UTILIZATION AND DISTRIBUTION OF SELECTED INVASIVE ALIEN SPECIES IN GERMANY AND NAMIBIA IN COMPARISON TO THE AREAS OF ORIGIN

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RUBEN ULBRICH

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Main Supervisor:	Dr E. G. Kwembeya (Department of Biological Sciences, University of Namibia)
Co-Supervisor:	Mrs V. De Cauwer (Department of Geospatial Sciences and Technology, Polytechnic of Namibia)

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Abstract

Leucaena leucocephala (Lam) de Wit, *Prosopis* L. spp, *Prunus serotina* Ehrh. and *Robinia pseudoacacia* L. originated in North America but are invasive alien species in different parts of the world. The aim of the study was to determine the actual and possible species distribution of *Leucaena leucocephala* and six *Prosopis* spp in Namibia as well as *Prunus serotina* and *Robinia pseudoacacia* in Germany. Species distribution modelling, using the software Maxent, was employed to predict the distribution of each species in the host region and to compare the actual and possible distribution according to the growing conditions of the donor region. Three different models were used. Model 1 included occurrence points and the ten most important environmental variables of the donor region. Model 2 used the same ten most important environmental variables but from the host area and Model 3 was calculated only with data of the host area. Occurrence points were obtained from the local herbarium, the GBIF database and road counts. Environmental variables consisted of different soil and climate variables. The results of the study calculated significant differences between the maps of Model 1 and 2, while Model 3 produced almost similar results to Model 2. The contribution of each variable to the model differed between the three models. Model 3 used three to five new variables. Response curves of each variable for univariate models showed different effects on the occurrence probability for each species. All species used a smaller range of environmental conditions in the host area compared to the donor region. The available and rarefied occurrence records and the time gap between species introduction to the rapid spread may explain the differences found in Models 2 and 3 in comparison to Model 1. The study demonstrated the importance of modelling invasive alien species with donor and host data in order to avoid wrong conclusions and underestimation of the potential threat of invasive alien species. Additionally, actual and reliable occurrence records are essential for accurate mapping predictions; regular monitoring and more intensive studies of invasive species especially in Namibia are necessary to accurately predict their range and impacts on native ecosystems.

Key words: *L. leucocephala, Prosopis* spp, *P. serotina, R. pseudoacacia,* Species Distribution Modelling, Maxent, Invasive Alien Species

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1 Introduction

1.1 Orientation of the Study

Since the beginning of agriculture people have influenced the spreading and dispersal of plants and animals. Today, 98 % of all agricultural products in the USA are from (former) alien species for example livestock in north western America but different other species in Australia and Argentina as well (Shine, Williams, & Gündling, 2000; Pimentel, Lach, Zuniga, & Morrison, 2005). Upon the discovery of America, new trade routes and thus a new age of species exchange began. Well-developed and far-reaching transportation methods and the increasing global trade in the current century enhance the dispersal of alien species (Shine et al., 2000; Perrings, 2005).

There are several reasons for the intentional introduction of new species like livestock (cows to Australia, Argentina) and crops (corn and wheat) as well as for ornamental purpose, timber, fodder, erosion control and/or reforestation (Shine et al.,, 2000; Pimentel et al., 2005). On the other hand, so-called ‘hitchhikers’ were brought unintentionally to the new environment and introduced through means of ornamental plants, soil, litter, luggage, or vehicles and planes. For instance, the Japanese alga (*Sargussum muticum* (Yendo) Fensholt) was introduced when Japanese oysters (*Parthenium hysterophorus* L.) were shipped as supplies for famine aid to Ethiopia (McNeely et al., 2001 in Chenje & Mohamed-Katerere, 2006).

According to the “Convention on Biological Diversity” invasive alien species are “species, subspecies or lower taxon, introduced outside its natural past or present distribution […] whose introduction and/or spread threaten biological diversity” (Shine et al., 2000). Often, the intentional or unintentional distribution of alien species has no effect as only an estimate amount of 0.1 % becomes invasive (Alpert, Bone, & Holzapfel, 2000).

According to a study of Pimentel et al. (2001) non-indigenous species caused an estimated damage of US$ 336 billion per year in the United States, United Kingdom, Australia, South Africa, India and Brazil together. The costs consist mainly of the control and prevention of future invasion, diseases spread by non-indigenous species (for example rats) and damages or losses to farmers. If this calculation included the effects of alien species on biodiversity losses, ecosystem services and aesthetics, the dollar amount would drastically increase (Pimentel et al., 2001). But not just the six listed states spend a tremendous amount of money every year, Chenje and Mohamed-Katerere (2006) estimated that the whole African continent has to spend US$ 60 million per year for the control of invasive alien species.

1.2 Statement of the Problem

Invasive alien species are seen as the second largest driver for biodiversity loss in the world. In the host region (area which receives foreign species) Europe, various endangered species are threatened by invasive alien species for example the European mink (*Mustela lutreola* L) by the American mink (*Neovison vison* Schreber). European forests changed on a larger scale due to Dutch elm disease brought from Asia (Genovesi & Shine, 2003; Shine et al., 2000).

Tree species like *Prunus serotina* Ehr. and *Robinia pseudoacacia* L. were introduced from the donor region (area from which the species is introduced to the host region) North America to Europe for forestry purpose (Brandes, 2000) but are today known for their impact on European economy in the forestry sector (Genovesi & Shine, 2003; Starfinger & Kowarik, 2003; Starfinger, 2010).

While in Europe certain awareness about the impact of invasive alien species is given invasive alien species seems to be a young field in Namibia. The Namibian Directorate of Forestry nurseries sold the non-indigenous tree *Leucaena leucocephala* (Lam.) de Wit since 1992 (Joubert, 2008) and *Prosopis* spp. were intentionally introduced as fodder and shade tree in the beginning of the 20th century (Smit, 2005). All four species (European and Namibian) are listed as major invasive alien plants in Germany or Namibia (Brandes, 2000; Lowe, Browne, Boudjelas, & De Poorter, 2000; Smit & Steenkamp, 2003; Zentralverband Gartenbau e.V., 2008).

Management tools to reduce the presence of these four species focus mainly on physical removal methods in areas of actual abundance or sanctions rather than precautionary approaches or protection of vulnerable areas (Smit, 2005; Zentralverband Gartenbau e.V., 2008). However, current management strategies in Germany and Namibia are limited by insufficient knowledge of potential distribution ranges for these invasive alien species. Few precautionary actions to combat invasive alien species have been developed on the basis of species distribution modelling. The rapid development and amount of different species distribution modelling approaches offer new opportunities to improve the precautionary actions and the identification of endangered areas of interests (such as national parks or nature reserves) on the basis of species distribution ranges.

