Razing Arizona: Introduced "wonder grass" plagues the American Southwest. The potential for modeling spread of a nonnative species.

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Abstract

A “wonder grass” introduced to the American Southwest has spread far beyond its expected range to the apparent detriment of native organisms. An assessment of current distribution and abundance related to environmental factors will allow land managers to target key areas for reclamation and preservation. We compiled a spatial database of 1,400 locations monitored for presence/absence of *E. lehmanniana*. From a subset of these locations, in association with environmental data, we developed a logistic regression model to predict probability of presence of *E. lehmanniana*. Based on our 90% probability model, we found that *E. lehmanniana* occurs on over 400,000 hectares, more than double the area covered only 20 years ago. We developed maps of potential future distribution of *E. lehmanniana* by integrating our logistic regression model with global climate scenarios. These models predicted the distribution of *E. lehmanniana* within Arizona will decrease substantially by 2030. Future work should include more monitoring locations beyond the boundary of our study area. We recommend that various land management agencies make a concerted effort to standardized monitoring protocols to facilitate larger scale studies.

Introduction

Nonnative plant species have the potential to alter species composition (across guilds), change hydrologic and nutrient cycles, and influence disturbance regimes (Mack and D’Antonio 1998). Contemporary concerns for preserving biodiversity have led to efforts to restore invaded areas to native flora. However, not only do we lack sufficient knowledge about the role of nonnative species in these areas but as Mack (2000) points out:

> We usually lack the ability to provide explicit answers to the obvious questions asked by policy makers: ‘Across and within what specific political boundaries are these invasion occurring?’ ‘How abundant are the invaders?’ ‘Which areas or habitats are next at risk of invasion?’ ‘Are these invading populations expanding, remaining static, or even contracting?’

Without ready answers, there is no sustained public interest, and more important, no sustained public support to control these pests (Office of Technology Assessment 1993).

Following severe overgrazing and drought in the late 1800s and early 1900s, land managers in southern Arizona were faced with virtually no plant cover and irreplaceable loss of topsoil. In a race for short-term solutions, the land managers introduced what turned out to be a long-term problem. In the 1930s, a nonnative grass, *Eragrostis lehmanniana*, was brought into the southwestern United States to control erosion and provide forage for cattle. By the late 1950s scientists began to express words of caution concerning the recently introduced grass from South Africa (Humphrey 1958): “Mesquite has made a good start on many of our southern Arizona ranges in driving out our native grasses; is [Lehmann] lovegrass going to finish the job?”

Indeed, numerous researchers have observed a convincing association between increasing proportion of *E. lehmanniana* and decreasing species richness in these grasslands (Cable 1971, Bock et al. 1986, Medina 1988, Whitford et al. 1999, McPherson et al. 2001). Whether this decrease across guilds occurred prior to or after occupation by *E. lehmanniana* is unknown; a recent study suggests the former scenario for native grasses (Angell and McClaran 2001). In addition to decreased species richness, *E. lehmanniana* has been implicated in alteration of ecosystem processes (Cable 1971, Bock et al.1986, Williams and Baruch 2000), modification of community composition (Anable et al. 1992, Kuvlesky et al. 2002), and changes in fire regimes (Ruyle et al. 1988, Burquez and Quintana 1994, Biedenbender and Roundy 1996). *E. lehmanniana* currently dominates these areas, not the suite of native species historically found. Just over half a century since its arrival, after doubling the area to which it was originally sown, scientists predicted that Lehmann lovegrass had reached the limits of its range (Cox and Ruyle 1986).

Published evidence indicates that sites with *E. lehmanniana* in Arizona vary from approximately 800 to 1500 meters in elevation (Cox et al. 1988), with summer rainfall exceeding 89 millimeters in 40 days (Anable 1990) or 30-40 days exceeding 150 mm (Cox et al. 1988) and temperatures rarely falling below 0 ºC (Cox and Ruyle 1986). Although researchers do not know the influence of soil characteristics on invasion by *E. lehmanniana*, the species apparently persists and dominates areas with sandy and sandy loam soils (Anderson et al. 1957, Cable 1971, Cox and Martin 1984, Cox and Ruyle 1986, Cox et al. 1988). Its spread is expected to continue under current climate conditions and land-management practices (Anable et al. 1992, McClaran and Anable 1992, Ruyle and Cox 1996). Indeed, several field ecologists have noted the spread of *E. lehmanniana* to areas originally believed beyond its range (Robinett, pers. comm., Ruyle, pers. comm.).

Eragrostis lehmanniana offers a unique opportunity to follow the introduction and spread of an invasive species. Unlike most nonnative species, the introduction history of *E. lehmanniana* is well-documented and includes knowledge of initial seeding sites, area seeded, and seed stock. Additionally, *E. lehmanniana* was selected for introduction after a world-wide search for a“wonder grass” that was perfectly suited to semi-arid conditions. Seventeen years ago, researchers delineated the range of *E. lehmanniana* (Cox and Ruyle 1986); however, since this time, it has expanded to areas beyond predicted climatic limitations. Land managers cannot make reliable decisions regarding native plant communities that are at risk of invasion because patterns associated with recent spread have not been identified. An up-to-date survey to determine new areas of colonization as well as current population abundance and distribution is needed. Analysis of trends associated with environmental or climatic changes may allow land managers to predict future patterns of spread and potential areas of invasion.

