The invasion risk in the Pacific Northwest of two closely related grass species in the Genus *Cortaderia*

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Abstract

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The distribution of *Cortaderia selloana* and *Cortaderia jubata* in the Pacific Northwest (PNW) has not been examined on a regional scale although geospatial information exists. *Cortaderia selloana* continues to be sold in nurseries across Oregon and Washington and both species are used as landscape plantings. With invasive tendencies in California and abroad, and multi-age populations found across Washington and Oregon, what risk of invasion do these two species pose for the Pacific Northwest? Research efforts focuses on two questions: 1) Is there a pattern to distribution of *Cortaderia* occurrences/records that might help offer more evidence for the invasion risk to the Pacific Northwest? 2) What is each species' potential for invasion in the Pacific Northwest? Two analyses were used to answer the above questions: geospatial and species distribution models. Geospatial analyses compared 83 existing records for both species with landscape features and other GIS data to find patterns or associations. Species distribution modeling was performed using a maximum entropy model program: MaxEnt. There are more *C. jubata* occurrences but they are mostly restricted to the mid and southern coast of Oregon whereas *C. selloana* is more likely to be found is more widely throughout the study area The majority of occurrences of both species were found in developed land cover types. There is a significant difference in the distribution of *C. selloana* and *C. jubata* with regard to distance to railroad, annual precipitation, and spatial location as measured by northing. Species distribution modeling outputs under current climate conditions indicate a broarder range for *C. jubata* than *C. selloana*. Both species increase potential areas of climate suitability under future climate scenarios. There does not seem to be a climate constraint for the future expansion of either species within the study area. It is likely that both species will continue to pose an invasion risk into the future. Early detection surveys should focus on developed areas, especially for *C. selloana*.

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Introduction

Biotic invasions are altering the world's natural communities and their ecological character at an unprecedented rate (Mack et al 2000). Invasions by non-native species are threatening conservation of native species and the integrity of ecosystems worldwide (Vitousek et al. 1996, Mack et al. 2000). Even before a species becomes, or is categorized as invasive, it needs to be introduced on to the landscape. Introductions can occur through natural or random events or through deliberate introductions. Focusing on plants, the horticultural trade is a major pathway of deliberate introduction for non-native species on to new landscapes (Reichard and White 2001). The large plumes of *Cortaderia selloana* (*Schult. & Schult.*) Ascherson *& Graebner* and *Cortaderia jubata* (*Lemoine ex Carrière*) (*Staph*) make them attractive as garden plants and they have become cultivated worldwide as a result of the global nursery trade (Lambrinos 2001). Both grass species, native to South America, are considered naturalized and/or invasive in Mediterranean climates of the world (EPPO 2014). *Cortaderia selloana* is native to Argentina, Brazil and Uruguay, where it grows along river margins (DiTomaso et al 1999). *Cortaderia jubata* is native to northern Argentina, and along the Andes of Bolivia, Peru, and Ecuador (DiTomaso et al. 1999, Costas-Lippmann 1976). The source of the cultivated stock, and since invasive, *C. jubata* is most likely from populations found in Ecuador and southern Peru (Okada 2009). Both species can attain a size between 2-4 meters height and 2 meters width (DiTomaso et al 1999). *Cortaderia selloana's* underground growth is just as prodigious, with roots 4 meters wide and reaching 3.5 meters in depth (Harradine 1991).

The invasiveness of *C. selloana* and *C. jubata* in California and other Mediterranean climates is documented in the literature. *Cortaderia selloana* has been the focus of study in

Europe (Domenech and Vila 2007, Domenech and Vila 2008, Bacchetta et al. 2013), New Zealand (Gosling et al., 2000, Okada et al 2009), South Africa (Robinson, 1984), and California (Ahmad et al. 2006, Lambrinos 2001 and 2002, Okada et al. 2007, Stanton and DiTomaso 2004, Vourlitis and Kroon 2013). *Cortaderia jubata* has been studied in New Zealand (Gosling et al., 2000), South Africa (Robinson, 1984), and California (Lambrinos 2001 and 2002, Stanton and DiTomaso 2004, Drewitz and DiTomaso 2004, Okada et al 2009). *Cortaderia selloana* and *C. jubata* both scored as "High Risk" for the USDA Weed Risk Assessment (USDA-APHIS 2014)

These two closely related species have different reproductive strategies and seem to have different tolerances for environmental conditions. *Cortaderia selloana* is an obligate outcrosser and considered gynodeiciuous (Conner 1973). There are female only plants and plants with functional male inflorescences and sterile female inflorescences so, while *C. selloana* is technically gynodeiciuous, it can be considered functionally dioecious (Connor and Charlesworth 1989). In its invaded range, where only females are known, *Cortaderia jubata* produces asexually with all offspring being clones of parent plant (Connor 1973). Regardless of reproductive strategy both species produce a large amount of small wind dispersed seed; as much as 1 million seeds per individual (Lambrinos 2002, Drewitz and DiTomaso 2004). The seeds of *C. jubata* have been shown to travel as far as 20 miles under ideal conditions and little or no longevity (Gadgil et al. 1984). Vegetative reproduction can occur through rooting of tillers under moist conditions (DiTomaso et al 1999). Research in California shows habitat preferences of the two species; *C. jubata* performs best in the narrow environmental conditions found along the coast, while *C. selloana* found in both coastal and inland habitats exhibits a greater tolerance for environmental conditions (Bossard et al 2000, Lambrinos 2002, Okada et al. 2007). Both species are restricted to low elevations (Lambrinos 2001). *Cortaderia jubata* is found in uplands along the coast where it occupies primarily open areas like road cuts and recently cleared sites (Bossard et al 2000, DiTomaso et al 1999). *Cortaderia selloana* is less restricted and is found along the coast as well as inland wetland and riparian systems (Bossard et al 2000). Compared to *C. jubata, C. selloana* can tolerate frost, warmer temperatures, more intense sunlight, and better drought resistance (Costas-Lippman 1976, DiTomaso 1999 et al).

The distribution of these two *Cortaderia* species in the Pacific Northwest has not been examined on a regional scale although, geospatial information exists. The two species are considered noxious weeds by Washington State, whereas only *C. jubata* is listed as a noxious weed in Oregon (WNWCB 2014, ODA 2015). Okada et al. (2007) concluded that the multiple introduction of *C. selloana* in California through landscape plantings contributed to the species invasive expansion in that state. Further contributions to the spread of *C. selloana* in California could be due to increased nursery production of the plant by seed, which increases the potential for male plants, since the presence of functionally male plants increases the potential for viable seeds (DiTomaso et al. 1999). The potential for increased seed production from landscape plants will likely increase the propagule pressure for *C. selloana* which could drive its expansion. Invasion biology theory suggests that disturbance and native community richness can drive or constrain invasion, however, propagule pressure can overcome these drivers resulting in successful establishment (Von Holle and Simberloff 2005). Propagule pressure is the cumulative effort of a plant's propagules by seed or vegetative parts, on a new or introduced landscape and often linked to probability of establishment on a site (Davis et al 2016). *Cortaderia selloana* continues to be sold in nurseries across Oregon and Washington and both species are frequently encountered as landscape plantings throughout the Pacific Northwest. If multiple introductions of *C. selloana* helped to contribute to the expansion of the invasive grass in California, does its presence as an ornamental planting in the Pacific Northwest create similar conditions for invasion? Herbarium records in Oregon and Washington of the two species seem to fit, more or less, the same pattern of preference in California: *C. jubata* is invasive along the coast and restricted to the southwest corner of Oregon and *C. selloana* is in scattered patches inland and some along the coast (Consortium of Pacific Northwest Herbaria 2014). This rests on the assumption of correct species identification.

With known invasive tendencies in California, and the number of non-intentional multi-age patches found across Washington and Oregon, what risk of invasion do these two species pose for the Pacific Northwest? This is the overall question this study is seeking to answer. This question is relevant since both *Cortaderia* species were added to the Washington State Noxious Weed list as a class C noxious weed in 2015. Class C noxious weeds in Washington State are defined as plants that, when established, are highly destructive, competitive, or difficult to control by cultural or chemical practices. These plants do not fit into the class A or B categories, and are typically common and widespread; control is generally not required for class C (RCW 17.10.010, WNWCB 2015). Although Class C category plants are typically widespread, this is not the case for the two listed *Cortaderia* species. While both plants are on the noxious weed list in Washington neither are on the quarantine list. It is still legal to sell and import them into Washington. The Oregon Department of Agriculture Noxious Weed Control Program lists *Cortaderia jubata* as a class B weed. *Cortaderia selloana* is not listed as a noxious weed in that Oregon, only *C. jubata*. In Oregon, class B noxious weeds are defined as a weed whose impact is of economic importance which is regionally abundant, but which may have limited distribution in some counties. Intensive action for control is site specific on a case-by-case basis (ODA 2015). In the state of Oregon listing a plant on the noxious weed list also restricts its import into and sale within the state (OAR 2016). Little research has been done on these species in Washington or Oregon. An unpublished report looked at the microsatellite diversity of two expanding populations of *Cortaderia* in Washington State. It was concluded that both populations have genetic diversity similar to what is expected in *Cortaderia selloana* and not *Cortaderia jubata* (Jasieniuk and Kern 2014).

Through analysis of *Cortaderia* populations in Oregon and Washington this study aims to gather all available evidence in order to answer the question of invasion risk for *C. selloana* and *C. jubata*. Also, by examining the geospatial records across landscape variables and other GIS information, a pattern might emerge that would indicate invasion trends for one or both of these species. I expect that human-impacted land-use types to be associated with *C. selloana* since the species responds best to conditions favoring ruderal plants with frequent disturbance and its major introduction pathway is through ornamental plantings (Lambinos 2002, Okada et al. 2007). Based on casual observations of *Cortaderia* patches (adventive or otherwise) in Washington, proximity to the railroad lines seems to be a similarity most patches share. This will be examined on a larger scale. The species distribution model will examine both species' potential climate niche under current climate conditions and future climate projections in 2050 and 2070 based on a moderate emissions scenario.

My research attempted to answer the overarching question of invasion risk that these two grass species pose in the Pacific Northwest, specifically in Oregon and Washington. Research efforts focuses on two more specific questions:

- What is each species' potential for invasion in the Pacific Northwest? The presence of *Cortaderia* as an ornamental feature in the landscape and the number of multi-age stands found across Washington and Oregon create conditions for invasion similar to California where multiple introductions of *C. selloana* helped to contribute to the expansion of the invasive grass. Examining the potential distribution of *Cortaderia* can offer insight about the expansion potential for both species.
- Is there a pattern to the distribution of *Cortaderia* occurrences/records that might help offer more evidence for the invasion risk to the Pacific Northwest? The pattern of distribution of available *Cortaderia* records of occurrences and potential association with landscape features might offer some evidence for the risk of invasion across Oregon and Washington.

Examining the distribution of both *Cortaderia* species will allow better understanding of the risk that *Cortaderia* does or does not pose. This will allow land managers and noxious weed programs to better allocate resources toward or away from *Cortaderia* control. This study will also establish strong baseline documentation for future researchers should these two grass species become more invasive across the Pacific Northwest.

Methods

Geospatial Analysis:

The spatial scope of this study was Oregon and Washington states and hereafter referred to as the study area. Through geospatial analysis I used all available geospatial records that exist for *C. selloana* and *C. jubata* to determine if any patterns or associations exist between the population, the location, and some features of the landscape. There are three major datasets and one other source used for reliable geospatial data:

- Consortium of Pacific Northwest Herbaria (Oregon and Washington)
- Oregon Department of Agriculture Weed mapper
- Oregon *iMap*Invasives
- Records from county noxious weed programs in Washington State

The collected occurrence records were analyzed using ArcGIS software (ESRI, Redlands, CA, USA) against available layers that might indicate site preference, identify pathways, or other associations to landscape features (Table 1). *Cortaderia* occurrences described as landscape plantings in the records were not used as part of this analysis. Any occurrences documented as one individual plant was also be omitted to prevent counting intentional plantings and single escapes in order to capture only the populations showing potential invasive behavior. Land use was determined based on the cell values from the National Land Classification 2011 database (Homer et al 2015) (Table 2). Linear features like road and rail lines used a point to feature tool in ArcGIS to determine distance from the occurrence record. Hydrologic soil group (HSG) and available water storage (0-150cm) (AWS) are two soil characteristics from the gSSURGO database that were examined. Available water storage is the volume of water that the soil, to a depth of 150 cm, can store that is available to plants (NRCS 2016). Stanton and DiTomaso found that *C. selloana* was significantly more tolerant of drought conditions in a greenhouse setting than *C. jubata* and Vourlitis and Kroon (2013) showed water table manipulation had no effect on total leaf area production of *C. selloana*. I expect that *C. selloana* to be associated with soils across a wider range of average AWS values than *C. jubata*. Hydrologic soil group is a classification of soil condition that categorizes the infiltration rate and by proxy soil properties (NRCS 1993). The groupings are described as followed:

- **Group A** - Soils having a high infiltration rate when thoroughly wet and consist mainly of deep, well drained to excessively drained sands or gravelly sands.
- **Group B** - Soils having a moderate infiltration rate when thoroughly wet and consist mainly of moderately deep or deep soils, moderately well drained or well drained soils that have moderately fine texture to moderately coarse texture.
- **Group C** - Soils having a slow infiltration rate when thoroughly wet and consist mainly of soils having a layer that impedes the downward movement of water or soils of moderately fine texture or fine texture.
- **Group D**- very low infiltration rates when thoroughly wetted and consist mainly of clay soils.
- **Group A/D, B/D, and C/D**- Soils having a two letter grouping indicates soil infiltration for drained areas (first letter) and undrained areas (/D). (NRCS 1993)

Domenech and Vila (2008) found *Cortaderia selloana* to have significantly higher germination rates in sandy soils. I expect both species to be associated mostly with well drained soils hydrologic soils group A or B.

Climate variables used were mean annual temperature and annual precipitation taken from the Worldclim Bioclim dataset (Hijmans et al 2005). Precipitation is known to drive plant growth and germination in Mediterranean climates (Espigares and Peco, 1993). Temperature, especially near freezing has been suggested as a driver of the distribution pattern of both species in California (Stanton and DiTomaso 2004). The distribution of the two species seem to be somewhat separated along a north-south gradient with most of the *C. jubata* in the south and more *C. selloana* north into Washington. Examining the occurrences based on the UTM equivalent of latitude, northing, will test this. Looking at only northing is appropriate since all but one of the records available are located west of the Cascade Mountains in a narrow east-west boundary.