The behaviour of invasive alien species in the host regions still needs more investigation to increase precautionary actions and the development of management strategies.

1.3 Objectives

The overall aim of this study was the testing and verification of the species distribution modelling for selected invasive alien species in Germany and Namibia with the help of the software Maxent. It was the first attempt to verify the distribution of invasive alien species in Namibia and tested limitations as well as explore potential applications. This was done with the following objectives:

- To predict the actual and possible distribution areas of *Leucaena leucocephala*, *Prosopis* spp, *Prunus serotina* and *Robinia pseudoacacia* according to species distribution modelling in Germany and Namibia
- To compare actual and possible/predicted distribution ranges of the selected species according to the growing conditions of the donor region (Northern America)

1.4 Research Hypotheses

- The predicted distribution range, based on the growing conditions of the donor region, will not differ from the potential distribution range, based on the environmental conditions of the host region of the selected species, due to the range of suitable environmental conditions in both regions

- The actual distribution range of the selected species will not differ from the potential/predicted distribution range in terms of preference to specified environmental conditions

1.5 Significance of the Study

Several international and national agreements (e.g. Convention on Biological Diversity, Bern Convention, Vision 2030 of Namibia) include the control, management or protection of natural habitats against alien species. Both Germany and Namibia do not view invasive alien species as an urgent problem but according to the precautionary approach both nations need to consider actions beforehand. The precautionary approach stays that all management and control actions are needed to solve the situation before the problem starts, for example before invasive alien species spread and threaten the indigenous ecosystem, (Mack et al., 2000; Bethune, Griffin, & Joubert, 2004; Klingenstein, Kornacker, Martens, & Schippmann, 2005; Joubert, 2008).

The knowledge of past and actual invasive alien species is necessary to limit future damage or prevent new invasions (Reichard & Hamilton, 1997 in Alpert, Bone, & Holzapfel, 2000). The information is important and necessary for management and nature conservation purposes in the different regions (Elith et al., 2006). Different studies with species distribution modelling software (for example Bioclim, Maxent, OpenModeller or Random Forest) were done to predict the distribution of invasive species such as invertebrates, mammals, mussels and plants (Eltih et al., 2006; Hoffman, Narumalani, Mishra, Merani, & Wilson, 2008; Jeschke & Strayer, 2008; Mingyang, Yunwei, Kumar, & Stohlgren, 2008; Baldwin, 2009). Such digital modelling methods are relatively new and most studies in Germany were focused on different future climatic scenarios or on a large number of different species (for example Kleinbauer et al., 2010). In Namibia the species distribution modelling has not been used for the purpose of modelling invasive alien species before but for the modelling climate change impacts on endemic organisms in Namibia (Thuiller et al., 2006).

1.6 Limitation of the Study

The study relies on present data (GIS - geographic information system, data sets for the species distribution modelling) of the donor region (Northern America) and the receiver countries (Germany, Namibia). Although, institutes like University and Polytechnic of Namibia, and Humboldt-Universität in Berlin, Germany, will ensure the access to the databases, there is potential bias of species observation records because of non-scientific listing or observation. This bias was reduced by actual datasets, records (last 20 years) and reliable sources (research stations, herbarium, ministries). However, the amount of species records for invasive alien species in Namibia remained low and the focus of species records from Germany and neighbouring countries might influence the output. A method of rarefying the occurrence points was used to reduce the effect on the models.

The weaknesses in modelling large areas like whole countries will be reduced by using the highest available resolution of GIS-datasets for each environmental variable (1 km).

2 Literature Review

2.1 General Aspects

For a long time problems and effects of invasive alien plants were overseen and only in the beginning of the last century policy, economy and conservationists groups start to focus on this urgent topic (Brandes, 2000; Klingenstein et al., 2005; Joubert, 2008). Today, Africa is home to hundreds of invasive alien species and Europe to estimated 12,000 alien plant species (Brandes, 2000; Chenje & Mohamed-Katerere, 2006). Invasive alien species in Germany and Namibia are not as problematic even though around 40 species in each country are declared as invasive alien species with actual or predicted impacts on biodiversity and economy (Smit & Steenkamp, 2003; Bethune, Griffin, & Joubert, 2004; Klingenstein et al., 2005; Joubert, 2008).

One of the reasons why invasive alien species were not seen as an urgent problem could be the time gap between the introduction of the species and its spread over the host region. Kowarik (1995) found evidence of a time gap between introduction and rapid spread of invasive alien species. This time gap was between 131 and 170 years for species in northern Germany (Kowarik, 1995). Other studies in Hawaii with tropical plant had time lags between 5 (herbaceous plants) and 14 years (woody plants) (Daehler, 2009). Both studies showed very different time gaps but were conducted under different climate situations as well. Such a time gap may explain why Germany and Namibia put less effort into the management of invasive alien species till this stage.

For this study four tree species were chosen which were either under worst invasive alien plant species worldwide or have a specific impact in the host region. According to Lowe et al. (2000) *Leucaena leucocephala* and *Prosopis* spp are under the 100 worst invasive alien plant species worldwide because of their serious impact on biodiversity. Both species are known to form dense thickets and change the soil composition which forms major threats to native fauna (Macdonald, Kruger, & Ferrar, 1986; Wells et al., 1986; Weber, 2003; Matthew & Brand, 2004; Orwa et al., 2009; Bromillow, 2010). They are listed among the "Nasty Nine" alien invasive species of Namibia (Smit & Steenkamp, 2003).

Prunus serotina and *Robinia pseudoacacia* have been ranked as species with main threats to biodiversity and economy in Germany (Brandes, 2000; Zentralverband Gartenbau e.V., 2008). The first one is also known as "forest pest" and out-shade the ground vegetation in European forests which suppress rejuvenation of the forests while on open land the effects are worse if rare species such as the rare *Calluna* spp Salisb in Denmark are effected (Starfinger, 2010). *Robinia pseudoacacia* changes the soil composition through nitrogen-fixation which threats the unique grasslands of Europe (Macdonald, Kruger, & Ferrar, 1986; Seitz & Nehring, 2013).

2.2 Study species

2.2.1 *Leucaena leucocephala*

Leucaena leucocephala (Lam.) de Wit belongs to the family *Fabaceae*. Former synonyms were *L. glauca* Benth, *Mimosa glauca* L., and *Acacia glauca* Willd. Some common names of the species are: wonderboom, white tamarind, reusewattle, stuipboom.