Objectives

The goal of this study was to synthesize a body of ecological knowledge, integrate it with other disciplines, and put it in the hands of land managers and policy makers to enhance decision-making. The knowledge regarding the range of and potential threats of *E. lehmanniana* to native grasslands was last assessed extensively in the 1980s. Most agencies, although they often struggle with similar problems, have no infrastructure for collaborating on monitoring projects or developing strategies to solve the problems. Here we provide an analysis of site-specific monitoring data from a multitude of land managers that relate the dynamics of *E. lehmanniana* to various environmental factors in an attempt to place the information in a regional context.

Our specific objectives for this study were to (1) compile a database containing known locations of *E. lehmanniana* from agencies in Arizona, (2) model and map the potential current distribution of *E. lehmanniana* based on environmental factors (soil texture, temperature, precipitation, etc.) associated with known locations, (3) compare our results to past and present assessments of *E. lehmanniana* distribution, and (4) generate future potential distribution maps under common general circulations models.

Methods

Compilation of location data for the response dataset

Spatial presence/absence information exists in the form of long-term monitoring data from multiple land managers and scientists working in disparate locations across the state of Arizona. We collated these site-specific data to generate a regional picture of *E. lehmanniana* extent. We compiled and managed observations of *E. lehmanniana* from various land management agencies (Table 1) across Arizona using a geographic information system (ArcGIS 8.1. ESRI). Individual observations were in the form of (1) distinct points marking small isolated patches, (2) point locations within larger continuous stands, (3) vegetation monitoring transects in which *E. lehmanniana* was recorded, and (4) boundaries of large patches. We calculated center points to represent transect and area data; when polygon centroids fell outside of their boundaries, we manually edited the point to fall within the polygon. (Figure 1).

We included in the analysis samples separated by a distance of greater than 1 km of each other (n = 183) to reduce autocorrelation and the influence of intensely sampled areas. The excluded *E. lehmanniana* observations were retained for evaluation of model performance. In addition, we used ArcInfo (ESRI) to generate a set of random locations (n = 217) to use in the analysis. Because *E. lehmanniana* presence points were available for only a portion of the state, a region surrounding these points was defined as the study area (Figure 1).

Climatic explanatory variables

We obtained continuous grids of modeled climatic variables at 1km resolution from DAYMET U.S. Data Center (www.daymet.org; July 23, 2003) including total precipitation June-Sep (cm); total precipitation Oct-Mar (cm); total annual precipitation (cm); annual average air temperature (°C); annual maximum air temperature (°C); annual minimum air temperature (°C); and daily shortwave radiation (MJ/m^2/day). Daymet models daily climatic variables as continuous surfaces from a network of weather stations and spatially continuous topographic surfaces (Thornton 1997). For our climatic variables, we acquired and summarized monthly and yearly data averaged over an 18-year period from 1980 to 1997.

Soil explanatory variables

We obtained a multi-layer soil characteristic data set in which we averaged the percent sand, clay, and silt over the top two 5-cm thick layers to estimate the percent of each in the top 10 cm, hereafter referred to as the surface layer (Miller and White 1998). To estimate the percent sand, clay, and silt in the soil profile, we averaged across the soil layers up to 1 m in depth. In addition, we included the depth to bedrock as an explanatory variable due to the previous observation of shallow soils at *E. lehmanniana* sites (Cox and Ruyle 1986). Using ArcInfo, we derived grids with 1km cells for each of the soil explanatory variables.

Topographic variables

We acquired a 30 m x 30 m Digital Elevation Model (DEM) covering the study area from USGS seamless data distribution (USGS 2002). We derived a grid of percent slope and aspect (in degrees) from the DEM within the GIS. We applied a cosine transformation to the aspect, resulting in values ranging from –1 (south-facing aspects) to 1 (north-facing aspects).

Sampling the explanatory variables at E. lehmanniana and random locations

At each *E. lehmanniana* and random location, we sampled the 1km grid of climatic variables, the polygonal coverage of soil variables, and the 30 m x 30 m topographic grids. After sampling the original format of the explanatory variables, each input spatial dataset was converted to a 1 km resolution grid for use in displaying the probability surface.

Statistical summary and analysis

We evaluated the correlation structure between explanatory variables (Appendix 1) using Pearson correlation analysis. We observed high correlation ($r^2 > 0.7$) among many of the soil variables. Additionally, elevation was correlated with winter low temperature; we selected winter low temperature for inclusion in the analysis because of its observed importance to the distribution of *E. lehmanniana* (Cox and Ruyle 1986). Variables considered for the analysis are listed in Table 2.

We used retrospective sampling, case-control logistic regression (Christensen 1997) to differentiate between *E. lehmanniana* sites and random sites based on environmental variables, a technique commonly used to model species' distributions (e.g. Franco et al. 2000, Kleinschmidt et al. 2000, Barbosa et al. 2003). This method produces a probabilistic model that predicts a binary response variable from a set of discrete or continuous explanatory variables.

We used a stepwise procedure in SAS 9.0 (SAS Institute) to select the variables and interactions between variables that best distinguish between *E. lehmanniana* locations and the random environment based on statistical criteria. We assigned a p-value to enter the model of 0.30 and a p-value to stay in the model of 0.10. We used a jack-knife (cross-validation) procedure which excluded each data sample in turn and then recalculated the maximum likelihood estimates of the coefficients. We used the Akaike Information Criterion (AIC) to select among the various models tested. The AIC value is based on deviance and number of parameters in the model (McPherson and DeStephano 2003).

