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Global terrestrial biomes at risk of cacti invasion identified for four species using consensual modelling

Mhosisi Masocha[a,*], Timothy Dube[b]

[a] Department of Geography and Environmental Science, University of Zimbabwe, Box MP 167, Mount Pleasant, Harare, Zimbabwe
[b] Department of Earth Sciences, University of the Western Cape, Private Bag X17, Bellville, 7535, South Africa

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ABSTRACT

Cacti invasion of natural ecosystems and grazing lands threaten native biodiversity and reduces economic output from infested grazing lands. Yet, few studies exist about potential hotspots of cacti invasion on a global scale. We used maximum entropy, boosted regression model and generalised additive models, calibrated using geo-referenced data from both the native and introduced ranges to construct ecological niche models for four invasive alien cacti species: *Opuntia ficus-indica* (the sweet prickly pear), *Opuntia stricta* (the sour prickly pear), *Cylindropuntia imbricata* (the tree cholla) and *Cylindropuntia fulgida* (the jumping cholla). The models were combined, using the average weighted method approach and projected onto the geographic space to predict terrestrial biomes, as well as areas of special conservation concern at risk of cacti invasion. The results indicate that the Mediterranean, tropical savanna and desert and xeric shrubland biomes are the most susceptible to cacti invasion. Eleven global biodiversity hotspots including the Mediterranean basin, Cape floristic region and Southwest Australia were associated with high risk of cacti invasion. The global maps of potential cacti distribution presented in this work have the potential to serve as an important contribution towards the implementation of a global policy to avoid the negative consequences of cacti invasion.

1. Introduction

Numerous cacti were introduced from the Americas into arid and semi-arid regions of the world to provide products, such as fruits and drought fodder for cattle, as well as to support the commercial production of red dye from a cochineal insect parasite (*Dactylopius coccus*) (Le Houerou, 2000; Foxcroft et al., 2008). Currently, more than a dozen introduced cacti have escaped cultivation and are spreading into grazing lands and natural habitats in the Mediterranean regions of Europe and savannas of Australia and Africa (Freeman, 1992; Cronk and Fuller, 2001; Vilà et al., 2003; Erre et al., 2009). Invasive alien cacti often form extensive monotypic stands, which out-compete desirable forage species and render huge tracts of farming and grazing lands useless. For example, at the peak of invasion in Australia in the 1930s, *Opuntia stricta* (sour prickly pear) infested 24 million hectares (ha) of farming and grazing lands in Australia, causing land desertion and affecting rural development (Freeman, 1992). In South Africa, another cactus, *Opuntia ficus-indica* (sweet prickly pear) had infested 900,000 ha of rangeland by the 1940s forcing many land owners to abandon their properties (du Toit, 1942; Dean and Milton, 2000). Cacti invasion of natural habitats and ecosystems have also been associated with declines in native diversity (Grice, 2006). For instance, in the Dom Antonio Xavier Pereira Coutinho Nature Reserve of Portugal, Monteiro et al. (2005) reported that sweet prickly pear and sour prickly pear suppress the establishment of native plant species. In the Kruger National Park of South Africa, it has been observed that sour prickly pear forms extensive monotypic thickets that affect plant community composition and insect assemblages (Robertson et al., 2011). Because invasive alien cacti damage natural ecosystems and reduce economic output from rangelands (Henderson, 2007; Masocha and Dube, 2017), they are of significant management concern in many countries. However, controlling alien cacti once they become invasive is difficult and costly (Van Wilgen et al., 2004; Ibáñez et al., 2009). Thus, predicting potential sites of invasion and preventing the introduction of alien invasive cacti have been pointed as the most effective and least expensive method for managing cacti invasions (Myers et al., 2000).