Table 1. GIS feature classes to use for analysis of Cortaderia and the type of analysis used. Note for raster layers the cell size in parenthesis.

Nominal quality	Feature class name	feature class type (cell size)	Type of analysis
Land use	NLCD2011	raster (30m)	count of cell value at point
pathway	WA Roads	polyline	distance to feature/buffered intersection
pathway	OR Roads	polyline	distance to feature/buffered intersection
soil characteristics	gSSURGO-WA	raster (10m)	count of cell value at point
soil characteristics	gSSURGO-OR	raster (10m)	count of cell value at point
pathway	WA Rails	polyline	distance to feature/buffered intersection
pathway	OR Rails	polyline	distance to feature/buffered intersection
climate variable	bio1- annual mean temperature	raster (91m)	count of cell value at point
climate variable	bio12- mean precipitation	raster (91m)	count of cell value at point

Table 2. List of land use values and classification/type used in the National Land Cover Database (NLCD). Values/Classes 51,72, 73,and 74 were omitted since they pertain only to Alaska (Homer et al 2015).

Class\ Value	Classification	Class\ Value	Classification
Water		**Shrubland**	
11	**Open Water**	52	**Shrub/Scrub**
12	**Perennial Ice/Snow**	**Herbaceous**	
Developed		71	**Grassland/Herbaceous**
21	**Developed, Open Space**	**Planted/Cultivated**	
22	**Developed, Low Intensity**	81	**Pasture/Hay**
23	**Developed, Medium Intensity**	82	**Cultivated Crops**
24	**Developed High Intensity**	**Wetlands**	
Barren		90	**Woody Wetlands**
31	**Barren Land (Rock/Sand/Clay)**	95	**Emergent Herbaceous Wetlands**
Forest			
41	**Deciduous Forest**		
42	**Evergreen Forest**		
43	**Mixed Forest**		

Processing of the geospatial data in GIS

Over 330 records existed in total from the three primary datasets within the study area. Of the total 39 specimen records found within the Consortium of Pacific Northwest Herbaria more records exist for *C. selloana* (31) than for *C. jubata* (8) with the more records coming out of Oregon (25) than Washington (12). The *iMap* Invasives and ODA Weedmapper had 157 and 151 records respectively, but many of these were duplicates. The Oregon *iMap* invasives dataset had substantially more records for *C. jubata* (144) than *C. selloana* (13). Point feature classes were created from the latitude and longitude coordinates listed in the records of occurrences within each dataset. All datasets were processed by removing erroneous or duplicate records, reducing the total number of records from over 300 to 176. Duplicates were determined based on spatial location and was identified using ArcGIS tool “Delete Identical”. Erroneous records were records in which the coordinate information did not match the information provided (e.g. a record whose spatial coordinates put it in Washington but the written description placed in a national park in New Zealand). An additional 16 occurrence points were removed from the *iMap* since the metadata described these occurrences as having only one plant. The post processing breakdown of records: 18 from PNW Consortium of Herbaria, 6 from Noxious Weed coordinators in Washington state, 9 from ODA Weedmapper, and 51 from *iMap* invasives Oregon, for a total of 83 occurrences; 27 *Cortaderia selloana* and 56 *Cortaderia jubata* (Figure 1). These 83 post processed records were used as the dataset in the GIS analysis. Of the 18 records within the PNW Consortium of Herbaria of 8 records describe the plant(s) as either adventive, naturalized, expanding, or spreading. All occurrence records were merged into one working shapefile and used the Universal Transverse Mercator UTM 10 N coordinate system and North American Datum (NAD) 1983 as the datum for display and analysis in ArcGIS.

Figure 1. Map display of the 83 post processed occurrence records; 55 records for C. jubata (white triangles) and 28 records for C. selloana (black circles). Study area is depicted in light gray and covers Oregon and Washington State.

Map created by D Sorensen using ESRI ArcGIS Software
Sources
Study area: 2006 Oregon Geosaptial Enterprise Office (GEO) http://www.oregon.gov/DAS/CIO/GEO/pages/alphalist.aspx accessed 04/06/2015
Herbarium Records: Consortium of Pacific Northwest website, www.pnwherbaria.org, accessed 03/15/2015

Species Distribution Model

To determine a potential species distribution in Oregon and Washington, the *Cortaderia* occurrence records and climate data were used to determine where these two species could be fully distributed, a potential climate niche. This was done using the modeling software package MaxEnt version 3.3.3 by Phillips et al. (2010). MaxEnt is the most widely used presence only species distribution model package (Yackulic et al. 2013). MaxEnt matches the locality of the species occurrence with the environmental variable specified in each raster cell or pixel. This package uses a prior that assumes equally uniform distribution, or maximum entropy, so all cells are equally likely to contain an individual (Merow et al 2013). The resulting model output is a probability distribution over all the raster cells of the study area. The objective of the MaxEnt modeling method is to predict environmental suitability for the species as a function of the given environmental variables (Phillips et al 2006). The climate variables used for this study were **bioclimatic variables** for current climate conditions (1950-2000) and future climate projections in 2050 and 2070. The “Bioclim” datasets were prepared and distributed by WorldClim (Hijmans et al 2005) derived from the monthly temperature and precipitation values (Table 3). The Bioclim data are an aggregation of 19 climate parameters of precipitation and temperature displayed as a raster cell surface all have cell resolutions of 91 meters. Future climate Bioclim projections used the Community Climate System model (CCSM) climate model under a 60 representative concentration pathway (RCP) emission scenario (CESM 2016).

Table 3. The 19 climate parameters of Bioclim data used in the MaxEnt species distribution model. (Hijmans et al 2005)

BIO1 = Annual Mean Temperature
BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3 = Isothermality (BIO2/BIO7) (* 100)
BIO4 = Temperature Seasonality (standard deviation *100)
BIO5 = Max Temperature of Warmest Month
BIO6 = Min Temperature of Coldest Month
BIO7 = Temperature Annual Range (BIO5-BIO6)
BIO8 = Mean Temperature of Wettest Quarter
BIO9 = Mean Temperature of Driest Quarter
BIO10 = Mean Temperature of Warmest Quarter
BIO11 = Mean Temperature of Coldest Quarter
BIO12 = Annual Precipitation
BIO13 = Precipitation of Wettest Month
BIO14 = Precipitation of Driest Month
BIO15 = Precipitation Seasonality (Coefficient of Variation)
BIO16 = Precipitation of Wettest Quarter
BIO17 = Precipitation of Driest Quarter
BIO18 = Precipitation of Warmest Quarter
BIO19 = Precipitation of Coldest Quarter

The *Cortaderia* datasets used for this species distribution model (SDM) was identical to what was used for geospatial analysis: 83 presence points; 55 *C. jubata* and 28 *C. selloana.* Potential species distribution was determined based on the probabilistic outcomes of model runs provided as a logistic output. Six model runs were performed in total. Three for *C. selloana*: current climate, 2050, 2070 and the for *C. jubata*: current climate, 2050, 2070. Each model run had ten replicates using a cross-validate method for replication. The cross-validate method divides the data into equally sized folds or groups and uses all but one fold for training. The remaining fold is then used for model testing (Philips 2006). Overall model performance was tested for significance using a receiver operator curve (ROC) and testing the area under the curve or AUC. The AUC of a model is the probability that the model ranks a random presence site higher than a random background site from the study area. (Phillips et al 2009) An AUC greater than 0.5 indicates the model is not a random guess, however, it is suggested that a model with an AUC greater than 0.75 is considered informative (Elith and Burgman 2002). For these model runs the test AUC was averaged over the 10 replicates. The lower bound of climate suitability was determined from the output probability at a threshold of maximum test sensitivity plus specificity. This threshold was provided by MaxEnt. The climate dataset from Worldclim uses the World Geodetic System (WGS) 1984 datum as a spatial reference, this was initially used for the MaxEnt model outputs but was transformed to North American Datum (NAD) 1984 for further analysis in ArcGIS. The raster layers and subsequent polygon layers used UTM zone 10N as the spatial reference and the NAD 1984 datum. Post model processing of MaxEnt outputs involved taking the raw .asi file and converting it to raster in grid in GIS, then using the reclassify tool to change the values from the probabilistic grid to a binary one based on the threshold that maximized test sensitivity plus specificity for each species.

Statistical analysis

A series of statistical tests were performed for both the continuous and categorical data. Given the difficulty of running statistical tests on data with location data based on observation and non-sampled records, tests compared the variables against the two species. For continuous data (distance to rail, distance to road, available water storage, mean annual temperature, mean precipitation, and northing) a univariate binary regression models was run as a generalized linear model (GLM). In order to run the models, the two species were treated as binary data:

0=*Cortaderia jubata* and 1= *Cortaderia selloana*. If differences exist then the slope of the curve functions should be significantly greater than 0. A logit transformation was used to obtain curves from GLM analysis using the following formula:

$$\boldsymbol{P(x|y) = \frac{e^{a+\beta x}}{1+e^{a+\beta x}}}$$

If the curve significantly differs from zero, the null hypothesis, then the variables are distributed differently for two species within the study area. Additionally, odds ratio analysis determined a break point or modeled progression should a different relationship exist between the two species for each measured variable. The NLCD 2011 land use classification and the gSURRGO hydrologic soil grouping uses categorical data to describe variable condition. In order to test the difference between the two species and these variables, a Chi-squared goodness of fit test was performed. All statistical tests and analyze used the software R studio (R Core Team 2016).

Results

Land use

Developed land use classifications, NLCD values 21-24, contained the most of both species with *C. jubata* found more in open space and medium density and *C. selloana* found mostly in medium density. For *C. jubata*, evergreen forest had the most occurrences in any one land use type and for *C. selloana* medium intensity development had the most occurrences. *Cortaderia jubata* had 10 occurrences in forest and *C. selloana* had zero. With wetland land use types, eight *C. jubata* occurrences were only found in woody wetlands while two *C. selloana* occurrences were found in emergent herbaceous wetlands and two in woody wetlands (Table 4).

Table 4. Breakdown of cell counts and percentages for C. jubata and C. selloana for land use. Land use groups based on NLCD 2011 data set. Cell counts were determined by extract to point tool in ArcGIS 10.3.

		C. jubata		C. selloana	
NCLD value	Description	cell count	Percent of total species counts	cell count	Percent of total species counts
11	Open Water	0	0%	0	0%
12	Perennial Ice/Snow	0	0%	0	0%
21	Developed, Open Space	9	16%	2	7%
22	Developed, Low Intensity	6	11%	4	15%
23	Developed, Medium Intensity	8	14%	8	30%
24	Developed High Intensity	1	2%	4	15%
31	Barren Land (Rock/Sand/Clay)	1	2%	0	0%
41	Deciduous Forest	0	0%	0	0%
42	Evergreen Forest	10	18%	0	0%
43	Mixed Forest	1	2%	1	4%
52	Shrub/Scrub	8	14%	3	11%
71	Grassland/Herbaceous	4	7%	0	0%
81	Pasture/Hay	0	0%	0	0%
82	Cultivated Crops	0	0%	1	4%
90	Woody Wetlands	8	14%	2	7%
95	Emergent Herbaceous Wetlands	0	0%	2	7%

Table 5. Contingency table of cell counts for C. jubata and C. selloana for land use groups used in test of independence. Land use groups based on NLCD 2011 data set.

Species	Developed	Developed Open Space	Barren	Forest	Scrub/ shrub	Grassland	Cropland	Wetlands
C. jubata	16	2	0	1	3	0	1	4
C. selloana	15	9	1	11	8	4	0	8

Roads and Rail lines

The distance to rail line was more variable for both species than distance to road with a larger mean value too (Table 6). The mean distance to the closest road for *C. jubata* was 163 meters (SE 63) and 225 meters (SE 91) for *C. selloana*. The maximum distance to road was 3,454 meters for *C. jubata* and 2,157 meters for *C. selloana*. Road distance distribution was tight for both species (Figure 3). Distance to rail lines was considerably larger for both species. The mean distance to the closest railroad line for *C. jubata* was 31,484 meters (SE 3,686) and 5,702 meters (SE 2,626) for *C. selloana*. For rail distances, *C. jubata* has a wider distribution than *C. selloana* (Figure 2).

Table 6. The summary statistics for distance to railroad and road features for Cortaderia jubata and Cortaderia selloana within the study area. Distance was determined by near tool in the ArcGIS 10.3

Rail					
Species	n	Mean Distance To Rail	Standard Deviation	Standard Error	95% Confidence Interval
C. jubata	56	31,484	27,584	3,686	24,097- 38,871
C. selloana	27	5,702	13,646	2,626	303- 11,100
Road					
Species	n	Mean Distance To Road	Standard Deviation	Standard Error	95% Confidence Interval
C. jubata	56	164	470	63	38- 290
C. selloana	27	227	471	91	41-413

Figure 2. A violin plot of distances to rail line for the 56 Cortaderia jubata and 27 Cortaderia selloana occurrences in study area. Width determined by density of occurrences around value. Plot was made using R (R software team, 2016) and ggplot2 package (Wickham 2010).