Its native range is in Central America, especially Mexico (Matthew & Brand, 2004; Orwa, Mutua, Kindt, Jamnadass, & Simons, 2009) (Figure 2.1). The plant can be found on forest margins, roadsides, wastelands, and riverbanks (Matthew & Brand, 2004). It grows in warm temperatures (annual mean 25 to 30 °C) and can tolerate dry seasons of 6 to 7 months (Orwa et al., 2009). The best growing conditions can be found over 1,200 mm rain/year, but the annual range of rainfall lies between 650 to 3,000 mm (Orwa et al., 2009). Mature *L. leucocephala* re-sprouts after cutting, fires and frost events although it prefers frost-free areas (Matthew & Brand, 2004; Orwa et al., 2009).

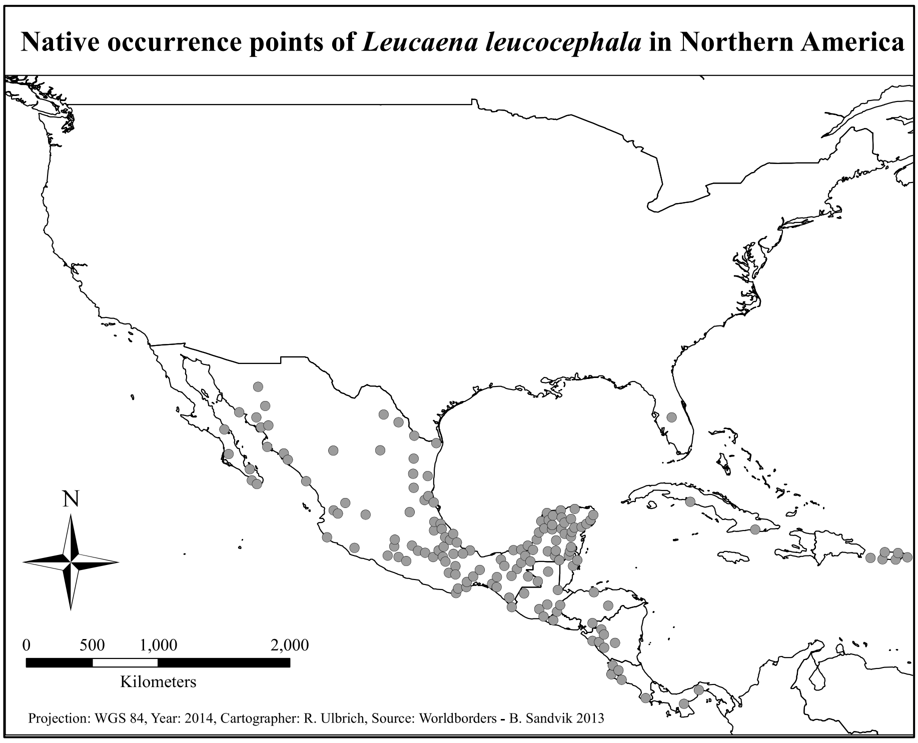


Figure 2.1 The native range of *Leucaena leucocephala* in Northern America retrieved from GBIF data and rarefied for the modelling

The fast-growing evergreen shrub or small tree grows up to 20 m (Figure 2.2) and occurs on lime soils, as well as alkaline soils up to pH 8 (Matthew & Brand, 2004; Orwa et al., 2009). The dark green leaves consist of 6 to 9 pairs pinnate with 13 to 21 pairs of leaflets (each 9 to 16 mm long) which folds up with heat, cold or lack of water (Henderson, 2001; Orwa et al., 2009). The species is self-fertilizing and the flowering and fruiting happens through out the year (Orwa et al., 2009). The white or

Figure 2.2 Mature *Leucaena leucocephala* in the north of Namibia (Ulbrich, 2014).

pale yellow flowers form groups of two or six flower heads with 100 to 180 flowers (Henderson, 2001; Orwa et al., 2009). The fruits are brown pods, 110 to 180 mm long and contain 8 to 18 dark-brown and hard seeds (Henderson, 2001; Orwa et al., 2009). The pod splits in two halves along the margins and releases the seeds.

The species was introduced in South Africa during the end of the 19th century as fodder and crop plant and eventually reached Namibia (Macdonald, Kruger, & Ferrar, 1986; Bromillow, 2001; Henderson 2001). No literature evidence was found about the time and place for Namibia.

The dense thickets reduce the native vegetation and species richness (Macdonald, Kruger, & Ferrar, 1986; Wells et al., 1986; Matthew & Brand, 2004; Bromillow, 2010). Also, the nitrogen fixation improves the soil fertility, which is in general cases an advantage for the ecosystem, the high tolerance, fast growth rate and the change of soil composition are disadvantages for the native vegetation. Furthermore, the competition with native flora for resources like water and nutrition's are the major challenges for host ecosystems (Wells et al., 1986; Macdonald, Kruger, & Ferrar, 1986; Mannheimer & Curtis, 2005; Orwa et al., 2009).

The whole plant is toxic to livestock in huge quantities (more than 25 % of the diet) and can cause problems for local farmers (Henderson, 2001).

2.2.2 *Prosopis* spp

There are six *Prosopis* species in Namibia: *Prosopis chilensis* (Molina) Stuntz, *Prosopis glandulosa* var. *glandulosa* Torr., *Prosopis glandulosa* var. *torreyana* (Benson) Johnst., *Prosopis juliflora* (Sw.) DC., *Prosopis pubescence* Benth., and *Prosopis velutina* Wooton (Smit, 2005). A potential seventh species (*P. cineraria*) failed to establish in Namibia, the reasons are seen in poor management rather than the ability of the species (Smit, 2005). *Prosopis* species are also known by the common names: honey mesquite, mesquite, ironwood, suidwesdoring.