Creation of the probability surfaces

To build the visual representation of the potential distribution of *E. lehmanniana,* we calculated the probability response (π) at every cell location in the study area using the raster array of explanatory variables to estimate the probability of potential *E. lehmanniana* presence. Using ArcInfo, each coefficient was multiplied by the cell value in the appropriate environmental grid. The resultant grids were summed at each cell location and the logit function was solved for the probability (π) at each cell location. In the resulting probability surface, values closer to 1 represent greater potential of *E. lehmanniana* occurrence; values close to 0 represent lower potential of *E. lehmanniana* presence.

Evaluation of model performance using known absence locations and presence locations

We derived a 1 km cell grid from the known point locations where *E. lehmanniana* was absent and a grid from the presence locations excluded from the analysis due to their proximity to included samples (less than 1 km). We sampled the probability surface at the grid cell locations coincident with known absences and excluded presences. Presence cells with probability ≥ 0.5 were considered true positives and contributed to the sensitivity rate. Absence cells with probability <0.5 contributed to the specificity rate.

Prediction of extent in 2030

The future extent maps are based on climate model results from the Canadian Centre for Climate Modeling and Analysis and from the Hadley Centre for Climate Prediction and Research (of the United Kingdom's Meteorological Office). These models predict increases in both temperature and precipitation in almost all seasons for 2030 (Table 3).

The climate grids were modified to reflect these predicted increases in precipitation and temperature. Then the probability surface was twice recalculated, referencing the modified climate grids in place of the long-term averages of climate variables. The first run referenced the grids reflecting the Hadley Center predictions; the second run referenced grids reflecting the Canadian Climate Center predictions.

Results

Predicted current distribution

Eragrostis lehmanniana presence probability is displayed in Figure 2. As can be seen by comparing Figures 1 and X, the predictions of the model closely match the distribution data available within the study area. Based on the cross validation (jack knife procedure), the overall accuracy of the model was 81.8%, with a high sensitivity (79.2%) and high specificity (83.9%) (Table 4).

This model predicted *E. lehmanniana* to be present (≥90% probability) in 4,146 km^2 cells, 414,600 ha. The parameters included in the model appear in Table 5. According to this model, the distribution of *E. lehmanniana* is defined by seasonal precipitation and temperature, soil texture, and slope. Increases in winter low temperature, summer precipitation (July, August, September), clay and sand in the soil surface, slope, and the interaction between winter low temperature and slope were all associated with an increased probability of *E. lehmanniana* occurrence. The interactions of winter low temperature with winter precipitation, and summer precipitation with winter precipitation, and slope with clay decreased the probability of occurrence. The estimates for the distribution of *E. lehmanniana* identified by the model increased nearly three fold since reported by Cox and Ruyle in1986, from 145,155 ha to 414,600 ha (Table 5).

Predicted distribution in 2030

The two future distribution scenarios appear in Figure 3. As displayed in Table 6, the area predicted to have a high probability of invasion by *E. lehmanniana* is drastically reduced from the current distribution map. The grass is predicted to nearly vanish from the region defined as the study area. The areas shown to still demonstrate some probability for invasion match, in general, areas predicted to have a high probability of invasion currently.

Discussion

Based on the model selected in this study, the distribution of *E. lehmanniana* is significantly affected by winter low temperature, summer precipitation, and soil texture (Tables 3 and 4) and other studies (Cox and Ruyle 1986, Anable 1989, McClaran and Anable 1992, TNC unpublished data). In addition, slope and interactions between the variables included in the model also significantly influence the distribution of this invasive grass. Cox and Ruyle (1986) predicted distribution where winter low temperatures exceeded 0°C whereas Crider (1945), who introduced the grass, predicted a lower limit for winter low temperature at –3°C. Our analysis confirms these earlier descriptions showing *E. lehmanniana* surviving at winter low temperatures below 0°C, but the probability of its persistence and spread are higher when winter low temperatures exceed 0°C.

E. lehmanniana has been documented to persist in areas receiving 89 mm of precipitation in 40 days (Anable 1989), an amount more than 100 mm lower than the originally predicted value limiting its distribution (Cox and Ruyle 1986). Our model confirms this lower precipitation limit and we see that the interaction between summer precipitation and winter climate variables (precipitation and winter low temperature) are also limiting the distribution of *E. lehmanniana*. Clay and sand in the surface layer are also demonstrated to be important variables in the distribution in *E. lehmanniana*, although their influence may be more evident on a microsite level. Including these variables in our model likely fine-tuned the probability rather than dramatically altering the distribution. Additionally, the effect of soil texture may be more obvious in the degree of dominance rather than as a limitation to distribution.

Slope also appeared as a significant variable in our model. It is possible that this is a result of southern slopes having higher temperatures than northern-facing slopes. Different slopes also have varying amount of runoff based on soil type and vegetation cover; the model may be reflecting these relationships. However, it is also possible that the inclusion of some of the variables is a result of the coarse input datasets that were used. The model could be rerun once better spatial datasets are available, to test if these relationships remain.

We believe the model presented here represents an accurate prediction of the current potential distribution of *E. lehmanniana* within our study area. Not only was the model objectively accurate based on the cross validation jack knife procedure (81.8% accuracy) and The Nature Conservancy's recent Apache Highlands Grassland Assessment (AHGA) study, it was also subjectively accurate when evaluated based on our knowledge of habitat boundaries of *E. lehmanniana*. Specifically, a comparison of high probability *E. lehmanniana* acreage with the AHGA we found that our values agreed fairly well both in size, our 414,600 ha compared to their 594,632 ha, and location (Figure 4). However, when our model predictions are compared to the seventeen year-old study of Cox and Ruyle (1986), we found that while the location of high probability areas of *E. lehmanniana* are consistent, our acreage is three times that of their study. This suggests that since the time of the Cox and Ruyle study, *E. lehmanniana* has continued to spread beyond the areas invaded by 1986.