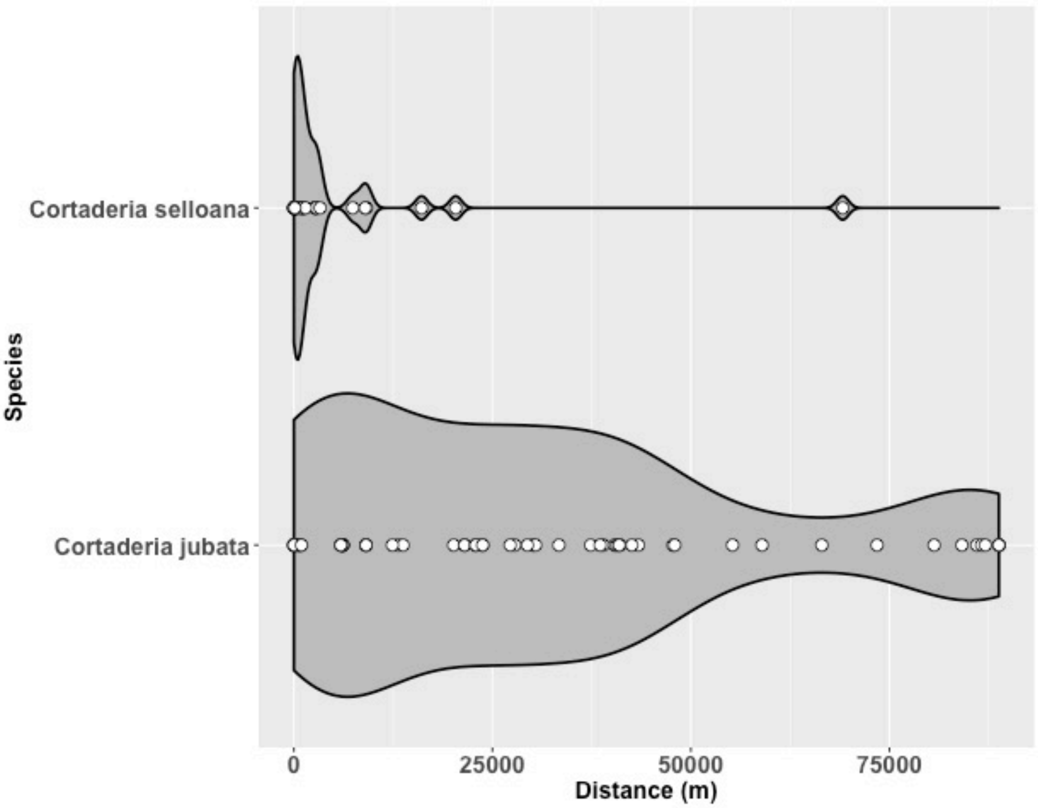
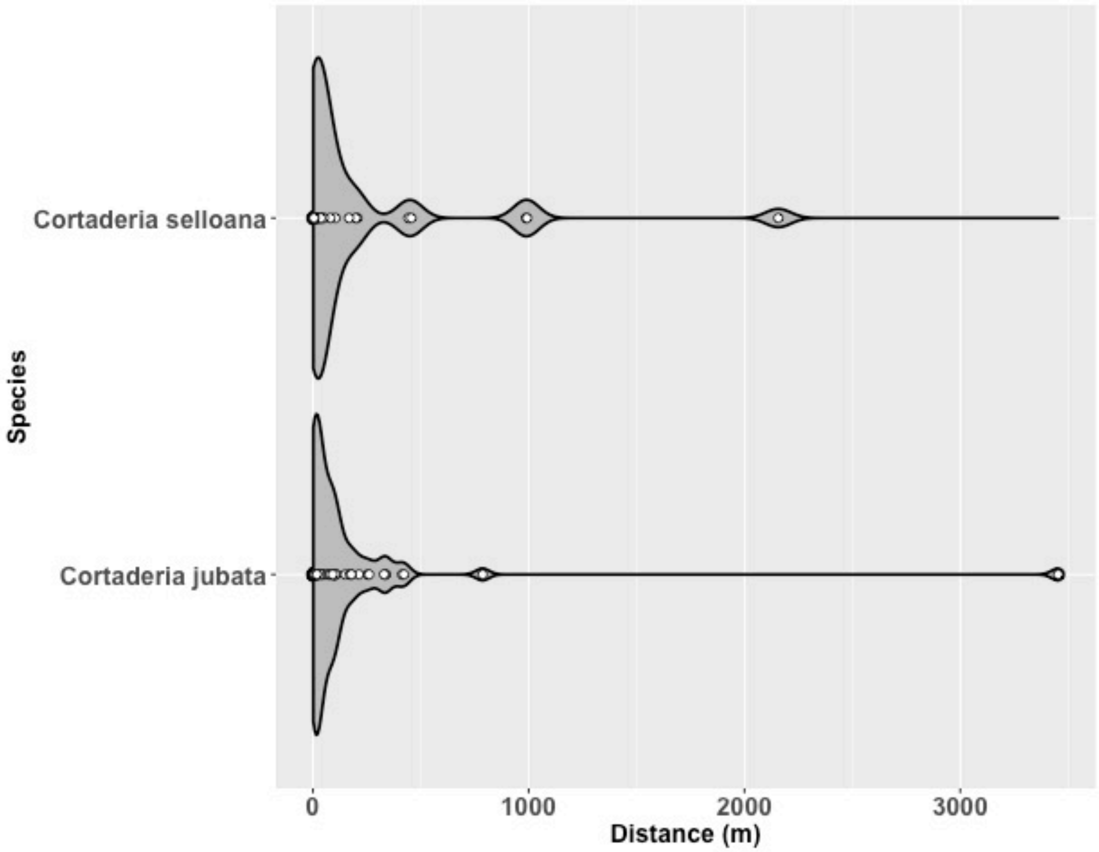


Figure 3. A violin plot of distances to closest road for the 56 Cortaderia jubata and 27 Cortaderia selloana occurrences in study area. Width determined by density of occurrences around value.



Soil characteristics

The distribution of available water storage values was very similar for both species (Figure 4). Using the weighted average available water storage (AWS) from 0-150 cm, the mean AWS for *C. jubata* was 19.54cm (SE 1.32) and 17.16 cm (SE 1.67) for *C. selloana*. *Cortaderia selloana* had a wider 95% confidence interval than *C. jubata* despite having a much lower sample size (Table 7). There were data missing from this layer resulting in 70 occurrence records used for analysis.

Table 7. The summary statistics for AWS in centimeters for Cortaderia jubata and Cortaderia selloana within the study area. AWS was determined by extract to point tool in the ArcGIS 10.3 using the gSSURGO dataset and the weighted average AWS 0-150 cm.

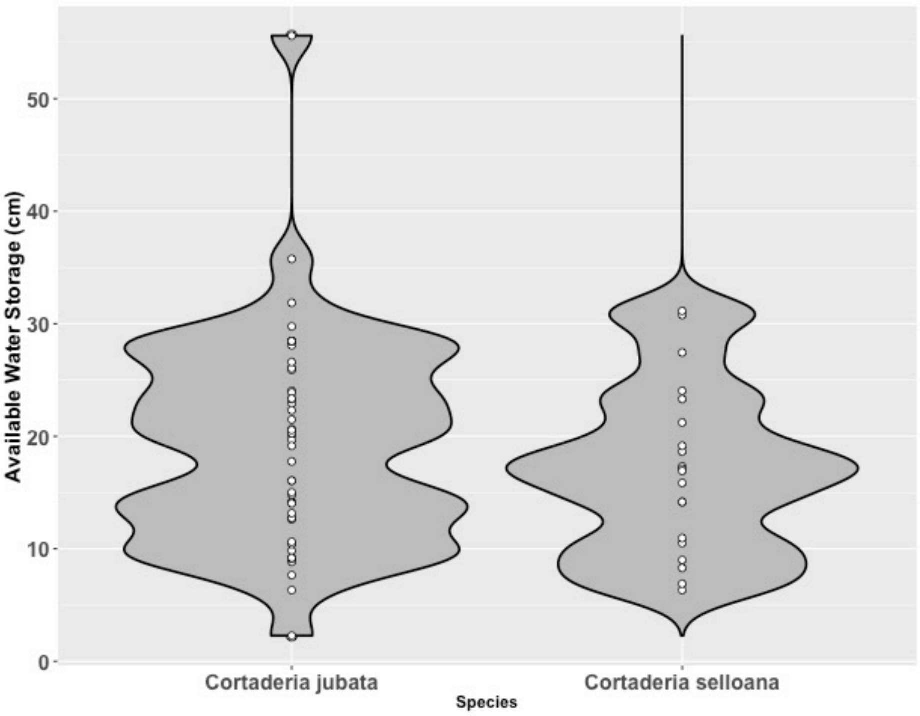
Species	n	Mean Aws (Cm)	Standard Deviation	Standard Error	95% Confidence Interval
C. jubata	50	19.54	9.36	1.32	16.88- 22.20
C. selloana	20	17.16	7.49	1.67	13.66- 20.66

Hydrologic soil groups B and C contained the most of either species (Table 8). Of the *C. jubata* occurrences, 65% were either in group B and C and 78% of *C. selloana* occurrences were either in group B or C. Fewer occurrences were found in soils classified as C/D, and D which have lower infiltration rates and tend to have more clay content (NRCS 1993). Five *C. jubata* occurrences were found in C/D classified soils and three found in D classified. While only one *C. selloana* occurrence was found in C/D classified soils and none found in D classified soils.

Table 8. Contingency table of cell counts for C. jubata and C. selloana for hydrological soil groups (HSG) used for test for independence. HSGs based on the gSSURGO data set.

Species	A	A/D	B	C	C/D	D
C. jubata	8	0	18	12	5	3
C. selloana	2	1	7	8	1	0

Figure 4. Violin plot showing the distribution of AWS weighted average from 0-150 cm values for Cortaderia jubata and Cortaderia selloana occurrences in study area. Width determined by density of occurrences around values.



Temperature and Precipitation

The mean annual mean temperature for both species was nearly identical although *C. jubata* had a wider distribution (Table 9 and Figure 5). The wider distribution is reflected in a larger 95% confidence interval for *C. jubata*. The mean annual mean precipitation for *Cortaderia jubata* was greater than *C. selloana* (Table 10). Both species had a similar range, *C. selloana* was more distributed across the range whereas most of the *C. jubata* occurrences were clustered at higher precipitation values (Figure 6).

Table 9. The summary statistics for mean annual temperature for Cortaderia jubata and Cortaderia selloana within the study area. Distance was determined by "Extract Values to Point" tool in the ArcGIS 10.3.

Species	n	Mean (C*10)	Standard Deviation	Standard Error	95% Confidence Interval
C. jubata	56	110.52	11.49	1.54	107.44- 113.59

C. selloana	27	110.56	4.63	0.89	108.73- 112.39

Table 10. The summary statistics for annual precipitation in millimeters for Cortaderia jubata and Cortaderia selloana within the study area.

Species	n	Mean (mm)	Standard Deviation	Standard Error	95% Confidence Interval
C. jubata	56	1674.91	397.99	53.18	1568.33- 1781.49
C. selloana	27	1364.96	469.12	90.28	1179.39-1550.54

Figure 5. Violin plot showing the distribution of annual mean temperature in degrees Celsius*10 values for the 56 Cortaderia jubata and 27 Cortaderia selloana occurrences in study area. Width determined by density of occurrences around values.

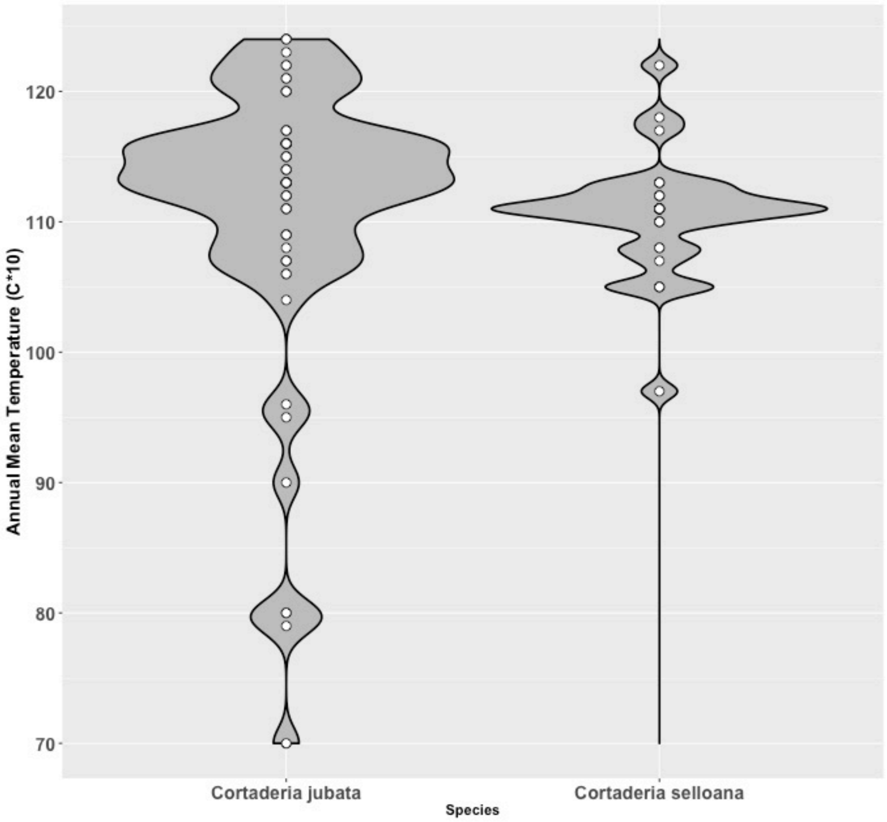
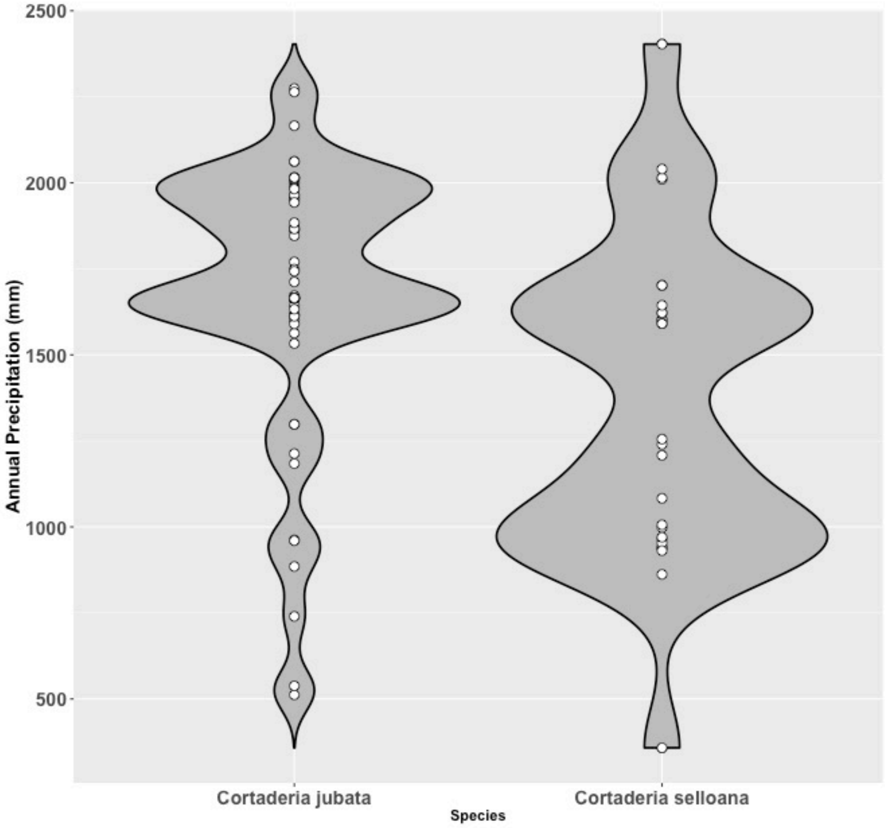


Figure 6. Violin plot showing the distribution of annual precipitation in millimeters (mm) values for the 56 Cortaderia jubata and 27 Cortaderia selloana occurrences in study area. Width determined by density of occurrences around value.