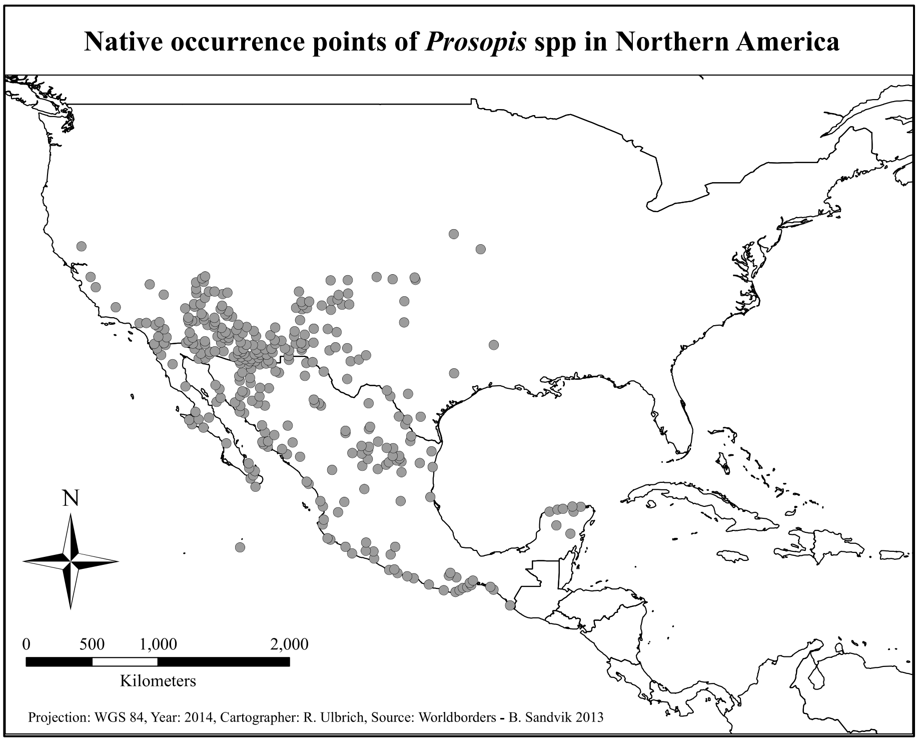


Figure 2.3 The native range of *Prosopis* spp in Northern America retrieved from GBIF data and rarefied for the modelling.

Most authors argue that *P. glandulosa* var. *torreyana* as the most common species in Namibia (Mannheimer & Curtis, 2005; Smit, 2005; Van Wyk & Van Wyk, 2011). During this study all six *Prosopis* species were pooled together due to high hybridization between the species, which makes the identification difficult and occurrence points unreliable (Henderson, 2001; Smit, 2005; Orwa et al., 2009; Bromillow, 2010; Van Wyk & Van Wyk, 2011). They will be named "*Prosopis* spp" throughout this study.

Prosopis spp belongs to the family *Fabaceae*, subfamily *Mimosoideae*. The six species' origins are in North America (Figure 2.3), especially south west USA and northern Mexico (Gilman & Watson, 1994a; Henderson, 2001; Smit, 2005). The distribution ranges from rocky slopes, gravelly foothills and washes as well as along streams and groundwater areas (Orwa et al., 2009). In Namibia and other host areas they can be found around homesteads, on roadsides and drainage lines (Macdonald, Kruger, & Ferrar, 1986; Smit, 2005).

Figure 2.4 *Prosopis* spp in the south of Namibia (Ulbrich, 2013).

They grow in a variety of substrates, including clay, loam, and sand as well as, well-drained, acidic and alkaline soils (Gilman & Watson, 1994a). The plants are very drought tolerant and grow in full sunlight (Gilman & Watson, 1994a). Studies report that lives in regions with mean annual temperatures of 18 to 21 °C and a mean annual precipitation between 200 to 1,000 mm is recorded in Orwa et al. (2009). *P. glandulosa* var. *torreyana* can grow up to altitudes of 1,500 m (Orwa et al., 2009).

Other *Prosopis* species like *P. chilensis* need less rain, 350 to 400 mm, and grow in lower altitudes – up to 1,230 m (Orwa et al., 2009). All six *Prosopis* species are salt tolerant, whereby, *P. juliflora* has the highest salt tolerance and can even survive waterlogged conditions (Orwa et al., 2009).

The six *Prosopis* species form mostly multi-stemmed 2 to 15 m high bushes or trees (Figure 2.4) (Pasiecznik, Harris, & Smith, 2004; Smit, 2005; Orwa et al., 2009). The deep root system (up to 18 m) allows the species a high drought tolerance (Orwa et al., 2009).

Most of the species are evergreen; the leaves have up to three pinnae with different pairs of leaflets (4 to 30) (Pasiecznik, Harris, & Smith, 2004; Smit, 2005; Orwa et al., 2009). While most distances between the leaflets are narrow, the exception is *P. glandulosa* var. *torreyana* with a distance of 6 to 18 mm (Orwa et al., 2009).

The species have yellow flowers, which are gathered to balls and produce straw-yellow pods (Gilman & Watson, 1994a; Weber, 2003; Pasiecznik, Harris, & Smith, 2004; Orwa et al., 2009). The woody pods are 10 to 25 cm long, cylinder-shaped and has slight constrictions between each of the 5 to 32 seeds (Weber, 2003; Pasiecznik, Harris, & Smith, 2004; Orwa et al., 2009). Mature trees produce 20 to 100 kg pods per year (Pasiecznik, Harris, & Smith, 2004). The seeds remain viable in the soil for years (Weber, 2003). Cattle eating the high nutritious pods aid germination and help to spread the immobile seeds, while the digestive system of pigs and goats kill most of the seeds (Macdonald, Kruger, & Ferrar, 1986; Pasiecznik, Harris, & Smith, 2004).

The six *Prosopis* species have more or less long pairs of spines, which allow the formation of dense thickets and pose a threat to car tires and animal feet (Weber, 2003; Pasiecznik, Harris, & Smith, 2004; Smit, 2005; Orwa et al., 2009).

The date and specific species of Prosopis that first reached southern Africa is highly debated. Bromillow (2010) notes that the first *Prosopis* species was planted 1897 in the Okahandja Experimental Garden. Other authors believe 1912 was the crucial year where *Prosopis chilensis* (Smit, 2005) or another *Prosopis* species (Brown, Macdonald, & Brown, 1985; Macdonald, Kruger, & Ferrar, 1986) reached Namibia. Still, others (Erkkilä & Siiskonen, 1992) reported first evidence of *Prosopis* species in a Windhoek nursery in 1905. The species were introduced for fodder and shade (Smit, 2005), although it is known that the pods are poisonous in quantities (Henderson, 2001).

The comparison with a map from 1985 (see appendix A1) as well as different studies showed that *Prosopis* spp is still spreading throughout the country (Brand & Matthew, 2004; Smit, 2005). Riparian zones are especially vulnerable, as seeds can be easily transported during flood events and, thus, spread the species in future (Brown et al., 1985; Boyer, D. C. & Boyer, H. J., 1989; Smit, 2005; Joubert, 2008).

