subset of the native range and most likely occupy an overlapping but different niche in the invaded range, it is likely best to use information from the plants' native and invaded ranges.

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