Understanding patterns of cacti invasion is important for achieving this goal. In Europe, Essl and Kobler (2009) evaluated the distribution of 26 established cactus species. They found that most alien cacti were restricted to the Mediterranean basin. In Australia, the Mediterranean biome was also observed to be prone to invasion by sour prickly pear, alongside the tropical savanna rangeland (Freeman, 1992). In South

* Corresponding author.
E-mail address: mmasocha@science.uz.ac.zw (M. Masocha).

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Africa, Henderson (1995) studied the distribution of sweet prickly pear and found that more than 50% of the country's total land area was prone to invasion. Currently, not much is known about terrestrial biomes and biodiversity hotspots at high risk of cacti invasion on a global scale (Novoa et al., 2015). Information on worldwide potential distribution of alien invasive cacti species is a pre-requisite for the successful implementation of a coordinated global strategy for managing cacti invasions (Masocha and Skidmore, 2011).

To map out the potential global distribution of cacti, environmental factors that determine their distribution need to be known (Austin, 2002; Jimenez-Valverde et al., 2011). Ecological information from the native distribution areas show that freezing temperatures, which destroy apical stems, limit cacti distribution (Rebman and Pinkava, 2001). For example, in Colorado (USA), the distribution of *Cylindropuntia imbricata* (tree cholla) is confined to tropical and subtropical regions with mean monthly temperature greater than −1 °C (Kinraide, 1978). In Sardinia (Italy), Erre et al. (2009) reported that sour prickly pear cannot survive at temperatures below −2 °C. In the Sonoran desert of Mexico, the northern distribution of *Cylindropuntia fulgida* (jumping cholla) is also controlled by freezing temperatures. Jumping cholla dies when exposed to sub-zero temperatures for more than 24 h (Yeaton and Cody, 1979). In South Africa, Snyman et al. (2007) documented that frost occurrence during spring causes the mortality of sweet prickly pear. Other major factors which influence the distribution of cacti are rainfall, solar radiation, canopy shading, and anthropogenic disturbance. Although cacti are known to occur in areas with little measurable (i.e., less than 450 mm of annual rainfall) to those receiving more than 5000 mm of annual precipitation (Tschirley et al., 1964), waterlogging causes rotting of roots (Rebman and Pinkava, 2001). Also, cacti require high amounts of photosynthetically active radiation. They etiolate rapidly in deep shade (Rebman and Pinkava, 2001) hence, shading by dense canopies constraints cacti distribution. On the other hand, anthropogenic disturbance may increase the realised niche of cacti species by opening up closed canopies through deforestation and removing resident plant species which compete with cacti and limit growth (Ansley and Castellano, 2007). There is also a great deal of literature suggesting that cacti thrive in overgrazed sites and human-dominated landscapes where biotic resistance to their invasion is low (Vilà et al., 2003). This information about factors which determine the distribution of cacti is useful for predicting areas at risk of cacti invasion. For example, temperature and rainfall are known to impose energy and water constraints on the distribution ranges of cacti (Coetzee et al., 2009). On the other hand, anthropogenic disturbance has proved key to predicting patterns of plant invasions. It integrates the effect of multiple factors such as propagule availability, invasion pathways, and residence time that interact to shape species distributions at regional and landscape scales (D'Antonio et al., 1999; Wilson et al., 2007; Chytrý et al., 2008; Ibáñez et al., 2009). However, it has to be clarified that the environmental factors mentioned above are limiting the distribution only of the invasive cactaceae, not of all the cactaceae.