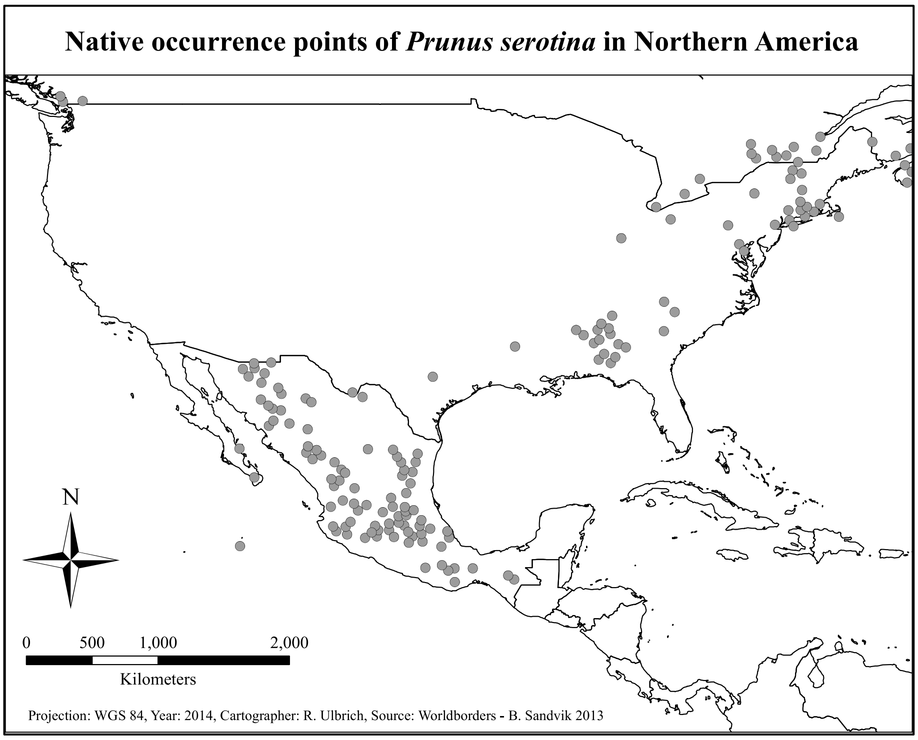
In 1986, Macdonald, Kruger and Ferrar mentioned the huge threat *Prosopis* spp invasions pose for arid and semi-arid biomes. In the same year, studies showed that *Prosopis* spp use more water than native tree species *Vachellia erioloba* (E. Mey.) P. J. H. Hurter, which were the comparison species for their studies (Brown, Macdonald, & Brown, 1985). Although, the initial nitrogen fixation provided by *Prosopis* spp seems to improve the soil quality, the eventual thick canopies result in a loss of grass cover and a consequent increase in soil erosion (Weber, 2003; Orwa et al., 2009). Today, the city of Windhoek prohibits the planting of any *Prosopis* spp by law (Mannheimer & Curtis, 2005).

2.2.3 *Prunus serotina*

The species *Prunus serotina* Ehr. is a member of the *Rosaceae* family and formerly known under *Padus serotina* (Ehr.) Borkh. and *Cerasus serotina* (Ehr.) Loisel. The most common names are: black cherry, rum cherry, Späte Traubenkirsche.

The native range is west and east Canada, but mainly the north central and north eastern parts of the USA (Seitz & Nehring, 2013) as well as Central Mexico (Figure 2.5). The species occurs in oak-pine forests, moorland and areas with minor vegetation (native range) but in host areas on waste land, coniferous and young woodland, forest clearings and mixed coniferous/deciduous forests (Weber, 2003; Klotz, 2007; Seitz & Nehring, 2013).

In its native range it grows up to 38 m, while in host regions like Europe it only grows to heights of 20 m or less (Figure 2.6) (Weber, 2003; Klotz, 2007). The deciduous plant has alternate, ovate to oblong-lanceolate leaves, which are 5 to 15 cm long, and have a finely toothed margin (Weber, 2003; Klotz, 2007).



Projection: WGS 84, Year: 2014, Cartographer: R. Ulbrich, Source: Worldborders - B. Sandvik 2013

Figure 2.5 The native range of Prunus serotina in Northern America retrieved from GBIF data and rarefied for the modelling.

The numerous white flowers consist of five petals and produce black berries (8 to 10 mm in diameter with huge stone: 6 to 8 mm), which are often spread by birds (Weber, 2003; Klotz, 2007; Seitz & Nehring, 2013). The species can produce huge seed banks in the soil where they germinate after three years and can stay viable for up to five years (Weber, 2003; Klotz, 2007; USDA NRCS, 2011). Root suckers are an alternative way of reproduction for *P. serotina*.

The shade-intolerant species grows on deep, rich and moist soils with clay, loam, sand, acidic, and alkaline partitions in their native range (Gilman & Watson, 1994b; Starfinger, 2010; Seitz & Nehring, 2013) and, in the host regions, they are found mainly in sandy and poor soils (Seitz & Nehring, 2013). The plant occurs in altitudes up to 2,000 m (Starfinger, 2010).

In 1623 the first specimens reached Europe as ornamental plants (Klotz, 2007) and in 1796 it was recorded in Berlin, Germany by Willdenow but the first proofs of

Figure 2.6 *Prunus serotina* in Central Europe (adapted from www.eol.org, 2014).

specimens in Berlin were only documented in 1825 (Kowarik, 1999 in Seitz & Nehring, 2013). The main purpose of the intentional introduction was as soil improver (due to low Carbon-Nitrogen-ratio in leaves it was hoped to speed up soil processes), fire- and windbreaker (Klotz, 2007; Starfinger, 2010). The species is cultivated in North America and also known for its toxin in leaves, twigs, bark and seeds for livestock (USAD NRCS, 2011).