In order to test for applicability of our model to areas outside of the study area, we compared the range of each input variable present in the study area to that in Arizona and New Mexico, outside of the study area. Spatial regions exhibiting values outside the range of a particular variable were excluded for model extrapolation. These excluded variables are shaded black in Figure 1. The model predicts 784,900 ha within Arizona to have a 90% probability of *E. lehmanniana* presence.

The predictions for *E. lehmanniana* retreat in 2030 are surprising. Both the Hadley Center and the Canadian Climate Center models project warmer, wetter conditions for the southwestern U.S. in 2030. As *E. lehmanniana* has been identified to be limited by winter temperatures and summer precipitation, this would suggest that the conditions in 2030 would be much more suitable for *E. lehmanniana* spread. Our prediction maps suggest that many variables are interacting in surprising ways in this model. These surprising results could be, at least in part, the result of coarse input datasets. The climatic data layers are the result of complex interpolation and terrain modeling from scattered weather stations. Precipitation, in particular, is very difficult to model accurately in complex terrain. As *E. lehmanniana* is very sensitive to precipitation amount, inaccurate datasets would lead to unexplainable model results. It is also important to realize that these predictions assume that *E. lehmanniana* would respond to an increase in average conditions in a linear fashion. However, it is possible that species are much more sensitive to extreme events rather than a shift in an average.

Conclusions

We compiled a spatial database of 1,400 locations monitored for presence/absence of *E. lehmanniana*. Presence points were put into a GIS and intersected with spatial distributions of abiotic factors to determine site-specific information. We developed a logistic regression model to predict probability of presence of *E. lehmanniana*. This map was compared to past and present assessments of *E. lehmanniana* distribution. We observed that *E. lehmanniana* spread beyond the limits originally predicted and is expected to continue to spread, particularly in southern Arizona. We also used our model to predict the future distribution of *E. lehmanniana* under various climate change scenarios. These models predicted the distribution of *E. lehmanniana* within Arizona will decrease substantially by 2030. Future work should include more monitoring locations beyond the boundary of our study area. We recommend that various land management agencies make a concerted effort to standardized monitoring protocols to facilitate meta-analysis using abundance measures rather than presence/absence data that have limited comparative value.

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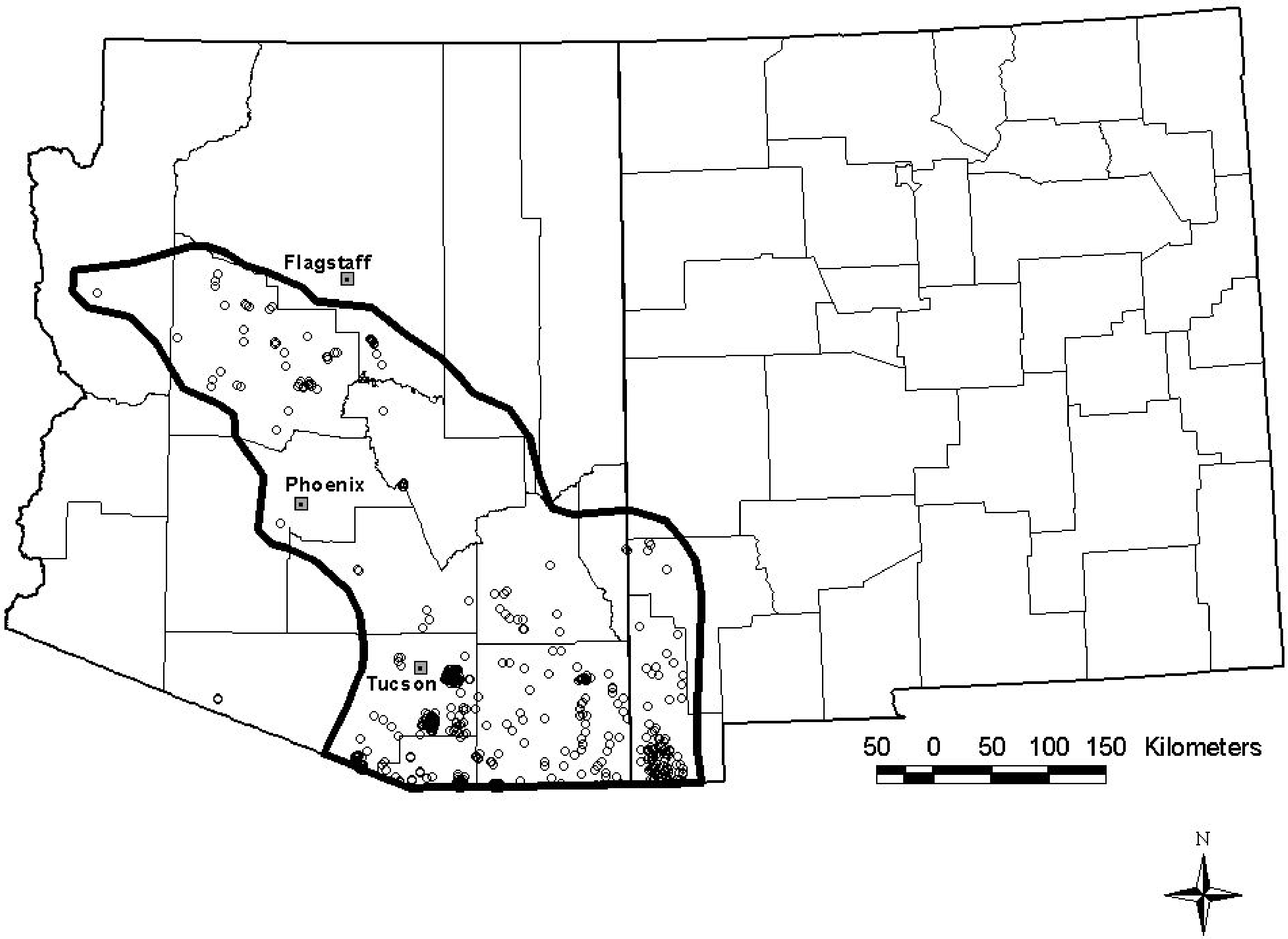