Latitude

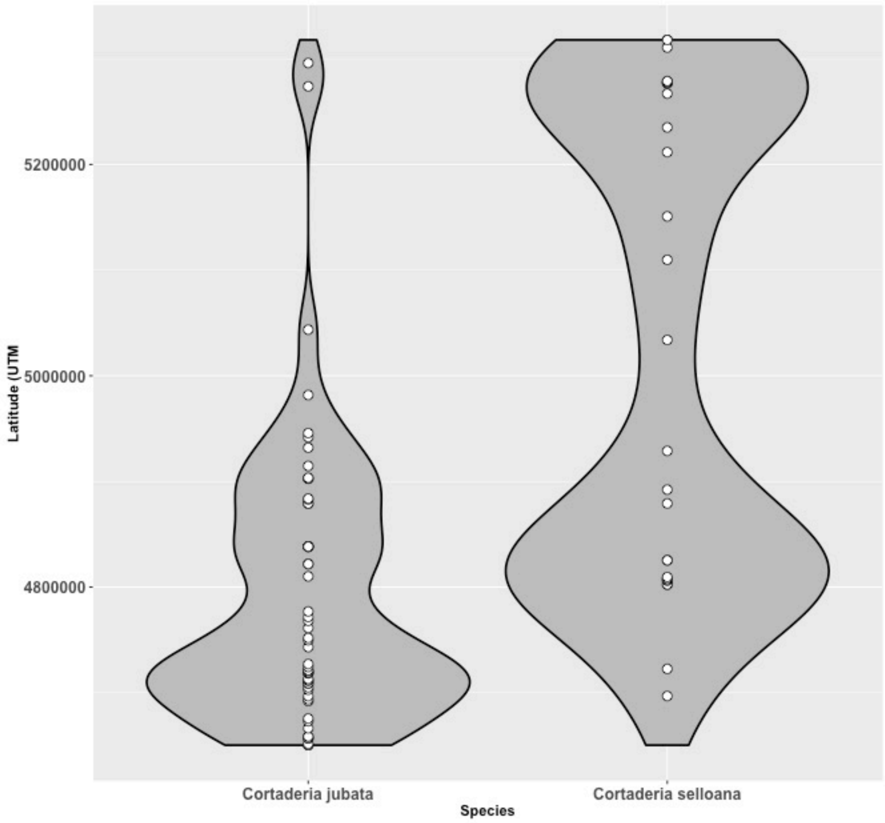
The breakdown of the two species across northing shows them to have a different north-south distribution. *C. jubata* occurrences have a mean UTM northing of 4,786,814 (SE 16081) which puts it south of the *C. selloana*'s mean northing of 5,026,241 (SE 42786) (Table 11). The distribution of the occurrences show *C. selloana* being distributed in two main area in areas of lower northing value (south), similar to *C. jubata*, and in areas with higher northing values (north) which differs from *C. jubata*'s more southerly distribution (Figure 7).

Table 11. The summary statistics for mean northing coordinate for Cortaderia jubata and Cortaderia selloana within the study area.

Species	n	Mean Northing	Standard Deviation	Standard Error	95% Confidence Interval

C. jubata	56	4,795,907	136,363	18,222	4,759,389 – 4,832,425
C. selloana	27	5,016,249	224,336	43,173	4.927,505- 5,104,993

Figure 7. Violin plot showing the distribution of northing (UTM) coordinates for the 56 Cortaderia jubata and 27 Cortaderia selloana occurrences in study area Width determined by density of occurrences around value.



Statistical Analysis

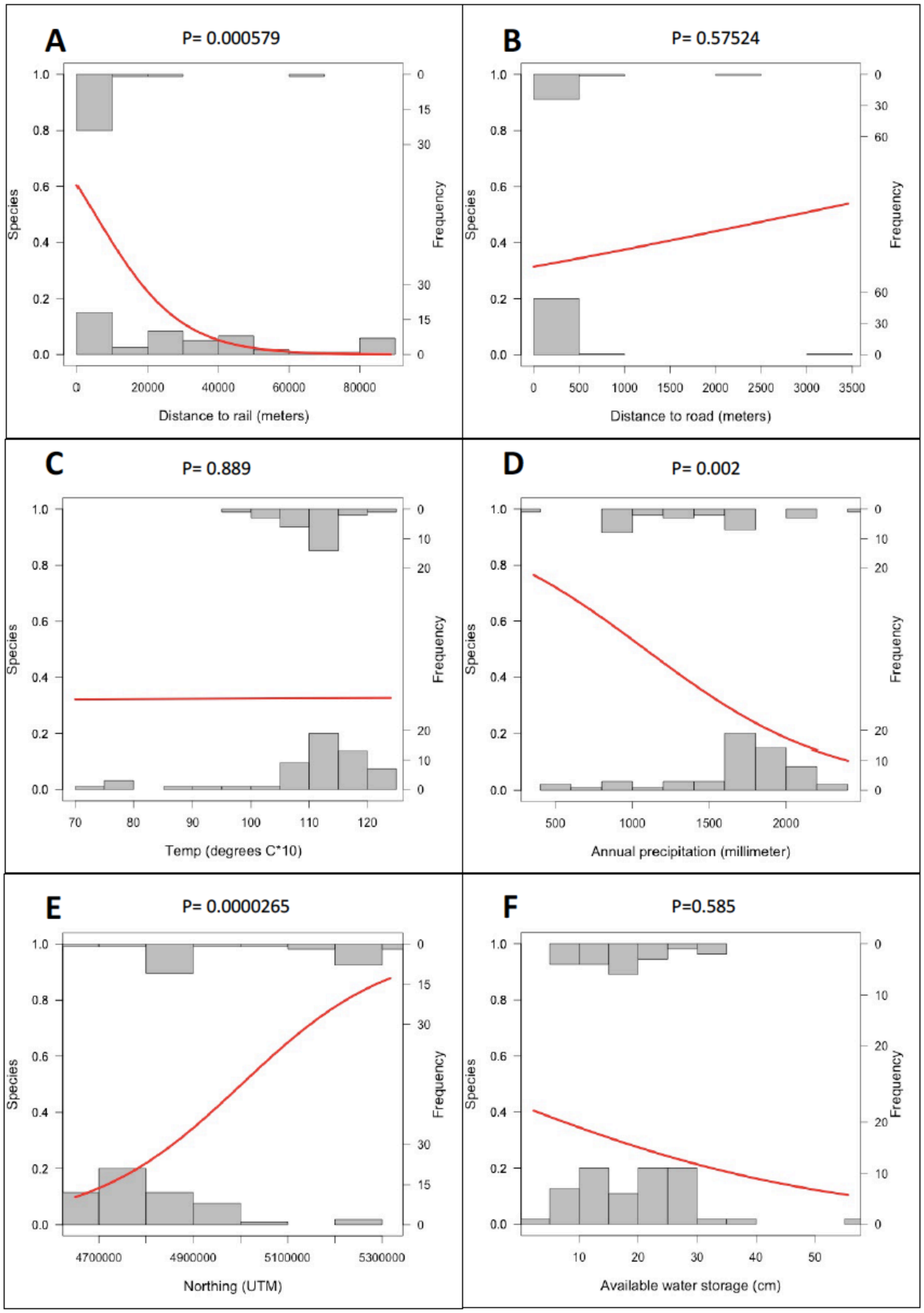
Logistic regression

The continuous variables were analyzed against the two species as general linearized model using the binomial distribution and a logit transformation. The slopes for distance to rail, annual precipitation, and northing were all significant from zero, meaning that for these variables, the distribution of *Cortaderia jubata* was different than the distribution of *Cortaderia selloana*. Distance to road, average water storage, and annual mean temperature were not significant from zero. Their slopes were not significantly different from zero (Figure 8). For the significant variables, odds ratios were calculated to determine the probability of one species occurring across the gradient of that variable. For distance to rail the estimated odds ratio was 0.000083 for each change in unit meter with a 95% confidence range 0.000141 to 0.000042. So for every increase in meter there is a 0.0083% increase in probability of being *C. jubata.* The change in probability between species is higher for annual precipitation. The odds ratio for annual precipitation was 0.00163, 95% confidence interval 0.0028 to 0.00055. For each one millimeter increase in precipitation there is a 0.163% in probability of being *C. jubata*. Conversely as precipitation decreased the probability of an occurrence being *C. selloana* increases by 0.163%. With each increase in northing the probability of an occurrence being *C. selloana* increase by 0.0006000%, 95% confidence range 0.0004000% to 0.0010000%. So the probability of an occurrence being *C. selloana* increases incrementally from south to north over the study area.

Chi-square Test for Homogeneity

The chi square value for the land use group results is 14.003 with a p-value = 0.051 making it equal to the significance level of 0.05. Under this condition the null hypothesis is rejected. The distributions of variables between the two species are not of equal proportions. The chi square value for hydrologic soil group results is 5.670 with a p-value = 0.34 much higher than the significant level of 0.05. The null hypothesis for hydrologic soil group is not rejected so the distribution of hydrological soil groups between the two species are of equal proportions.

Figure 8. Curves and p values of logistic GLM analysis comparing Cortaderia species to single variables extracted from geospatial analysis in ArcGIS. A) Distance in meters to nearest rail line. B) Distance in meters to nearest road. C) Available water storage potential of soil as a weighted average in centimeters. D) Annual temperature. E) Annual precipitation, F) Degrees latitude in metric units of UTM. Species are represented on the graph as 0 (Cortaderia jubata) or 1 (Cortaderia selloana). Gray bars are histogram of cell counts and match with frequency on the right y-axis. Plots were created using the popbio package in R (Stubben and Milligan 2007).



Overview of significant findings

The results of this analysis so far have looked at individual variables and not addressed overall pattern or associations between the occurrences and variables. To look at overall patterns and association of the variables and species' occurrences, significant findings were plotted. Distance to rail, precipitation, and northing coordinate were plotted and overlayed with species (shape) and land use (color) (Figures 9, 10, and 11). The plots show occurrences found in developed land use had closer distance to rail values and lower precipitation values. The plotting of northing and distance to rail show similar pattern (Figure 10). UTM northing and annual precipitation plot shows an association between developed land use, lower mean precipitation, and higher northing. There is a cluster of *C. selloana* located in Washington, above northing 51000, associated with developed land use and lower annual precipitation (Figure 11). There is also a cluster of *C. jubata* in the southern part of the study area, southern Oregon, associated with more forest, scrub, and grassland land use and range in annual precipitation between 1500 and 2000 millimeters (Figure 11).

Figure 9. Distance to rail meters plotted against annual precipitation for Cortaderia jubata and Cortaderia selloana. Selected land use classifications used to determine point color. Plots were created in R using the popbio package (Stubben, and Milligan 2007).

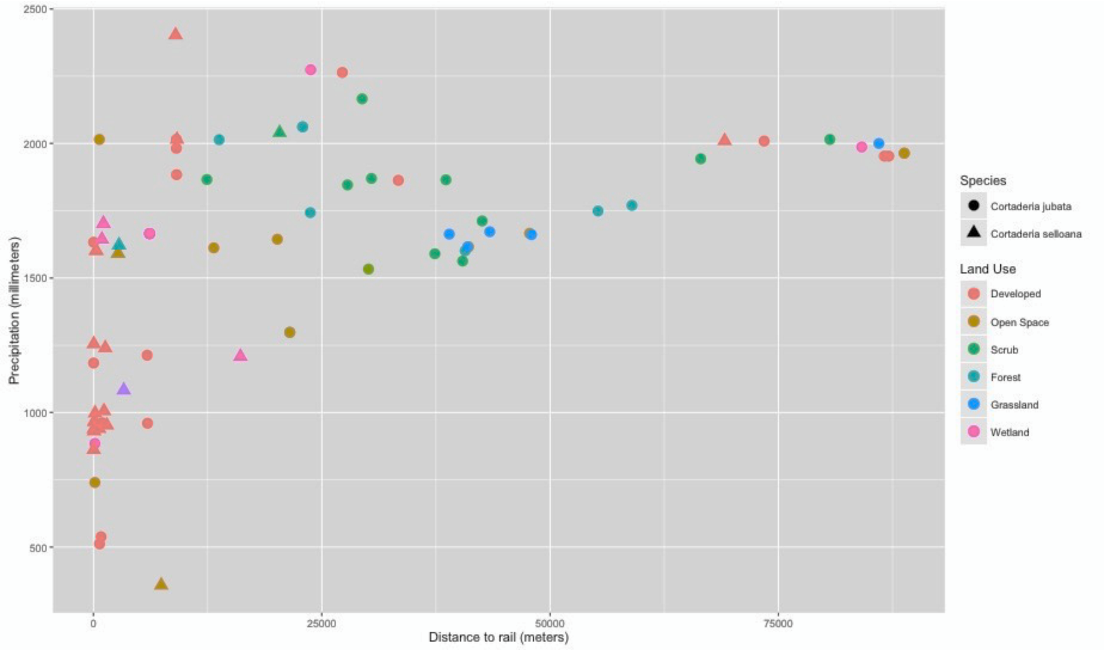


Figure 10. Distance to rail in meters plotted against the northing UTM coordinate for Cortaderia jubata and Cortaderia selloana. Selected land use classifications used to determine point color.