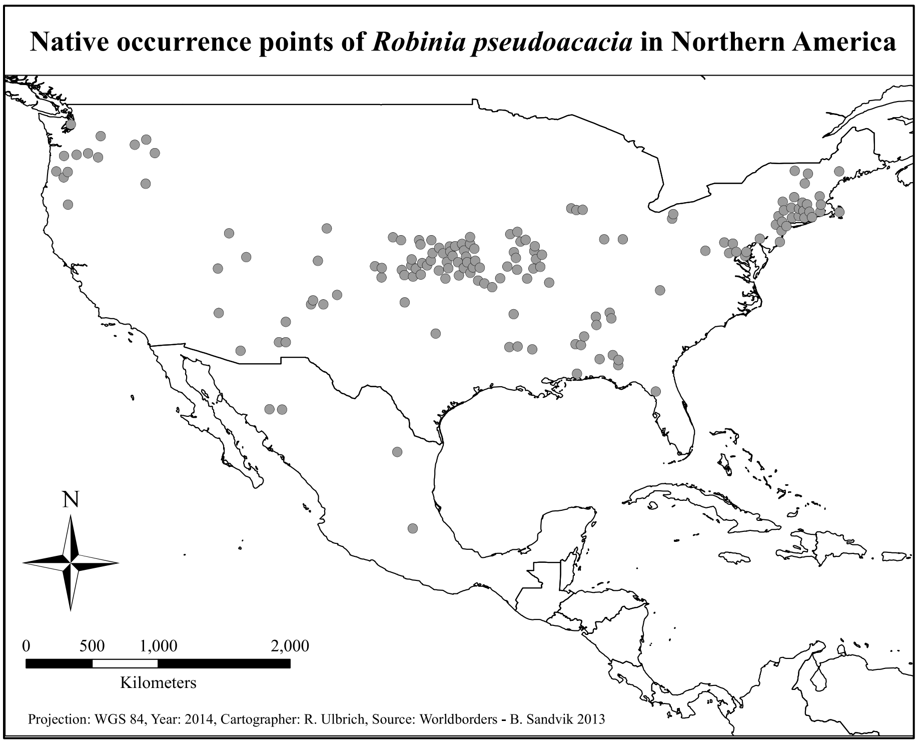
Prunus serotina reduces the species abundance and suppresses regeneration in forests (Seitz & Nehring, 2013). Dense stands outcompete native vegetation and the litter changes the humus quality (Macdonald, Kruger, & Ferrar, 1986; Klotz, 2007; Seitz & Nehring, 2013).

2.2.4 *Robinia pseudoacacia*

Robinia pseudoacacia L. belongs to the family *Fabaceae* and has two related species: *R. viscosa* and *R. hispida*. Several synonyms were used for *R. pseudoacacia*, namely *Pseudoacacia communi*s Simkovics, *Pseudoacacia pseudoacaci*a Borbás, *Robinia acacia* L., *Robinia pseudacacia* L., and *Robinia pseudacacia* var. *rectissima*

(L.) Raber. Some of the common names of *R. pseudoacacia* are: black locust, false acacia, witakasia, Robinie, Scheinakazie.

The species native range is the eastern part of North America, especially in the Appalachian Mountains (Bromillow, 2010; Starfinger & Kowarik, 2010; Seitz & Nehring, 2013) (Figure 2.7). The shade intolerant pioneer plant uses forest gaps and grows rapidly to dense pure stands (Weber, 2003). In its native range it prefers limestone derived, moist soils (Orwa et al., 2009). In the host regions, it is mainly found in dry grassland, forb habitats and young woodlands as well as acidic and polluted sites (due to is nitrogen fixation ability) are the main habitats of the species in host regions (Başnou, 2006; Starfinger & Kowarik, 2010; Seitz & Nehring, 2013).



Projection: WGS 84, Year: 2014, Cartographer: R. Ulbrich, Source: Worldborders - B. Sandvik 2013

Figure 2.7 The native range of *Robinia pseudoacacia* in Northern America retrieved from GBIF data and rarefied for the modelling.

The cold tolerant species prefers a mean annual precipitation of 1,000 to 1,500 mm and grows in altitudes up to 1,500 m (Orwa et al., 2009; Starfinger & Kowarik, 2010).

The deciduous tree (Figure 2.8) reaches up to 30 m height and has alternate, pinnate compounded leaves (Weber, 2003; Orwa et al., 2009). The leaves consist of 7 to 19 leaflets with a terminal leaflet and two characteristic spines at the base of each leaf (Orwa et al., 2009). The leaflets are oval with a smooth margin and 30 to 50 mm long (Orwa et al., 2009).

Figure 2.8 *Robinia pseudoacacia* in Central Germany (Ulbrich, 2014).

The white, pea-like flowers form dropping racemes of 10 to 20 cm length (Macdonald, Kruger, & Ferrar, 1986; Bromillow, 2001; Henderson, 2001; Orwa et al., 2009). The fruits are brown pods, 7 to 10 cm long, and contain 5 to 8 dark, beanlike seeds per pod (Orwa et al., 2009). The pods on a central stalk remain on the tree over the winter month (Orwa et al., 2009). The wind-dispersed seeds can survive several years in the soil but require a lot of sunlight to start germination (Başnou, 2006; Starfinger & Kowarik, 2010).

R. pseudoacacia was brought to Europe around 1630 as an ornamental plant (Başnou, 2006; Bromillow, 2010). Around 40 years later the first specimens were mentioned in Berlin, Germany. During the 18th century the species was used in forest cultivation in Brandenburg and Sachsen-Anhalt (Starfinger & Kowarik, 2010) but the first proof of specimens in Germany are from 1824 in Frankfurt (Oder) (Seitz & Nehring, 2013).

All parts of the plants are toxic for humans and most animals except cattle and deer, which can bear the toxins (Başnou, 2006). The nitrogen-fixing species changes the soil composition and fertility levels in host regions, especially in the unique dry grasslands of Europe where the higher soil fertility outcompete species which are highly adapted to low fertility areas (Macdonald, Kruger, & Ferrar, 1986; Seitz & Nehring, 2013).

2.3 Species Distribution Modelling

Several studies were made on invasive alien trees (*Elaeagnus angustifolia* L. in North America – Hoffman et al., 2008; Janrevich & Reynolds, 2011; *Pinus* L. spp. on global scale – Nuñez & Medley, 2011; *Tamarix* L. spp. in North America – Evangelista, Stohlgren, Morisette, & Kumar, 2011; *Sapium sebiferum* (L.) Small in western Himalaya – Jaryan, Datta, Uniyal Kumar, Gupta, & Singh, 2013), weeds (several hundred species in Australia – Wilson, Downey, Leishman, Gallagher, Hughes, & O'Donnell, 2009), or mussels (*Dreissena polymorpha* Pallas in North America – Mingyang, Yunwei, Kumar, & Stohlgren, 2008) using Maxent and/or another modelling program. Most of those studies used occurrence points and environmental variables of the host area and projected the distribution range of species to the host region under current climate condition or future changing scenarios (Hoffman et al., 2008; Evangelista et al., 2011, Jaryan et al., 2013). For example Nuñez and Medley (2011) modelled the possible distribution range of different *Pine* spp across the world using the occurrence points and environmental conditions of the donor area North America. They used different climate and environmental settings; and tested the accuracy of their models with known occurrence points of host areas around the globe (Nuñez & Medley, 2011). All of these previous species distribution models included a projection to a new set of environmental variables but used only one area, the host region. Different studies using species distribution modelling are listed in Table 2.1.