Figure 1. Known presence/absence locations for Eragrostis lehmanniana across Arizona and New Mexico, USA.

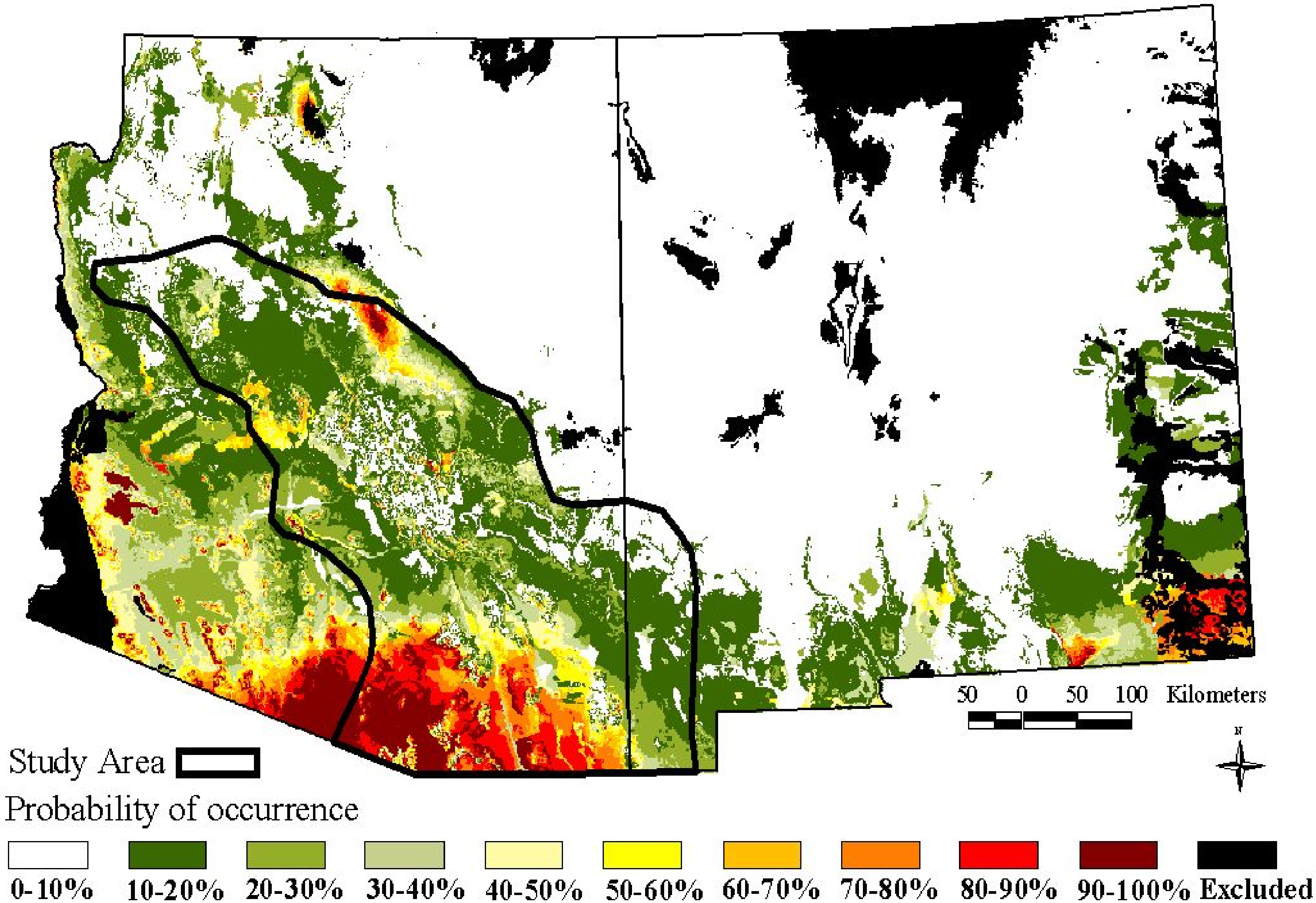

Figure 2. Potential current distribution of Eragrostis lehmanniana (Lehmann lovegrass) in Arizona, USA generated using logistic regression with several abiotic factors.