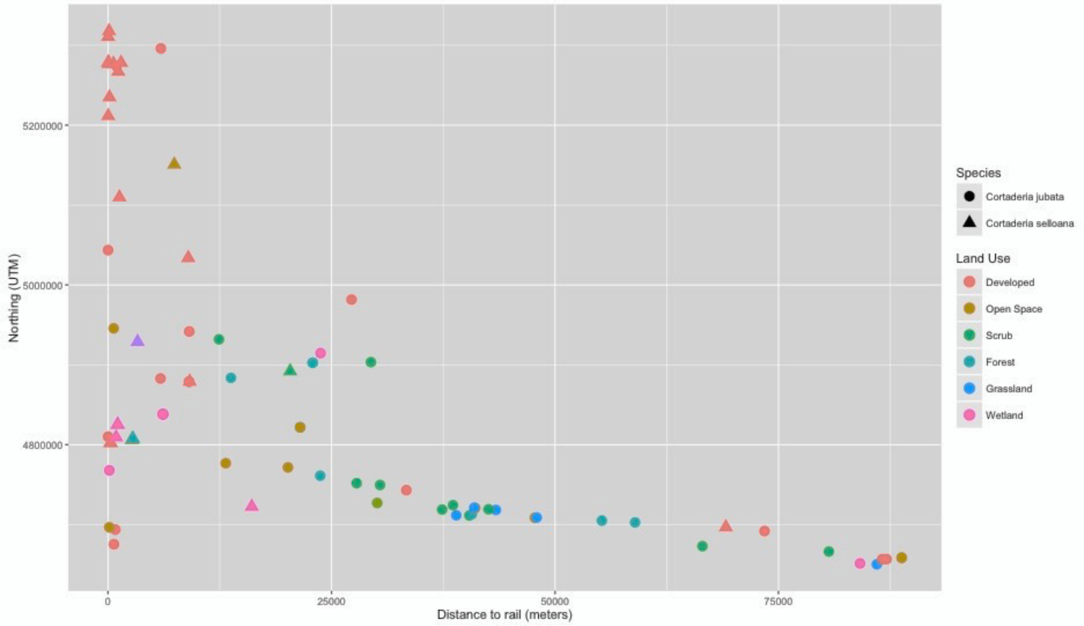
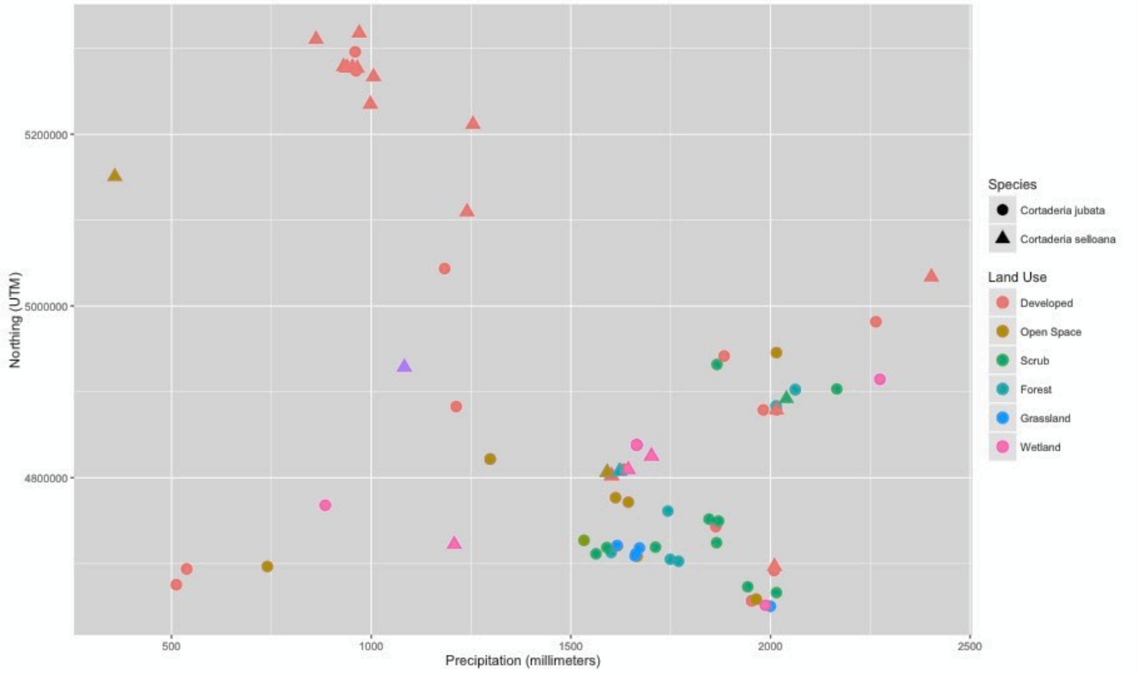


Figure 11. Plot of significant findings. Annual precipitation plotted against the northing UTM coordinate for Cortaderia jubata and Cortaderia selloana. Selected land use classifications used to determine point color.



Species Distribution Modeling in MaxEnt

Model outputs from MaxEnt resulted in high AUC values for both species indicating highly significant outputs. The high outputs for both species show more deterministic models not created by random chance. The averaged AUC values over 10 replicates were nearly identical: 0.9704 (standard deviation of 0.014 for *C. jubata* and 0.9697 for *C. selloana* with a standard deviation of 0.0139 (Figure 12). Thirty-eight or 39 samples per replicate were used for training for the *C. jubata* runs and four or five samples for testing data. Twenty or 21 samples were used for *C. selloana* for training and two or three samples for test data. Using the logistic threshold of maximum test sensitivity plus specificity suitable habitat was calculated based on the MaxEnt results for current climate condition and future projects given as a logistic output. Mean area for suitable habitat under current conditions was 1,823,340 hectares for *C. jubata* and 849,053 hectares for *C. selloana*. Under projected climate conditions there is an increase in suitable area for both species (Table 12 and Figure 13).

Table 12. Hectares of suitable habitat area for Cortaderia jubata and Cortaderia selloana based on mean, max, and average logistic outputs from MaxEnt. Suitable habitat was determined based on occupancy probabilities greater than the maximum test sensitivity plus specificity logistic threshold (0.1194 for C. jubata and 0.3145 for C. selloana). Area values are shown for western part of the study area, west of the Cascade Mountains.

	Current Climate (1950-2000)	Climate conditions projected in 2050	Climate conditions projected in 2070	% change in area 2050	% change in area 2070
Cortaderia jubata					
min	1,096,360	5,350,540	5,939,020	388%	442%
average	1,823,340	6,462,530	7,130,120	254%	291%
max	2,417,200	7,212,320	7,982,620	198%	230%
Cortaderia selloana					
min	487,352	2,784,150	3,473,780	471%	613%
average	849,053	5,397,970	6,610,800	536%	679%
max	1,146,540	6,294,460	7,986,000	449%	597%

Model runs for both species had a minimum temperature parameter as the top contributor to the respective model. *C. jubata* models were most influenced (61.4%) by the Mean Temperature of Coldest Quarter (Bio 11) and *C. selloana* models were most influenced (62.5%) by Min Temperature of Coldest Month (Bio 5). Climate parameters contributions were determined by the mean contribution of the 10 individual replicate model for each species (Appendix B). Mean Annual temperature decreased the model gains, for all model runs most when omitted which means that this variable contains the most information not present in the other climate variables.

Figure 12. Receiver Operator Curves and mean area under the curve (AUC) for MaxEnt outputs for (A) Cortaderia jubata and (B) Cortaderia selloana averaged for 10 replicates.

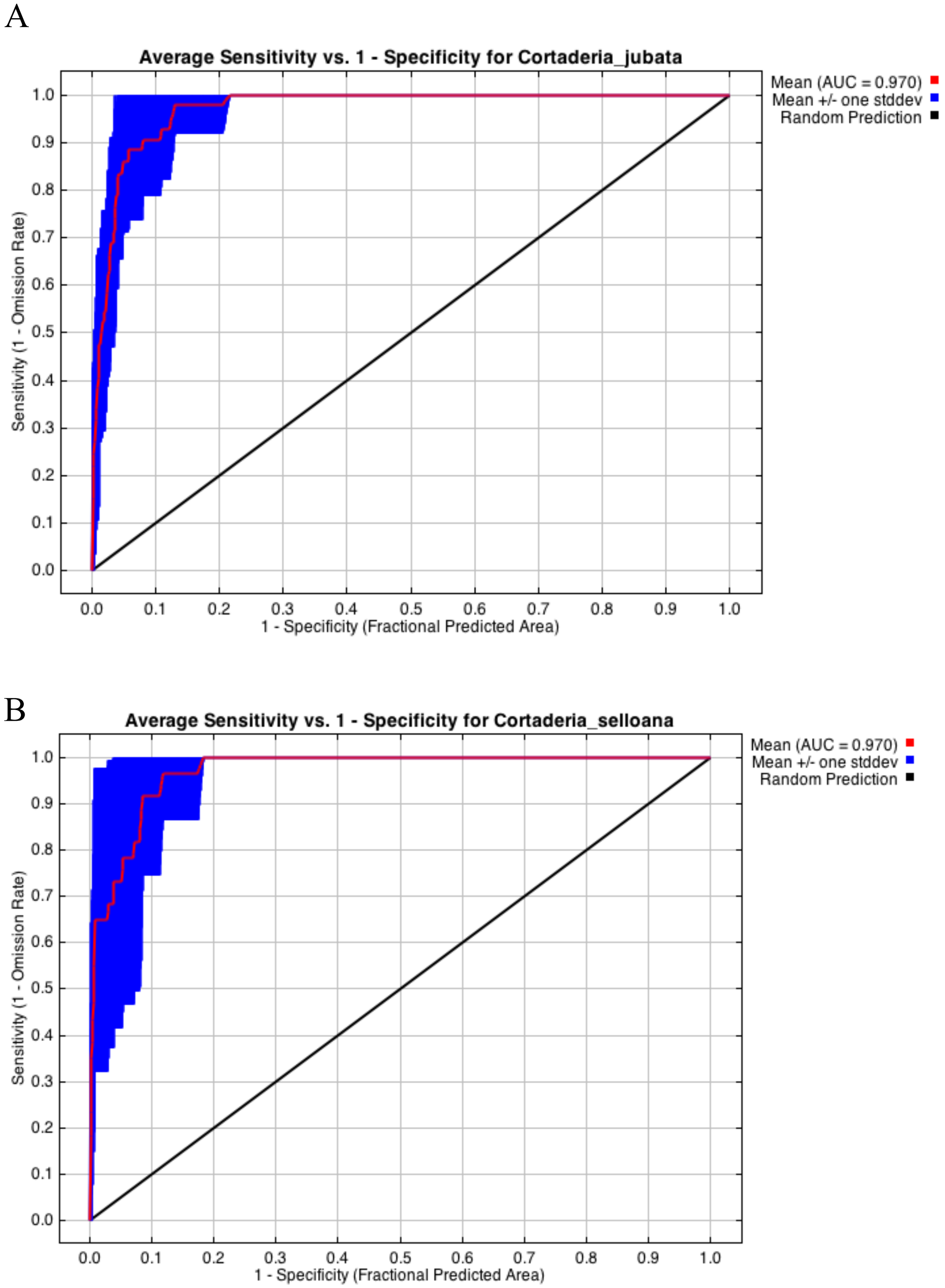
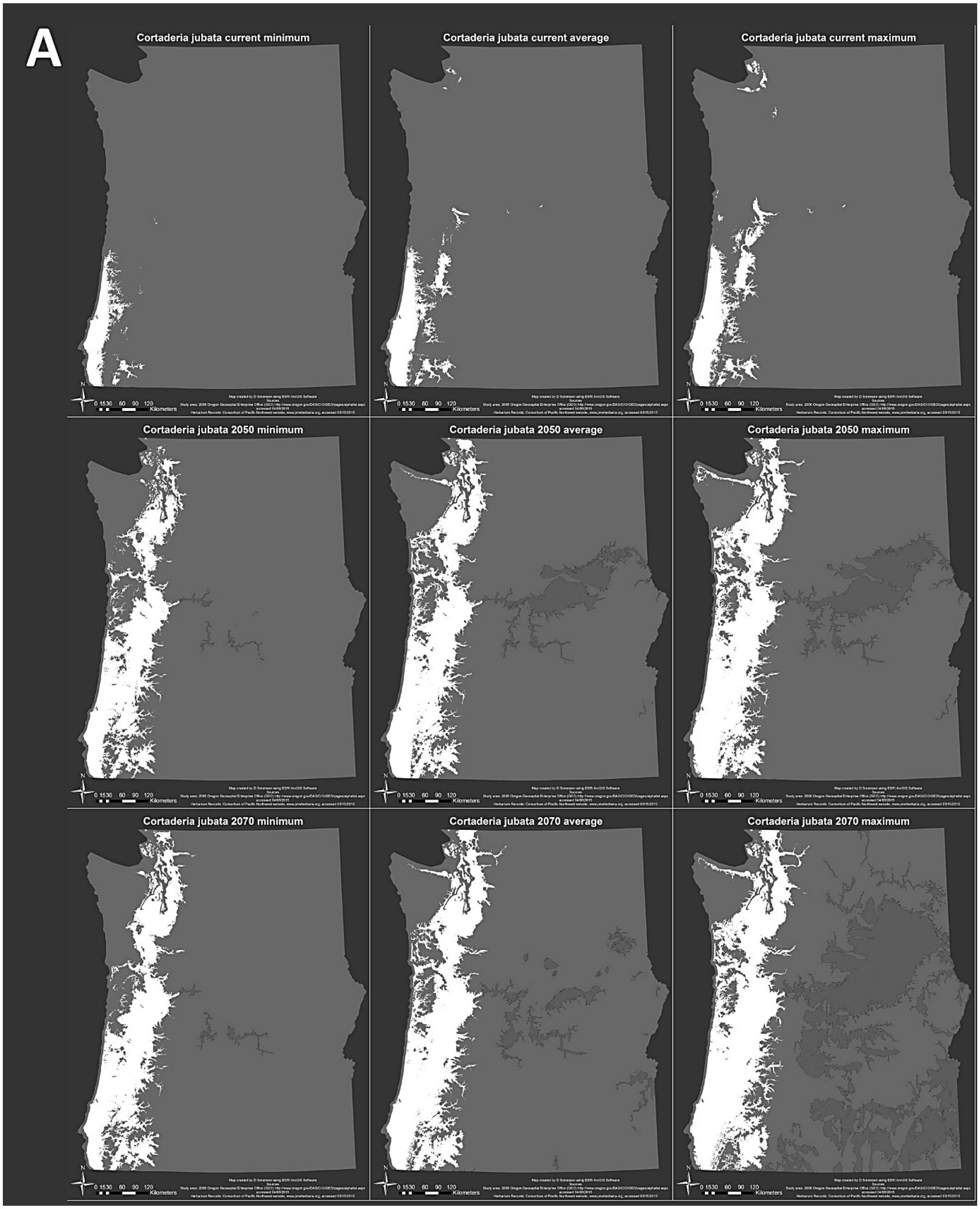
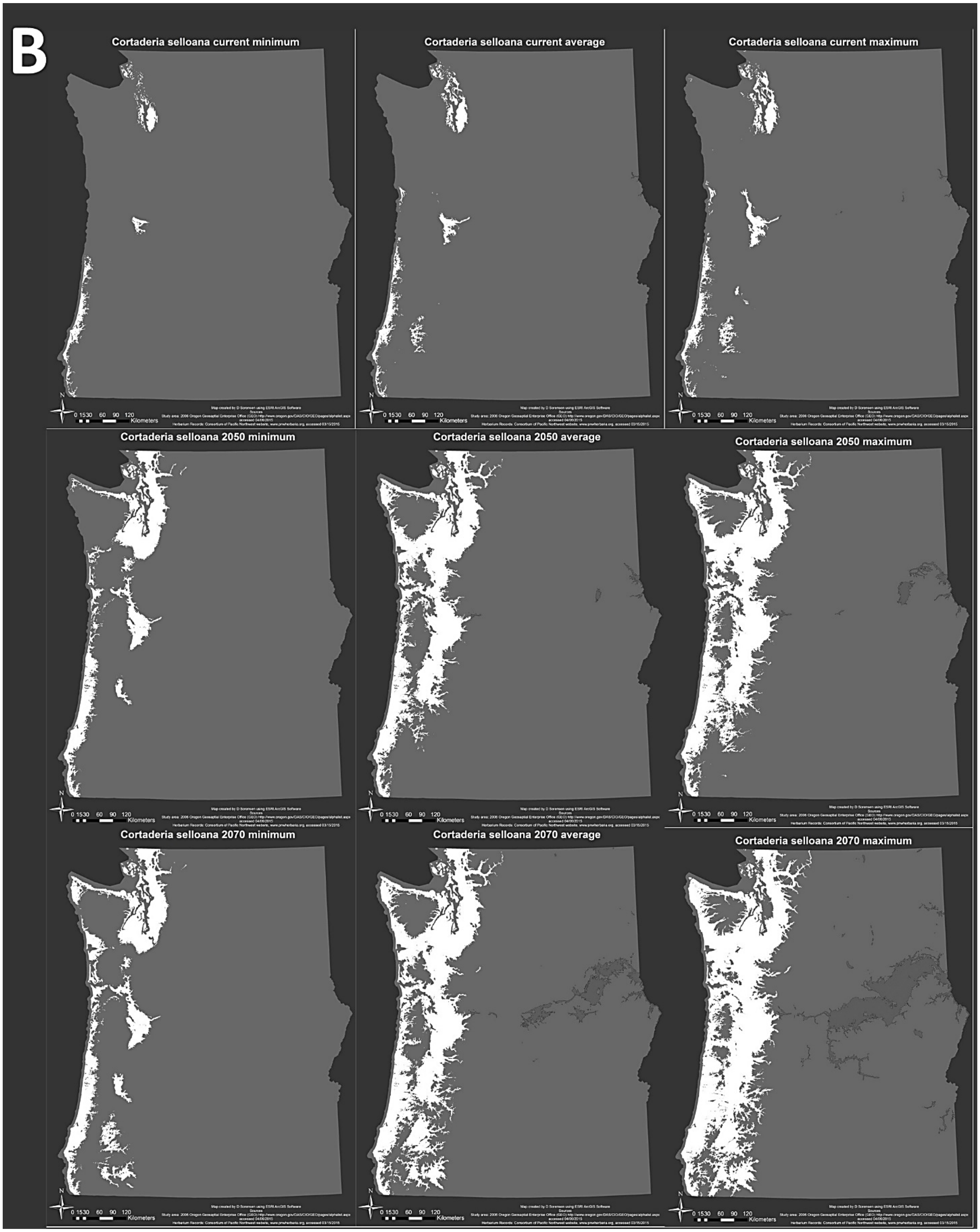