The objectives of this research were to predict the potential global distributions of invasive alien cacti and identify terrestrial biomes as well as biodiversity hotspots at high risk of invasion. Out of more than ten introduced cacti species, we analysed the potential expansion of four species: *O. ficus-indica*, *O. stricta*, *C. imbricata*, and *C. fulgida*. The rationale for selecting these four species is that although the species are native to the semi-arid and desert regions of central and south America, they have been reported as dominant and invasive in several regions with different climates such as southern Africa, southern Europe, as well as in eastern and southern Australia (Freeman, 1992; Henderson, 2007; Essl and Kobler, 2009; Masocha and Dube, 2017). This makes the results of the present work broadly applicable to other different regions of the world. Like other members of the cactus family, *Opuntia* and *Cylindropuntia* species have evolved strategies to minimise water loss and achieve water use efficiency (Hernandez et al., 2003). Since these cacti are sensitive to sub-zero temperatures and tolerant to drought, we hypothesised that terrestrial biomes with warm to hot and dry climates, characterised by a seasonal water deficit are the most susceptible to cacti invasion. We used the generalised additive model (Yee and Mitchell, 1991), boosted regression model (Elith et al., 2006) and maximum entropy (Phillips et al., 2006) to construct separate environmental niche models for four cactus species in order to test the prediction of our hypothesis that terrestrial biomes with long hot and dry seasons such as the Mediterranean, tropical savannas and tropical deserts are at great risk of invasion by cacti. Results from the above three modelling techniques were combined using the weighted-average approach to generate consensual global potential distributions for cacti (Araujo and New, 2007; Coetzee et al., 2009; Stohlgren et al., 2010). Invasion risk was computed in a geographic information system as the proportion of each biome predicted suitable for the four target invasive alien cacti.

2. Methods

2.1. Species occurrence data

We downloaded geo-referenced occurrence data for *Opuntia ficus-indica, Opuntia stricta*, *Cylindropuntia imbricata* and *Cylindropuntia fulgida* (Plate 1) from the Global Biodiversity Information Facility (http://data.gbif.org), the Australia's virtual herbarium (http://www.chah.gov/au/avh), and the South African Biodiversity Information Facility (SABIF) (http://sibis.sanbi.org). The species occurrence data were supplemented by occurrence data derived from published literature (Tschirley et al., 1964; Kinraide, 1978; Crosta and Vecchio, 1979; Spears, 1987; Zimmermann and Moran, 1991; Khan-Jetter et al., 2001; Foxcroft et al., 2004; Bobich, 2005; Monteiro et al., 2005; Shackleton et al., 2011) as well as field data collected from Zimbabwe. Species occurrence data points consisted of pairs of geographic coordinates recorded as latitude and longitude. A total of 818 records for *O. ficus-indica*, 390 for *O. stricta*, 252 for *C. imbricata* and 191 for *C. fulgida* were available for model training and validation.

2.2. Environmental and human disturbance datasets

We used minimum temperature of the coldest month, mean temperature of the warmest quarter, annual precipitation, human population density, cattle density, and mean annual normalized difference vegetation index (NDVI) to characterize the environmental space suitable for the four cacti species. These seven environmental variables encompass a broad spectrum of abiotic and biotic determinants influencing the potential distributions of cacti species (see the Introduction for details). Human population and cattle density datasets were used as surrogates of anthropogenic disturbance. Bioclimatic variables were downloaded from the WorldClim (http://www.worldclim.org) as raster grids with a spatial resolution of 30 arc-seconds or approximately 1-km (Hijmans et al., 2005). Specifically, mean temperature of coldest quarter (bio 11), annual mean temperature (bio 1), and mean temperature of warmest quarter (bio 10) were used as proxies for thermal energy influencing cacti growth (Currie, 1991; O'Brien, 1998) whereas precipitation of driest quarter (bio 17) and annual mean precipitation (bio 12) were included as predictors to evaluate the influence of moisture on cacti growth and distribution.

Data on human population density for the year 2005 were downloaded from the Gridded Population of the World database, version 3 (GPWv3) at http://www.sedac.ciesin.columbia.edu/gpw (CIESIN, 2005). Data on global cattle density for the year 2005, corrected for cattle unsuitability and adjusted to match FAOSTAT totals for the year 2000, were obtained from the Food and Agricultural Organisation's Animal Production and Health Division (FAO-AGA) at http://www.fao.org/geonetwork. The global NDVI dataset generated from satellite remote sensing of the earth was obtained from the NASA-MODIS/Terra dataset in raster format at grid cell resolution of 500 m. NDVI data were

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