Although previous studies have explored the topic of invasive alien species in Germany and Namibia, most studies and articles deal with the disadvantages on biodiversity and management purposes rather than possible future distributions and insights for precautionary control (Brandes, 2000; De Wit, Crookers, & Van Wilgen, 2001; Smit, 2005; Chenje et al., 2006; Joubert, 2008; Zentralverband Garten e.V., 2008).

The knowledge and understanding of species ecology and evolutionary determinants in spatial patterns are essential for conservation planning and projects (Elith et al., 2006). It allows conservationists to mobilize and focus resources in advance on possible target areas of invasive alien species distribution. In contrast to general approach, which relies on assets to cover a generalized area that is assumed to be threaten by invasive alien species without any evidence. Species distribution models come in hand to fill this gap.

Species Distribution models are empirical models, which relate occurrence points to environmental variables on the basis of statistically or theoretically derived response surfaces aiming for the best reflected ecological tolerances (Guisan & Thuiller, 2005; Elith et al., 2006; Rupprecht, Oldeland, & Finckh, 2011). Depending on the available occurrence data, models of presence-only, presence-absence or abundance observations can be calculated.

Around 80 years ago the first known species distribution models were done by Johnston who modelled the invasive spread of cactus species in Australia while the earliest computer-based models occurred in 1970s (Guisan & Thuiller, 2005).

In most cases, herbaria, natural history collections in museums, national biological-data record centres or similar institutes only have presence-only data (Guisan et al., 2007), which restricts the kind of model and/or the quality of the output.

The availability of few absence data from herbaria or database led to the creation of own absence points for example areas outside of known occurrence points which should be done with caution. Especially in the case of invasive alien species, which did not cover their full ecological range, this could ignore possible suitable sites and underestimate the possible thread of the species (Václavík & Meentemeyer, 2009; Jiménez-Valverde et al., 2011).

Species distribution modelling was first based on analyses of presence-only data including calculations of envelopes or distance based measures (Gómez, Pompa and Nevling, 1970; Rapoport, 1982; Silverman, 1986; Busby, 1991; Walker & Cocks, 1991; Carpenter et al., 1993 - all in Elith et al., 2006). Distribution modelling advanced with the adaption of presence-absence methods to model presence-only data using samples of background environment (random points) or pseudo-absences (Stockwell & Peters, 1999; Boyce et al., 2002; Ferrier et al., 2002a; Zaniewski et al., 2002; Keating & Cherry, 2004; Pearce & Boyce in press - all in Elith et al., 2006).

In 2004 Phillips, Dudík and Schapire developed the machine-learning software "Maxent", a presence-only modelling software.

Maxent was and is used for different purposes: predicting distribution in current, past or future climate setting, predicting species richness or diversity, forecast distributions to understand changes with climate change and predicting potential distribution for invasive species (Elith et al., 2011). Institutes like the Natural Resources Canada (NRCan) uses Maxent models for current and future distribution models of different native and alien species in North America (http://planthardiness.gc.ca).

The more detailed concept of Maxent will be explained in section 3 Methodology.

Table 2.1 Different studies using Maxent or other software to model species distribution of divers organism and different geographic extend.

Objectives of Study	**Studied Organism**	**Geographic Extend**	**Study listed in**
Predict species distribution	Geckos (*Uroplatus* spp.)	Madagascar	Baldwin, 2009
Model geographical distributions and fundamental niches	Brown-backed bearded sakis (*Chiropotes israelita* Black uakaris (*Cacajao* spp.)	Western Amazon, Brazil	Baldwin, 2009
Assess habitat use	Mule deer (*Odocoileus hemionus*) Gemsbock (*Oryx gazelle*	South-central New Mexico, USA	Baldwin, 2009
Predicting potential occurrence of invasive plant species	5 different tree species	Nebraska, USA	Hoffman, Narumalani, Mishra, Merani, & Wilson, 2008
Prediction potential distribution of invasive riparian tree	Russian olive (*Elaeagnus angustifolia*)	North America	Janrevich & Reynolds, 2011
Climate and prediction of invasion	*Pinus* spp.	Global scale	Nuñez & Medley, 2011
Potential habitats for alien species	Zebra mussel (*Dreissena polymorpha*)	North America	Mingyang, Yunwei, Kumar, & Stohlgren, 2008
Predict species richness or diversity	Amphibians and reptiles	California, USA	Elith et al., 2011
Predict current distributions as input for conservation plan- ning, risk assessments or IUCN listing, or new survey	Humming birds Stony corals	Andes, South America Global	Elith et al., 2011
Understand environmental correlates of species occurrences, groups of species, or other	Macrofungi European wildcat	Norway Portugal	Elith et al., 2011