Figure 13. Maps of suitable climate(white) within the study are as predicted by MaxEnt using the occurrence data for both Cortaderia jubata (A) and Cortaderia selloana (B) modeled under 19 climate variables. The minimum, average, and maximum area are left to right while the current climate, 2050 projection, and 2070 projection read top to bottom. Logistic outputs were transformed into areas of suitable occupancy for either species using a threshold of maximum test sensitivity plus specificity. The cross-hatched areas were omitted from the final area calculations.




B
Cortaderia selloana current minimum
Cortaderia selloana current average
Cortaderia selloana current maximum
Cortaderia selloana 2050 minimum
Cortaderia selloana 2050 average
Cortaderia selloana 2050 maximum
Cortaderia selloana 2070 minimum
Cortaderia selloana 2070 average
Cortaderia selloana 2070 maximum
N
0 15 30 60 90 120
Kilometers
Map created by D Sorensen using ESRI ArcGIS Software
Sources
Study area: 2006 Oregon Geospatial Enterprise Office (GEO) http://www.oregon.gov/DAS/CIO/GEO/pages/alphalist.aspx accessed 04/06/2015
Herbarium Records: Consortium of Pacific Northwest website, www.pnwherbaria.org, accessed 03/15/2015

Discussion

Geospatial analysis

The land use types occupied by both species are consistent with my predictions. I expected *C. selloana* to be more associated with human altered landscape and that was supported by the land use results with more than half, 16 of 27, of the *C. selloana* occurrences found in developed land use area. *Cortaderia jubata* occupied more forest area than *C. selloana* in the study which seemed to fit in other parts of the world where it has invaded logged coastal forests in California and forestry operations in New Zealand and Australia (Harradine 1991, Lambrinos 2002, USDA 2014). Eight records of *C. jubata* were found in land use classified as woody wetlands. I did not expect this since it primarily occupying upland sites in California (Lambrinos 2001). The wetland occurrences of *C. selloana* are consistent with other invaded regions where it is reported growing along the margins of wetland and riparian areas (Bossard et al 2000, Bacchetta et. al. 2010). The chi square test for homogeneity determined that the two species are independent of each other and are distributed differently across land use type. Perhaps these two species are both relatively early in invasion expansion but on different trajectories within the study area.

Although the mean distance to railroads is closer for *C. selloana* than *C. jubata* it is outside what would be considered a rail line right of way corridor. While the typical right of way width is 10m, with multiple tracks these corridors can be up to 120m (Schmick and Strachota 2006). Rail corridors tend to be open sites consisting of mostly mineral soils which seem like an ideal space for establishment of either *Cortaderia* species. Although only five *C. selloana* records are found within 120m of what could be considered a rail corridor, the fact there is a significant difference exists between *C. selloana* and *C. jubata* for the whole study area does not examine what might be happening at a smaller spatial scale. Rail line could be playing an important role in expanding *C. selloana* for only a part of the study area. Road distances do not differ between the species and were considerably closer than the rail lines measurements. There are a few explanations for this result. Roads are associated with human altered landscapes and a majority of the records for both species are found in the developed land use classifications (NLDC values 21-24). Also the road network layer used for this analysis is very dense and include all roads, local, state, and federal. This covers a lot of the area across the study area. This is likely the reason for such a close association and not very informative in answering the question about finding patterns or associations in the distribution of *Cortaderia*.

The literature documents *C. selloana*'s ability to resist drought stress (Stanton and DiTomaso 2004, Domenech and Vila 2008, Vourlitis and Kroon 2013), but that characteristic does not seem to impact where the plant is found when soil is classified by available water storage capacity since there was no significant difference between the two species and they seem to occupy the same range of values (Figure 4). Seed germination studies of *C. selloana* have shown optimal germination in sandy soils and *C. jubata* tends to be associated with sandy well drained soils (Domenech and Vila 2008, Bossard et. al. 2000). However, this analysis showed occurrences in soils that were less sandy, using hydrologic soil groupings as a proxy. The majority of occurrences for both species are found in soils in the B and C hydrologic soil groups meaning a slower infiltration rate and being composed mostly of moderately course grained and moderately fine grained components.

The results of the MaxEnt modeling showed temperature variables were the most informative parameters driving the modeled distribution of both species and there was no difference between the distributions of mean annual temperature values of the two species. This offers evidence that temperature is driving the current distribution for both species across the study area. Although no statistical difference exists, I was surprised to find *C. jubata* occurrences occupying the lower ranges of temperature. DiTomaso et al. (1999) document *C. selloana* as being more cold tolerant, yet, there are six *C. jubata* records occurring in areas with a mean temperature value less than that of the lowest mean temperature value for *C selloana*. A possible explanation for this might be that the *C. jubata* occurrences are in warmer microclimates. Another explanation could be increased propagule pressure of *C. jubata* overcoming environmental constraints in the southwest corner of the study area. Although not shown in soil characteristics, the results between the two species and precipitation indicate what research has shown: *C. selloana* is more tolerant of drier conditions than *C. jubata*. While the overall range of precipitation values of the two species did not seem to differ (Figure 6), the GLM analysis shows a significant difference in distribution. *Cortaderia selloana* occupying more areas with lower annual precipitation values than *C. jubata*. The results comparing northing show that there is a significant difference in the north south distribution of the two species, *C. jubata* found more in the southern latitudes of the study area and more *C. selloana* found in northern latitudes of the study area. These two species are distributed differently across some environmental gradients and also across a spatial gradient. These different distributions offer evidence that these two species might be undergoing different invasion and expansion trajectories.

Species Distribution Model

MaxEnt created a climate envelope for both species to model a potential climate niche. Under current climate conditions MaxEnt outputs suggests a restricted distribution which more or less matches where it is currently found. Outside of known locations it seems like the northern Puget Sound area, in particular the San Juan Islands, have the climate suitability for *C. selloana* and with less certainty *C. jubata*. This, of course, is driven by the presence points, still climate might be strong driver in dictating where *C. jubata* and *C. selloana* can occupy. Occupancy under future climate projections show both species expanding across much of the western part of the study area and portions of the drier eastern part of the study area. The maximum 2070 *C. jubata* model shows that species in large parts of eastern Oregon and Washington. This seems to run counter to what is seen invaded areas around the world. This discrepancy might be explained by the models being primarily driven by temperature parameters. The maximum model for a 5- replicate test model ran with only precipitation parameters, Bio 12-Bio 19, shows a very small area of *C. jubata* on the east side of the study area under 2070 climate conditions. Although the MaxEnt models did not have much contribution from precipitation variables, in reality precipitation and humidity drive, in part, where *Cortaderia* is distributed in California (Lambrinos 2002).

The output from all models were showed to be statistically significant as indicated by the AUC of 0.97. MaxEnt might give a high AUC if the background points show high contrast which may have little to do with the distribution or model fit given the data (Yackulic et al. 2013). The relatively narrow geographic scope used in this analysis strikes a good balance with avoiding too much landscape contrast for background points while offering the model enough landscape heterogeneity to train and test the model. There is debate about how appropriate it is to consider background areas synonymous with absence areas in MaxEnt (Yackulic et al. 2013). This creates some uncertainty for this analysis when considering the modeled distribution for each species. Given this uncertainty, the models were effective in distinguishing between presence and background not presence and absence. The models showed relative increases in area of suitable climate for both species under predicted future climate conditions, these actual area measures should not be taken as prediction but rather potential trends. Caution should be given when making conclusions regarding projecting into future climate scenarios since it is unlikely that it reflects the biological reality (Merow et al 2013). The more cautious conclusion is not that *C. selloana* and *C. jubata* will increase their range in the next 30-40 years, rather, based on the MaxEnt results and predicted climate conditions there does not seem to be any climate constraints on their range in the western parts of Oregon and Washington going into the future. This offers more evidence that both species continue to pose an invasion risk for both Oregon and Washington and potentially elsewhere in the Pacific Northwest.

Error and uncertainty

The working dataset for both analyses was 27 *C. selloana* records and 56 *C. jubata* records. It seems like a small sample size for two states, especially for *C. selloana*. Most likely it is a function of under-detection or just very limited occurrences outside of intentional plantings. The occurrence data used for this study came mostly from herbarium records (Consortium of Pacific NW Herbarium) and observation records (Oregon Weedmapper and iMap Invasive Oregon). Local abundance affects the plant probability for detection. (Chen et al 2013) Most samples came from the SW corner of Oregon where *C. jubata* is more established and can be thought of as the northern movement of the California invasion. The dataset is biased towards that part of the study area which drives the explanatory variables in the geospatial analysis and the MaxEnt outputs for *C. jubata*. Plants of both species are large and noticeable as they contrast from other grasses, native or otherwise, in the landscape so they probably have a fairly high detection probability. Throughout most of the study area either species will most likely not avoid intentional detection. Since the two species were only listed in Washington as noxious weeds in 2015, it is unlikely that “adventive” or expanding populations are being recorded or looked for to the same extent as in Oregon which listed *C. jubata* in 2007 (ODA 2008).

Another possible source of error is the accuracy of the data. The occurrence records used for both analyses were collected using GPS to document spatial location and manual methods, and span from 1950 to 2015. Spatial accuracy varies depending on how location data were collected. GPS units can be off several meters or larger. In addition, the recorded location could represent the location of the recorder not the actual plants. An example of this would be an occurrence documented along a road by the recorder while the actual plants might be a couple meters away inaccessible but observable. This may account for some error since the x and y (latitude and longitude) coordinates may not have represented the exact location of the plants. Any errors related to this would more likely affect the road and rail distance measures since measurement was taken from that point location. If spatial errors exist, I would expect them to have little impact on the raster layers unless the spatial errors were larger than the cell sizes of the raster data (Table 1). Temporal accuracy of the data is also something to consider. The occurrence data are mostly snapshots of what is happening on the ground and while there were some duplicate points, there were not enough to show any expansion trajectory. Datasets like herbarium records are not always effective in showing trajectories of invasive species since records are often only collected once they have expanded or become widespread pests

(Lambrinos 2001).

One of the constraints of this study was finding datasets to fit a study area that encompassed two states at a spatial grain to produce meaningful results. Both Oregon and Washington have multiple GIS portals and clearinghouses that contain potentially useful variables but they did not always fit together. The states' land use layers are a good example for this; Washington maintains a state-wide vector based land cover layer which is based on tax parcels. Oregon does not have a state wide land use/land cover but instead has land use layers for municipalities and metro areas (Oregon GEO 2016). For some variables I relied on national and world databases; NLCD 2011, gSURRGO, and WorldClim. By relying on these datasets I compromised on spatial grain. The larger the spatial grain or raster cell size the higher probability of this analysis not taking into account small changes on the landscape like micro climates. Spatial grain issues were less problematic for the rail and road datasets which were state based and vector type feature classes.