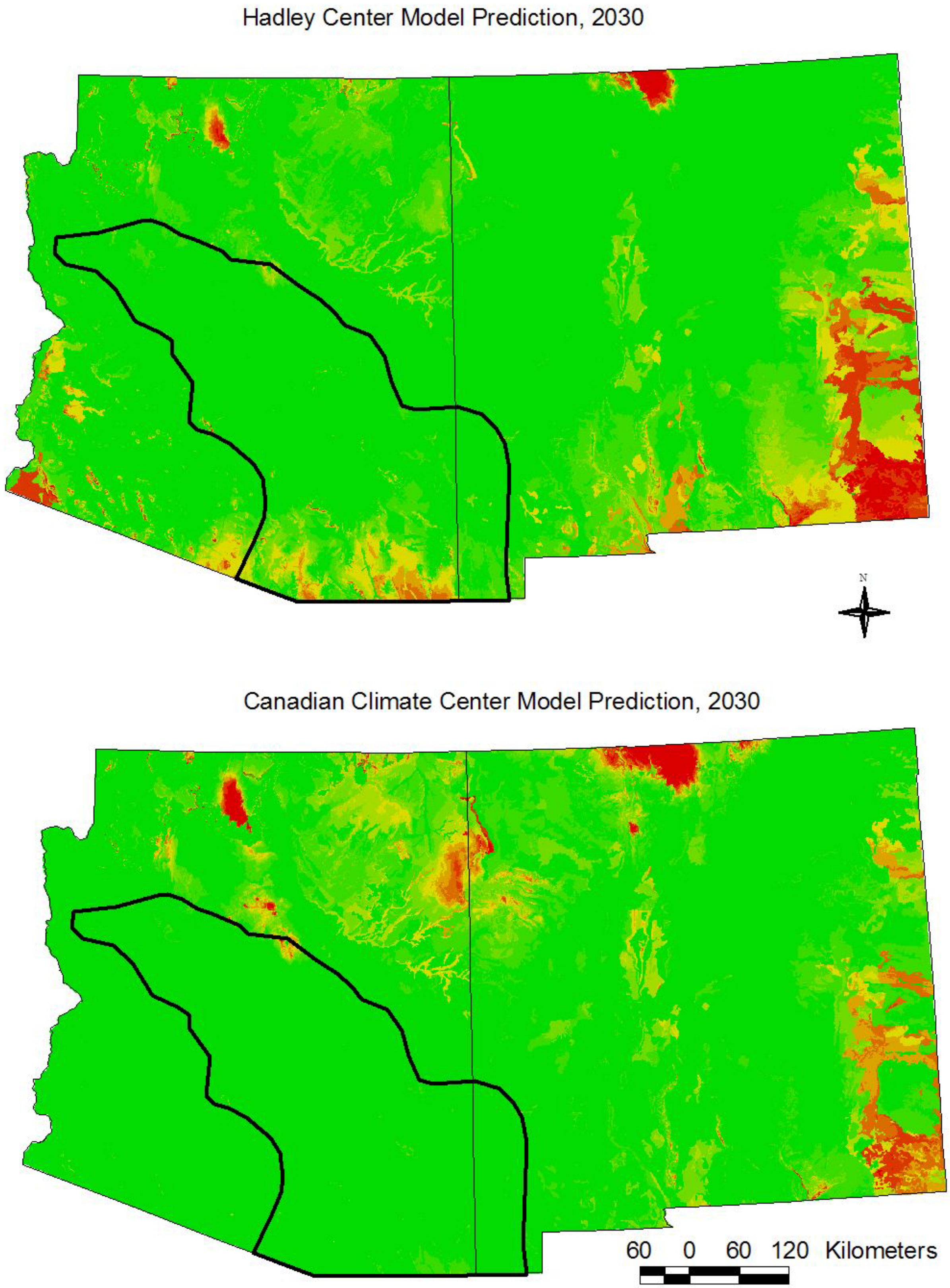

Figure 3. Predicted distribution of E. lehmanniana in 2030 generated using two common general circulation models.