Lack of absence data constrained the type of analyses done in this study. A multivariate regression model with location as the response variable could not be constructed due to the presence only data. If such a model were constructed, variable data could be combined and step-wise regression would elucidate which, if any, of the variables most explained the distribution of the two species within the study area and predict invasion-prone areas. MaxEnt was used to help overcome this obstacle and provided a predictive model of climate occupancy. Using an integrated approach would require both absence and presence data, however it could generate likelihood for colonization, dispersal and proliferation of an invader across specified areas at multiple spatial scales. Even small amounts of this type of data could be used to explain ongoing invasion processes (Ibanez et al 2014). The factors that drive early invasion vary across ecosystems however propagule pressure is often cites as primary contributor (Taylor et al 2016). This analysis is weakened since did not take into account seed pressure from intentional plantings. Integrating both absence data and propagule pressure would have strengthened and added more certainty to this study

Site based considerations

This study looked at *Cortaderia* across a large geographic area and, as a consequence of such a large spatial scope, smaller scale considerations that might drive the pattern of distribution were not examined. Smaller scale drivers, like competition, might be contributing to the two species' distribution across the study area. *Cortaderia* plants are a common occurrence in residential and commercial landscapes. If enough plants are present, then perhaps there are enough accidental male plants planted to produce some viable seeds. If the assumption of some viable seeds being available is true, why aren't there more plants found throughout the study area? The MaxEnt outputs show a limited range under current climate conditions which may be a constraint for the expansion for these two grasses. However, the two species might be kept in check by constraints other than climate. Competition studies on these two species have shown them to be poor competitors on the landscape. In simulated landscapes, *C. selloana* was found to thrive under conditions of frequent disturbances. The greater the disturbance, the larger the invaded area will be (Pausas et al 2006). The same study found the *C. selloana* disappears from the landscape with no disturbance. Lambrinos (2002) found similar results experimentally with both species having significantly enhanced seedling emergence due to disturbance across different habitats under field conditions.

Competition studies in Spain, show *C. selloana* was not a better competitor, as measured by growth parameters, than native counterparts, but rather was found to optimize water efficiency so it out-performed selected natives under water stress conditions (Domenech and Vila 2008). Given both species positive response to disturbance, perhaps the areas in proximity to seed sources do not frequently have disturbance to create the necessary opening for the plant to get established. The two largest known patches of *C. selloana* in WA state are located in open site with mineral soils (WNWCB 2014, Juiseniek and Kern 2014). The largest site, with over 1000 individuals, was previously cleared of multiple noxious weeds and only then did the *C. selloana* become abundant. (Rick Johnson, personal communication) The propagules were perhaps on the site from adjacent seed producing plants but never could get established until the appropriate disturbance created the right conditions. To that end *Cortaderia* could be a backseat driver type of invasive species where a disturbance event is needed to get established but once established can start to drive the landscape it is invading (Bauer 2012). This sit and wait strategy might have played out with the above mentioned invasion at the Olympia Washington site and similarly observed at two *Cortaderia* patches at recently cleared sites in southwest Oregon (Figure 14)

Figure 14. Photographs of two sites in southwest Oregon where Cortaderia is rapidly expanding following a disturbance event that cleared the landscape. Photo A is in Gold Beach and Photo B is in Bandon. Photo credit C. Pirosko and D. Sorensen.

Future studies

Genetic analysis across a sample of occurrences to confirm identification to species was initially part of this study. Since identification between these two *Cortaderia* species can be difficult, especially for immature plants, the proposed genetic analysis would have removed any doubt about species and provide clarity of what *Cortaderia* species is present where. I believe there might still be some confusion of species especially in the Oregon records where both species coexists near the same location. Further only *C. jubata* is listed as a noxious weed in Oregon which might create the assumption that all *Cortaderia* plants displaying invasive behavior are *C. jubata*. If landscape plantings of *C. selloana* are present and producing viable seed in southwest Oregon, then they could be reproducing. Whether or not there is a discrepancy in species between some of the recorded occurrences is an important question that remains unanswered.

If the documented occurrence records are correct then the two species seem to fit more or less the same pattern of preference in California: *C. jubata* being invasive along the coast and restricted to the southwest corner of Oregon and *C. selloana* in scattered patches inland and some along the coast throughout both Washington and Oregon. If not, then perhaps there is something different happening with the invasion of one or both of these plants here than other parts of the world. Genetic testing using the same protocols as Okada et al (2009), microsatellite allele diversity can be examined to see if different genotypes are invading in different locations within the study area, or if those in the study area differ from the results found in California from past *Cortaderia* genetic research (Okada et al 2007). Similar work was done looking at invasive blackberry across California, Oregon and Washington (Clark et al 2012).

The reproductive strategies of the two plants are different and could have consequences for expansion throughout the study area. Because it is an obligate asexual reproducer, there is less of a biological constraint on *C. jubata* from expanding, but *C. selloana* needs male plants in the vicinity to produce seed, a constraint for expansion. However, propagule pressure has been shown to overcome landscape resistance and be drivers of early invasion of plant species (Von Holle and Simberloff 2005, Taylor et al 2015). Accounting for propagule pressure from residential plantings can improve the predictive power of species distribution models especially for species with strong ties to human dominated landscapes (Davis et al 2016). This study focused only on occurrences of either species with multiple individuals and did not look at seed/propagule sources. It might be harder to infer potential propagule pressure from residential/intentional plantings for *C. selloana* since plant fertility is not consistent, given its reproductive strategy. A good first step might be a study looking at the seed viability or sex breakdown of intentional *C. selloana* plantings. In New Zealand invasive populations of *C. selloana* have equal sex-form ratios (Connor and Charlesworth 1989). If some baseline rate for seed viability could be determined for the intentional plantings within the study area, then the impact of propagule pressure to the invasion risk of these two species could be elucidated. Further, Davis et al. (2016) concluded that any predictive or species distribution model that does not include residential propagule pressure will be “wildly inaccurate” when predicting risk of invasion by non-native species, especially species that have strong associations to human dominated landscapes. If *Cortaderia* risk is to be assessed in the future, then residential propagule pressure should be examined.

The study area of this analysis was Washington and Oregon, and it utilized research done close by in California. Both *Cortaderia* species have a longer history of invasion in California then in the study area. An interesting research project could treat California as a saturated invasion and the current study area as the early invasion for both species. Are some trends, like land use associations, found in this analysis true for California? To some extent this study was guided by the invasion trajectory in California, what would be the results if this analysis was replicated using only California *Cortaderia* occurrence data?

Conclusion

To answer the question of invasion risk of these two grass species in the Pacific Northwest, this study analyzed land use, distance to rail and road networks, and soil water availability, hydrologic soil groups, annual mean temperature, annual precipitation, and northing to help explain the distribution of these two species across Oregon and Washington. A potential species distribution was created using MaxEnt and climate variables to determine suitable climate for both species using current climate data and future climate projections. No statistical differences between the species and road distance, available water storage in soil, annual mean temperature were found. Significant differences exist in the distribution of occurrences of the two species with regard to land use, distance to rail, annual precipitation, and northing. The two species are probably on different expansion trajectories. There are more *C. jubata* occurrences but they are mostly restricted to the mid and southern coast of Oregon whereas *C. selloana* is likely to be found more widely throughout the study area. If greater genetic diversity and a wider tolerance of environmental conditions of *C. selloana* in California was a result of repeated horticultural introductions, then perhaps *C. selloana* might be adapting to the climate conditions in the Pacific Northwest being selected from the abundant intentional plantings.

I expected both species to be more associated with human altered land use and this was supported by the data. *C. jubata* occurrences are occupying more variable land use than *C. selloana* but that may reflect it being more saturated in the southwest Oregon landscape. Given the strong association with developed land use for both species, the unknown impact of propagule pressure from landscape plantings, and preference for disturbance, it seems likely that new populations would be found at open spaces in developed areas. Early detection surveys should focus on developed areas, especially for *C. selloana*. Based on studies that examined environments conditions for germination and growth of the two species, it seemed likely that *C. selloana* would be found in soils with higher soil water available values and both species would be found in soils with higher infiltration rates. This was not the case as suggested by the soil characteristic variables. *Cortaderia selloana* occupies areas with less annual precipitation than *C. jubata,* supporting the claim that *C. selloana* is better at maximizing water resources than *C. jubata*. Based on the MaxEnt results, there are no constraints on suitable climate for either species in the future in the western part on the study area and possibly eastern parts of the study area too.

Overall this analysis offers little evidence, if any, to show that these two species won't expand: they do continue to pose a threat to suitable habitats. Being poor competitors and having specific establishment requirements make early detection surveys and rapid response for these two plant species a well suited control and prevention strategy. The tendency for them to rapidly expand on a site (Figure 14) stresses the importance of prevention. The unknown quantity of seed for intentionally planted *C. selloana* and the uncertainty in identification to species are compelling reasons to further study these species in the Pacific Northwest. If these two species, *C. jubata* and *C. selloana* , do indeed expand and become problem pests in the landscape, then there will be more occurrence records available to compare. A strength of this study is that it can serve as a strong baseline for future studies on these two plants in the Pacific Northwest.

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Appendix A: Raw Data from Geospatial Analysis

Id	Scientific	Obs date	County	State	Mapunit Key	AWS_Weight_avg	HSG	RR_DIST_m	nlcd2011_group	Rd_DIST_m	sp_code
1	Cortaderia jubata	10/25/2003	Curry	OR	65334	26.04999924	C	86005	70	107.377753	0
2	Cortaderia jubata	1/1/2007	Curry	OR	65069	21.48999977	C	84128	90	7.44868604	0
3	Cortaderia jubata	1/1/2007	Curry	OR	64990	17.31999969	C	86606	20	19.6376781	0
4	Cortaderia jubata	1/1/2007	Curry	OR	65511	27.44000053	C	87081	20	39.9997817	0
5	Cortaderia jubata	6/19/1997	Curry	OR	65324	14.15999985	B	88785	21	3.05286976	0
6	Cortaderia jubata		Curry	OR	65324	14.15999985	B	88784	21	2.16824207	0
7	Cortaderia jubata	7/8/1998	Curry	OR	64998	17.10000038	C	80636	40	213.760645	0
8	Cortaderia jubata	1/1/2007	Curry	OR	65463	9.869999886	C	66493	40	22.4791651	0
9	Cortaderia jubata	7/15/2002	Jackson	OR	469720	22.31999969	D	661	20	5.93028395	0
10	Cortaderia jubata	1/1/2007	Curry	OR	65005	16.04999924	A	73439	20	17.3095237	0
11	Cortaderia jubata	7/15/2002	Jackson	OR	469718	15.01000023	A	818	20	15.7684515	0
12	Cortaderia selloana		Curry	OR	65427	18.63999939	B	69114	20	43.9080455	1
13	Cortaderia jubata	7/15/2002	Jackson	OR	469633	21.21999931	C	144	21	10.9502351	0
14	Cortaderia jubata	1/1/2007	Curry	OR	65429	13.5	B	58958	50	7.3184498	0
15	Cortaderia jubata	1/1/2007	Curry	OR	65522	12.48999977	C	55244	50	20.3914181	0
16	Cortaderia jubata	1/1/2007	Curry	OR	65162	15.93000031	B	47754	21	3.13029963	0
17	Cortaderia jubata	1/1/2007	Curry	OR	65195	22.92000008		47957	70	337.617309	0
18	Cortaderia jubata	1/1/2007	Curry	OR	65590	8.840000153	B	40420	40	3.42509791	0
19	Cortaderia jubata	1/1/2007	Curry	OR	65162	15.93000031	B	38956	70	3.60574706	0
20	Cortaderia jubata	1/1/2007	Curry	OR	65587	19.87999916	C	40690	50	5.487161	0
21	Cortaderia jubata	1/1/2007	Curry	OR	65590	8.840000153	B	43387	70	42.6229611	0
22	Cortaderia jubata	1/1/2007	Curry	OR	65067	14.77000046	A	37375	40	6.23603913	0
23	Cortaderia jubata	1/1/2007	Curry	OR	65570	13.25	B	42557	40	5.09591221	0
24	Cortaderia jubata	1/1/2007	Curry	OR	64975	28.07999992	B	41061	21	12.5356441	0
25	Cortaderia jubata	1/1/2007	Curry	OR	65488	17.37000084	B	40971	70	178.395139	0
26	Cortaderia selloana	10/23/2007	Josephine	OR	469531	2.279999971	D	16081	90	2156.97123	1
27	Cortaderia jubata	1/1/2007	Curry	OR	65340	15.85000038	C	38585	40	150.233742	0
28	Cortaderia jubata	1/1/2007	Curry	OR	65195	22.92000008		30111	30	3453.7906	0
29	Cortaderia jubata	9/7/2006	Curry	OR	65420	17.76000023	B	33377	20	57.3115715	0
30	Cortaderia jubata	7/15/1997	Curry	OR	65421	16.92000008	B	30430	40	786.208755	0
31	Cortaderia jubata	10/6/1997	Curry	OR	65122	12.61999989	C	27811	40	170.31459	0
32	Cortaderia jubata	7/15/1997	Coos	OR	61236	6.889999866	C/D	23738	50	253.651401	0
33	Cortaderia jubata	7/15/2002	Douglas	OR	66571			148	90	26.4382932	0

easting	northing	bio_12	bio_1	nlcd2011	Latitude	Longitude
400036.313	4650336.5	2000	114	71	41.9987	-124.207
401512.094	4651482	1987	116	90	42.009201	-124.18938
395225.938	4656720	1953	117	22	42.055556	-124.26621
394664.906	4656748	1953	117	23	42.055733	-124.27299
391754	4658517.5	1964	115	21	42.07127	-124.30849
391753.219	4658521	1964	115	21	42.0713	-124.309
396543.906	4666294.5	2015	107	42	42.14194	-124.25198
408904.344	4673031	1943	113	42	42.204136	-124.10348
520838.25	4675498	512	113	23	42.231383	-122.74747
384029.469	4691975	2009	117	23	42.371404	-124.40852
505895.188	4693805	538	121	23	42.396515	-122.92837
383164	4696830.5	2010	117	23	42.415	-124.42
482200.125	4696690	740	120	21	42.422315	-123.21637
404624.438	4702767.5	1770	70	52	42.47138	-124.16023
407764.5	4705045.5	1749	90	52	42.492272	-124.1224
414343.625	4708634.5	1666	122	21	42.525345	-124.04289
413909.594	4708906.5	1661	122	71	42.527746	-124.04822
421323.719	4711454.5	1563	80	42	42.55148	-123.95831
413082.563	4711697.5	1663	121	42	42.556005	-123.9405
419872.688	4712997.5	1601	96	52	42.565225	-123.9762
412594.563	4718380.5	1672	114	71	42.612906	-124.06568
419534.656	4718804.5	1590	79	42	42.61748	-123.98114
410227.5	4719179.5	1712	95	42	42.619829	-124.09466
413900.563	4720706.5	1616	120	21	42.633998	-124.05011
413728.563	4721188.5	1616	120	71	42.638318	-124.05228
444448	4722533.5	1208	118	95	42.65326	-123.67775
396707.344	4724371	1865	80	42	42.664874	-124.26043
422807.688	4727115.5	1533	108	31	42.692652	-123.94236
379136.281	4743110.5	1863	114	23	42.83102	-124.47878
378925.063	4749642.5	1870	113	42	42.88979	-124.48277
380823.313	4751854.5	1846	113	42	42.91	-124.46
382840.938	4761237.5	1743	113	52	42.994784	-124.43726
471809.125	4767975	885	123	90	43.063954	-123.34622