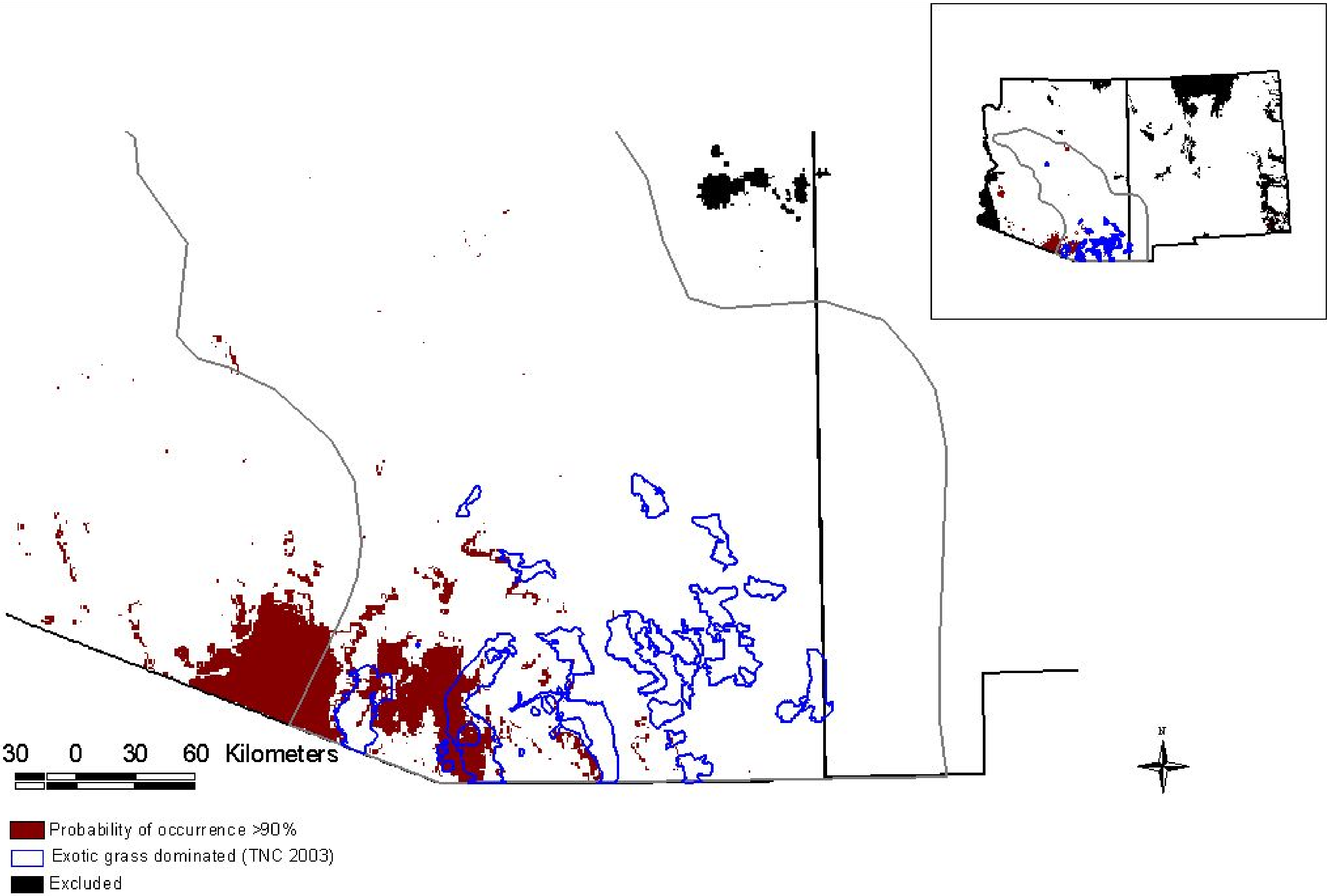

Figure 4. Probability of E. lehmanniana presence >90% (this study) and the Arizona Chapter of The Nature Conservancy's Apache Highlands Grassland Assessment distribution of E. lehmanniana.

Table 1. Summary of observations included in the LOCATION table of the Access database.

Land management area/ dataset	Record numbers	Observation type(s)
Bureau of Land Management		
Empire-Cienega Conservation Area	147-154	
Empirita Ranch	155-157	Transects
National Parks Service		
Coronado National Monument	133-146	Points
Organ Pipe Cactus National Monument	158-162	Points
Saguaro National Park	964-1080, 1423-1431	Points, transects, polygons
The Nature Conservancy		
Apache Highlands grassland assessment	1081-1366	Points, transects
U.S. Department of Defense		
Fort Huachuca Military Reservation	1423-1431	Transects
U.S. Fish and Wildlife Service		
Buenos Aires National Wildlife Refuge	1367-1400	Transects
U.S. Forest Service		
Prescott National Forest	1401-1406	Points
U.S. Geological Survey		
Southwest Exotic Plant Mapping Program	163-174	Points
University of Arizona		
Santa Rita Experimental Range	1-132	Transects
Survey of National Parks	175-963	Points

Table 2. Variables evaluated for inclusion in the logistic regression model, bold text indicates variables selected for model.

Variable	Explanation
Summer precipitation	Total precipitation from June to September (cm)
Winter precipitation	Total precipitation from October to March (cm)
Annual precipitation	Total annual precipitation (cm)
Summer high temperature	Average daily maximum air temperature Jun – Sep (°C)
Winter low temperature	Average daily minimum air temperature Oct – Mar (°C)
Annual average temperature	Annual average air temperature (°C)
Annual high temperature	Annual maximum air temperature (°C)
Annual low temperature	Annual minimum air temperature (°C)
Radiation	Daily total shortwave radiation ($MJ/m^2/day$)
Surface sand	Percent sand in the top 10-cm
Surface clay	Percent clay in the top 10-cm
Surface silt	Percent silt in the top 10-cm
Sand in profile	Percent sand in the soil layers to 1-m depth
Clay in profile	Percent clay in the soil layers to 1-m depth
Silt in profile	Percent silt in the soil layers to 1-m depth
Depth to bedrock	Depth to bedrock (cm)
Elevation (m)	
Slope (%)	
Aspect (cosine; range +1 to –1)	

Table 3. Results from global climate model calculations averaged over the southwestern United States region for 2030.

	Temperature °C		Precipitation (mm/day)	
	Hadley Center	Canadian Climate Center	Hadley Center	Canadian Climate Center
Winter	2.5	3	1	1.5
Spring	1.5	2	0.5	0.3
Summer	1.5	2	0.3	0
Fall	1.5	1.5	0	0.5

Table 4. Summary of accuracy assessment of the logistic regression based on evaluation dataset of known absence locations and the presence observations excluded from the analysis.