Id	Scientific	Obs date	County	State	Mapunit Key	AWS_Weight_avg	HSG	RR_DIST_m	nlcd2011_group	Rd_DIST_m	sp_code
34	Cortaderia jubata	7/22/2007	Coos	OR	61267	14.03999996	B	20126	21	15.9217072	0
35	Cortaderia jubata	9/6/2006	Coos	OR	61268	14.11999989	B	13167	21	17.7538524	0
36	Cortaderia selloana	10/5/1997	Coos	OR	61231			282	20	17.8151172	1
37	Cortaderia selloana		Coos	OR	61231			282	20	17.8178124	1
38	Cortaderia selloana	10/5/1997	Coos	OR	61240	23.30999947	C	2681	50	9.23029764	1
39	Cortaderia selloana		Coos	OR	61240	23.30999947	C	2684	21	11.3840214	1
40	Cortaderia selloana	10/5/1997	Coos	OR	61167	24.04000092	C	2786	50	205.648675	1
41	Cortaderia selloana		Coos	OR	61167	24.04000092	C	2782	50	198.833129	1
42	Cortaderia selloana	10/15/1997	Coos	OR	61171	9	A/D	913	90	442.55468	1
43	Cortaderia jubata	6/15/2006	Coos	OR	61238	9.18999958	A	6	20	35.5332753	0
44	Cortaderia jubata		Douglas	OR	67084	12.72999954	B	21489	50	336.001444	0
45	Cortaderia jubata	12/8/2010	Douglas	OR	67084	12.72999954	B	21496	21	329.603249	0
46	Cortaderia selloana	10/6/1997	Coos	OR	61151	6.329999924		1077	90	987.438593	1
47	Cortaderia selloana		Coos	OR	61151	6.329999924		1081	90	992.087612	1
48	Cortaderia jubata	8/17/2010	Douglas	OR	66890	28.45999908	C/D	6156	90	99.5671039	0
49	Cortaderia jubata		Douglas	OR	66890	28.45999908	C/D	6145	90	98.6527318	0
50	Cortaderia jubata	8/17/2010	Douglas	OR	66890	28.45999908	C/D	6136	90	102.1774	0
51	Cortaderia jubata	8/17/2010	Douglas	OR	66890	28.45999908	C/D	6138	90	99.3655627	0
52	Cortaderia jubata	8/17/2010	Douglas	OR	66890	28.45999908	C/D	6141	90	96.8169927	0
53	Cortaderia jubata		Lane	OR	62646	19.14999962	B	9067	20	70.9345958	0
54	Cortaderia jubata		Lane	OR	62768	13.15999985	A	9066	20	99.3669673	0
55	Cortaderia selloana	10/14/2005	Lane	OR	62646	19.14999962	B	9137	20	103.945441	1
56	Cortaderia jubata	7/15/2002	Lane	OR	62771	23.87999916	A	5870	20	7.28455827	0
57	Cortaderia jubata		Lane	OR	62765	26.60000038	C	13753	50	94.4319941	0
58	Cortaderia selloana		Lane	OR	62588	55.59999847	B	20376	40	456.276782	1
59	Cortaderia jubata		Lane	OR	1426000	10.61999989	B	22879	50	413.145759	0
60	Cortaderia jubata		Lane	OR	1425960	20.55999947	C	22916	50	422.349067	0
61	Cortaderia jubata	6/14/1959	Lincoln	OR	64701	35.75999832	C	29411	40	104.915457	0
62	Cortaderia jubata		Lincoln	OR	1426020	31.86000061	B	23781	90	260.293786	0
63	Cortaderia selloana		Lincoln	OR	85295	30.78000069	B	3306	80	80.5844859	1
64	Cortaderia jubata		Lincoln	OR	64612	29.76000023	B	12409	40	79.2240015	0

easting	northing	bio_12	bio_1	nlcd2011_	Latitude	Longitude
383378.188	4771620	1644	111	21	43.08833	-124.43284
388304.875	4776853	1612	109	21	43.13618	-124.37338
401495.313	4802410.5	1602	111	24	43.3681	-124.2158
401495.344	4802410.5	1602	111	24	43.3681	-124.216
403791.406	4806241	1591	113	52	43.40288	-124.18814
403794.656	4806243	1591	113	21	43.4029	-124.188
403779.375	4807726.5	1622	111	52	43.41625	-124.18855
403775.406	4807732	1622	111	52	43.4163	-124.189
397175.219	4809438	1644	111	95	43.43078	-124.27043
399743.906	4810090	1633	112	22	43.437	-124.23882
453389.25	4821800.5	1298	124	52	43.547699	-123.577
453381.938	4821801.5	1298	124	21	43.54771	-123.57709
402067.531	4825337.5	1702	112	90	43.57457	-124.21286
402064.344	4825341	1702	112	90	43.5746	-124.213
419343.813	4838246	1665	116	90	43.692852	-124.00086
419332.781	4838252	1665	116	90	43.692902	-124.001
419323.063	4838252	1665	116	90	43.692903	-124.00112
419325.188	4838254	1665	116	90	43.692923	-124.00109
419327.594	4838256	1665	116	90	43.692938	-124.00106
412029.938	4878977	1982	112	22	44.058682	-124.09832
412067.406	4879006	2015	111	22	44.058946	-124.09786
412097.438	4879122.5	2015	111	22	44.06	-124.0975
496400.188	4882908.5	1213	116	23	44.099348	-123.04498
410408.75	4883707.5	2014	112	52	44.101068	-124.11936
411328.406	4892197	2040	113	43	44.1776	-124.109
437162.344	4902612	2062	113	52	44.274038	-123.7874
437087.25	4902668	2062	113	52	44.274537	-123.78835
411474.063	4903394.5	2166	107	42	44.27841	-124.10937
426617.938	4914656	2274	107	90	44.381472	-123.92121
481476.313	4928855	1083	112	82	44.5128	-123.233
446220	4931948	1866	111	43	44.538857	-123.67695

Id	Scientific	Obs date	County	State	Mapunit Key	AWS_Weight_avg	HSG	RR_DIST_m	nlcd2011_group	Rd_DIST_m	sp_code
65	Cortaderia jubata	11/18/2007	Lincoln	OR	64739	10.40999985		9090	20	80.0310127	0
66	Cortaderia jubata	7/12/2006	Lincoln	OR	64718	25.89999962	B	638	21	91.5166186	0
67	Cortaderia jubata	7/16/2005	Lincoln	OR	64629	23.36000061	D	27244	20	7.48382866	0
68	Cortaderia selloana		Tillamook	OR	67149	10.94999981	A	8978	20	8.33104613	1
69	Cortaderia jubata	7/15/2002	Multnomah	OR	61846	20.26000023		5	20	18.1032566	0
70	Cortaderia selloana	2011	Cowlitz	WA	72226	9.119999886	A	1278	20	19.3832692	1
71	Cortaderia selloana	2013	Asotin	WA	69411	20.63999939	B	7412	21	1.6764	1
72	Cortaderia selloana	2013	Thurston	WA	2454649			23	20	32.0691937	1
73	Cortaderia selloana	2014	Pierce	WA	2511989			165	20	167.214184	1
74	Cortaderia selloana		King	WA	2511988			1144	20	18.0025651	1
75	Cortaderia jubata		King	WA	2511988			955	20	18.3137949	0
76	Cortaderia selloana		King	WA	2511988			75	20	50.2479469	1
77	Cortaderia selloana		King	WA	2511988			612	20	20.5730442	1
78	Cortaderia selloana		King	WA	2511988			19	20	8.86128819	1
79	Cortaderia selloana		King	WA	2511988			1461	20	31.4229983	1
80	Cortaderia selloana		King	WA	2511988			55	20	36.7931867	1
81	Cortaderia jubata	2000	Snohomish	WA	74936	7.659999847	B	5914	20	177.88611	0
82	Cortaderia selloana	2014	Snohomish	WA	74900	8.300000191	A	16	20	6.66241775	1
83	Cortaderia selloana	2002	Snohomish	WA	74967			124	20	4.82908111	1

easting	northing	bio_12	bio_1	nlcd2011_	Latitude	Longitude
415685.563	4941773.5	1884	106	22	44.62437	-124.06285
432747.188	4945729.5	2015	109	21	44.66178	-123.84832
420138.844	4981750	2264	106	23	44.9847	-124.013
424812.281	5033910	2403	97	22	45.45467	-123.96161
536772.25	5043625.5	1184	115	22	45.545197	-122.52895
507982	5109791	1240	110	23	46.1416	-122.897
956600.938	5150862.5	358	122	21	46.357	-117.064
506516.281	5211653	1255	105	23	47.0584	-122.914
545906.75	5235112	998	107	23	47.26788	-122.3931
552453.25	5267100	1006	108	22	47.5552	-122.303
550097.375	5273911	962	109	24	47.6167	-122.333
546361.688	5276917.5	965	108	23	47.64399	-122.3827
550591.188	5277031	940	111	23	47.6447	-122.3264
547933.313	5278153.5	939	110	24	47.655	-122.362
552296.563	5278224	953	111	22	47.6553	-122.3036
546905.25	5278910	931	110	24	47.66188	-122.3753
554207.063	5296025.5	960	104	23	47.8153	-122.276
551975.75	5310724	862	105	23	47.94772	-122.3039
560408.563	5317914.5	970	105	23	48.0117	-122.19

Appendix B: Contribution of variables for MaxEnt model outputs

Table B-13. Estimates of relative contributions of the environmental variables to the Maxent model for Cortaderia jubata

Variable	Percent contribution	Permutation importance
bio_11	61.4	0
bio_3	11.6	3.6
bio_1	7.6	7.2
bio_15	7.4	0
bio_4	2.7	28.3
bio_2	2.4	6
bio_6	2.2	45.7
bio_14	1.5	4.2
bio_7	1.4	2.3
bio_13	0.4	1
bio_18	0.4	0.5
bio_19	0.4	0
bio_5	0.2	0.8
bio_17	0.2	0
bio_16	0.2	0
bio_8	0.1	0
bio_12	0	0
bio_9	0	0.4
bio_10	0	0

Figure B-15.Jackknife test of variable importance for Cortaderia jubata MaxEnt models.

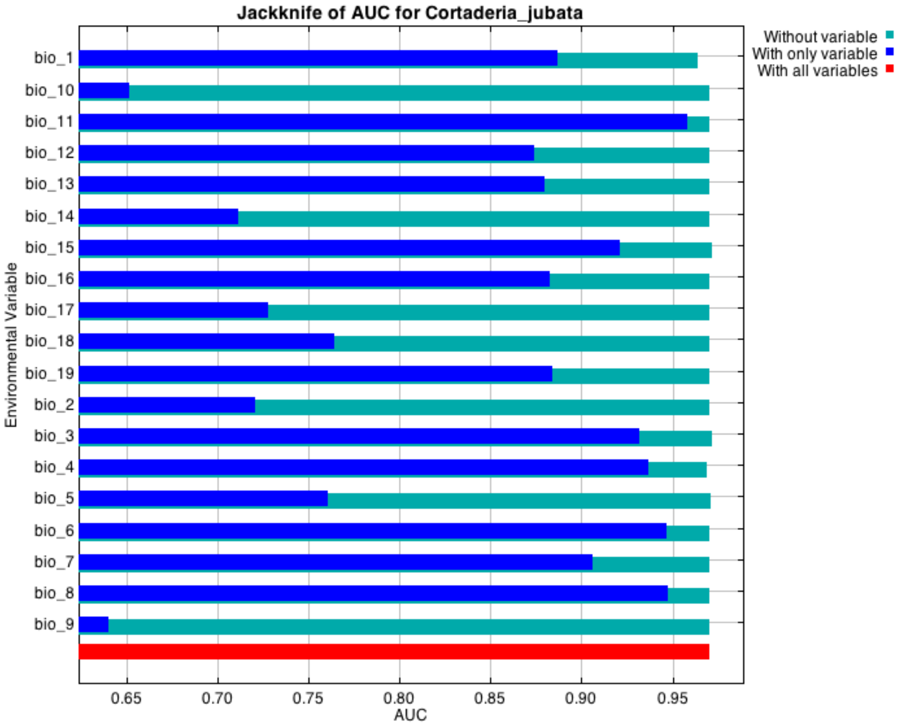

Table B-14. Estimates of relative contributions of the environmental variables to the Maxent model for Cortaderia selloana

Variable	Percent contribution	Permutation importance
bio_6	62.5	41.1
bio_1	17	53.5
bio_2	5.4	1.8
bio_14	3.1	0.8
bio_11	2.8	0
bio_13	2.6	1.3
bio_7	2.2	0
bio_3	1.5	0.5
bio_12	1.1	0
bio_16	0.8	0
bio_18	0.5	0.7
bio_4	0.2	0
bio_17	0.1	0
bio_19	0	0
bio_9	0	0
bio_15	0	0.1

bio_5	0	0
bio_8	0	0
bio_10	0	0

FigureB- 16. Jackknife test of variable importance for Cortaderia selloana MaxEnt models