		Observed Response	
		Present	Absent
Predicted	Present	145	35
Response	Random	38	182
	Total (n)	183	217

Accuracy Assessment		
Sensitivity	145/183	79.2%
Specificity	182/217	83.9%
Overall Accuracy	$\frac{(145 + 182)}{(183 + 217)}$	81.8%

Table 5. Summary statistics for coefficients of variables selected in the stepwise logistic regression procedure to distinguish between *E. lehmanniana* locations (n = 183) and random locations (n = 217).				
Parameter	**Estimate**	**Standard Error**	**Wald ChiSq**	**Pr > ChiSq**
Intercept	-14.5496	3.093	22.1285	<.0001
Percent clay in soil surface	0.1655	0.0376	19.3366	<.0001
Percent sand in soil surface	0.1165	0.0282	17.1078	<.0001
Average winter low temperature	1.1328	0.2963	14.6195	0.0001
Total summer precipitation (Jul-Aug-Sep)	0.5308	0.1471	13.0122	0.0003
Winter low x Summer precipitation	0.0446	0.0154	8.4093	0.0037
Total winter precipitation (Nov-Dec-Jan)	0.0194	0.121	0.0257	0.8727
Winter low x Winter precipitation	-0.0658	0.00858	58.7679	<.0001
Summer precipitation x Winter precipitation	-0.0122	0.00617	3.9228	0.0476
Slope	0.2743	0.071	14.9372	0.0001
Clay x slope	-0.0088	0.00355	6.1405	0.0132
Winter low temperature x slope	0.0227	0.0136	2.8053	0.094

Table 5. Estimates of the amount of area invaded by *Eragrostis lehmanniana*

Acreage (hectares)	Methods	Reference
145,155 ha	Qualitative field assessment, areas where *E. lehmanniana* was planted and spread	Cox & Ruyle 1986
594,632 ha	Qualitative field assessment, areas classified as dominated by *E. lehmanniana*	The Nature Conservancy 2003
414,600 ha	Quantitative and qualitative field assessments incorporated into statistical model, areas with a 90% probability of *E. lehmanniana*	Geiger et al. , this study

Table 6. Area predicted to be invaded by *E. lehmanniana* based on current conditions and under two common general circulation models in 2030.

	Study Area (ha)	Arizona (ha)
	Current Probability Model	
90%	414,600	784,900
80%	1,124,100	1,727,900
70%	1,663,800	2,489,300
	Hadley Center Model	
90%	5,000	109,800
80%	27,700	247,400
70%	193,100	489,200
	Canadian Climate Center Model	
90%	500	96,100
80%	1,100	146,800
70%	9,900	251,300

Appendix 1. Pearson product moment correlation coefficient between explanatory variables assessed for inclusion in the model based on all cell locations in the study area.

Climate Variables	Summer high	Winter low	Summer precip.	Winter precip.	Percent summer rain	Annual avg. temp.	Annual max. temp.	Annual min. temp.	Annual precip.	Radiation
Summer high temperature (°C)	1.00									
Winter low temperature (°C)	0.86	1.00								
Summer precipitation (mm)	-0.56	-0.20	1.00							
Winter precipitation (mm)	-0.09	0.31	0.37	1.00						
Percent summer rain	-0.35	-0.44	0.45	-0.64	1.00					
Annual average temperature (°C)	0.87	0.92	-0.27	0.19	-0.38	1.00				
Annual maximum temp. (°C)	0.80	0.85	-0.22	0.20	-0.34	0.98	1.00			
Annual minimum temp. (°C)	0.91	0.97	-0.32	0.17	-0.41	0.97	0.90	1.00		
Annual precipitation (mm)	-0.36	0.08	0.69	0.92	-0.31	-0.04	-0.01	-0.07	1.00	
Short-wave radiation	-0.34	-0.42	0.29	-0.28	0.56	-0.31	-0.21	-0.43	-0.10	1.00

Appendix 1 cont. Pearson product moment correlation coefficient between explanatory variables assessed for inclusion in the model based on all cell locations in the study area.

Soil Variables	Surface clay	Profile clay	Surface sand	Profile sand	Surface silt	Profile silt	Depth to bedrock
Surface clay (%)	1.00						
Profile clay (%)	0.91	1.00					
Surface sand (%)	-0.70	-0.63	1.00				
Profile sand (%)	-0.72	-0.75	0.92	1.00			
Surface silt (%)	0.07	0.10	-0.26	-0.17	1.00		
Profile silt (%)	-0.03	-0.12	-0.11	-0.09	0.81	1.00	
Depth to bedrock (cm)	0.04	0.13	0.06	0.03	0.09	-0.06	1.00

Topographic Variables	Elevation	Slope	Cosine (Aspect)
Elevation (m)	1.00		
Slope incline (%)	0.16	1.00	
Aspect (cosine)	0.01	-0.04	1.00

Appendix 2. Pearson product moment correlation coefficient based on the samples in the binary response dataset between explanatory variables included in the model.

	Surface clay	Surface silt	Depth to bedrock	Winter low	Summer precip	Winter precip	% summer precip	Radiation	Elevation	Slope	Cosine (Aspect)
Surface clay	1.00										
Surface silt	0.08	1.00									
Depth to bedrock	0.11	0.03	1.00								
Winter low	-0.17	-0.08	0.12	1.00							
Summer precip	0.05	0.13	-0.02	-0.25	1.00						
Radiation	0.24	0.18	0.09	-0.50	0.30	-0.24	0.49	1.00			
Slope	-0.20	-0.02	-0.34	-0.02	0.10	0.23	-0.11	-0.17	0.18	1.00	
Cosine (aspect)	0.05	0.03	0.12	0.00	0.09	-0.12	0.19	-0.13	-0.04	-0.17	1.00