3 Methodology

3.1 Study Area

3.1.1 Donor Region

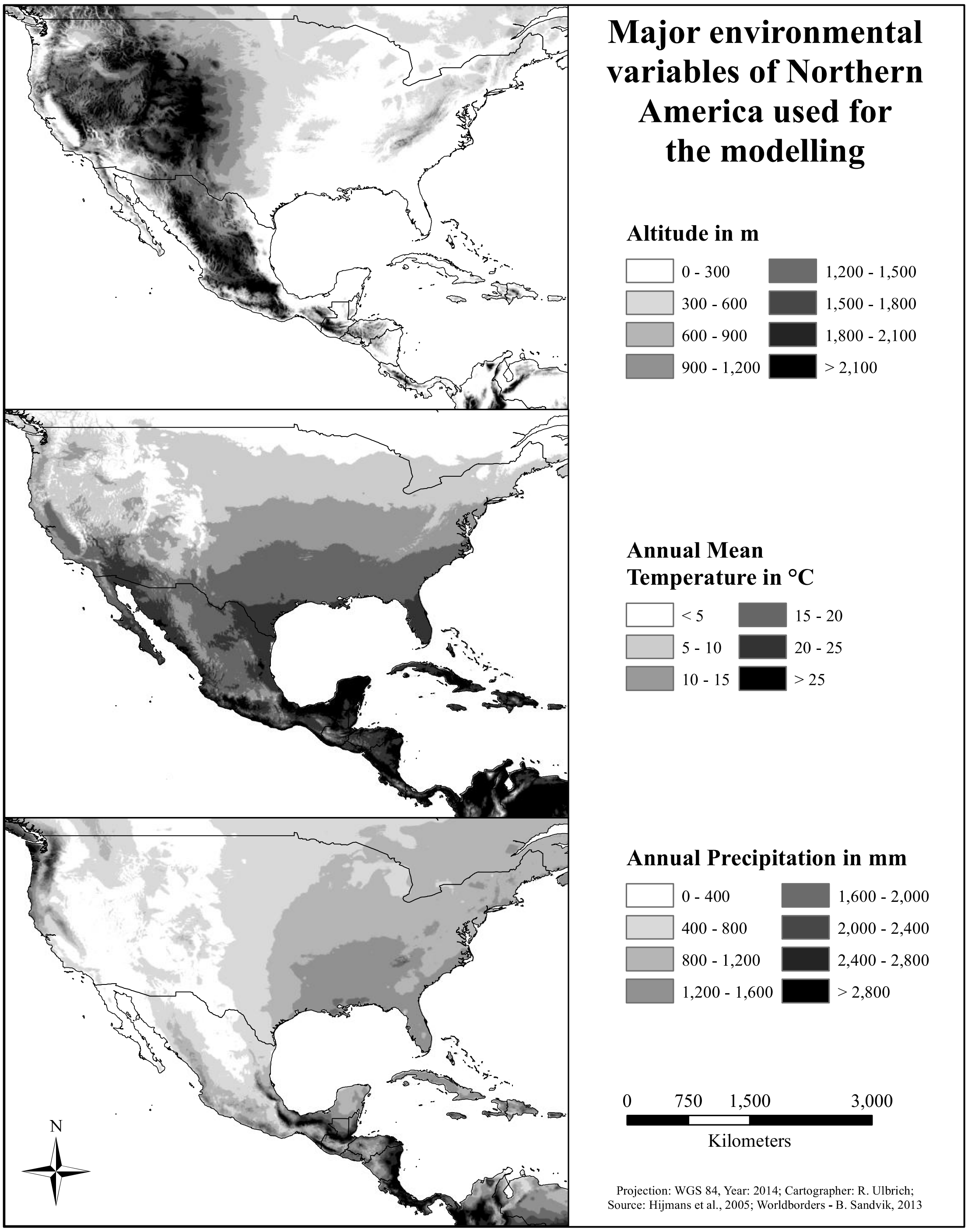
3.1.1.1 Northern America

The donor region “Northern America” used in this study include parts of North America as well as Central America but in specific the following countries Belize, Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama, the United States of America (without Alaska), the northern parts of Colombia and Venezuela, and the southern part of Canada (Figure 3.4 below). Only the main land was included. The extent of the area is listed in Table 3.1 below.

The environmental descriptions of the donor region are not for the full geographical extent but restricted to the set study area extent (see Table 3.1).

The northern part of the donor region is situated in the temperate climate zone, while the southern region is in the tropic climate zone and inner regions have continental climate. The highest rainfall areas in North America can be found on the north western coast of the USA (2,800 mm) and from the south of Mexico up to Panama (800 to 2,400 mm) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) (Figure 3.1). From the central USA to the east coast the rainfall ranges from 800 to 1,200 mm while the south east coast has rainfall up to 1,600 mm per year; from central USA to the west coast the rainfall drops to less than 200 mm per year (Hijmans et al., 2005).

The average temperature increases from north to south, with 0 °C in southern Canada over 19 °C in southern USA and 25 °C in Panama (Hijmans et al., 2005). The mountain ranges in western USA and Mexico are separated with temperatures around 7 °C respectively 18 °C (Hijmans et al., 2005).



Projection: WGS 84, Year: 2014; Cartographer: R. Ulbrich; Source: Hijmans et al., 2005; Worldborders - B. Sandvik, 2013

Figure 3.1 Altitude, Annual Mean Temperature and Annual Precipitation of Northern America used during the modelling. Darker colours represent higher values.

Coniferous forests are found in the north eastern part of the donor regions, while the central regions have mixed forests and the south consists largely of deciduous forests. Most of the central areas are savanna and changes to desert vegetation in the southwest (Kaiser, 2001). Northern Mexico and the highlands host succulents while southern Mexico and Central American countries have mainly tropical forests (Kaiser, 2001).

The eastern part of the USA with an altitude around 150 m (except the Appalachian Mountains near the coast with 1,000 m) (Hijmans et al., 2005) consists of the dominant Acrisols and Phaeozem soils; some Podzols can be found in the north east USA (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). The western USA has Kastanozems and Luvisols in the Rocky Mountains with elevation from 1,500 up to 3,000 m (Hijmans et al., 2005). Mexico and Central American countries have a variety of soils like Calcisols, Leptosols, Nitisols and Regosols (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). The highlands of Mexico spread from north to south with elevations up to 3,000 m (Hijmans et al., 2005).

3.1.2 Host Regions

3.1.2.1 Europe

In this study, the host region "Europe" included Austria, Belgium, Bosnia Herzegovina, Croatia, Czech Republic, Denmark, France, Germany, Great Britain, Italy, Liechtenstein, Luxembourg, Montenegro, Netherlands, Portugal, Slovenia, Spain, and Switzerland; parts of Albania, Hungary, Norway, Poland, Serbia, and Sweden (in alphabetical order) (Figure 3.4). The extent of the study area "Europe" is listed in Table 3.1.

The environmental descriptions of the host regions (Europe and Namibia) are not for the full geographical extent but restricted to the set study area extent (see Table 3.1). Average and maximum/minimum areas are listed.

Europe is positioned in the temperate climate zone with a maritime climate in most of the parts of Western Europe (coastal areas) and a Mediterranean climate in the south. The southern areas experiences distinctive dry and rainy seasons whereas the other areas have four seasons. The inner parts of Europe have a continental climate influence.

The average temperature in Europe is around 8 to 10 °C, whereby, the temperatures in Italy (around 14 °C) and Portugal/Spain (15 °C) are higher (Hijmans et al., 2005). Another exception is the Alps and the Pyrenean mountains with an average around 0 °C per year (Hijmans et al., 2005) (Figure 3.2).

The average precipitation is between 500 and 800 mm in Europe (Hijmans et al., 2005). The west coast of Great Britain (1,200 to 2,000 mm), south coast of Norway (2,600 mm) and the Alps region (1,400 to 2,000 mm) have higher rainfall per year while driest area is in Spain with only 300 to 500 mm rain per year (Hijmans et al., 2005).

The vegetation can be split in two main parts: Italy, Portugal and Spain host mixed deciduous broadleaved forests adapted to higher temperatures and sclerophyllous forests as well as shrubs adapted to dry and hot areas; the other countries included in this study are characterised by a mixture of deciduous broadleaved and coniferous forests. The Alps have vegetation, which is more adapted to the higher rainfall consisting mainly of coniferous forests, shrubs and forbs (Bohn et al., 2000 in European Environment Agency, 2007).

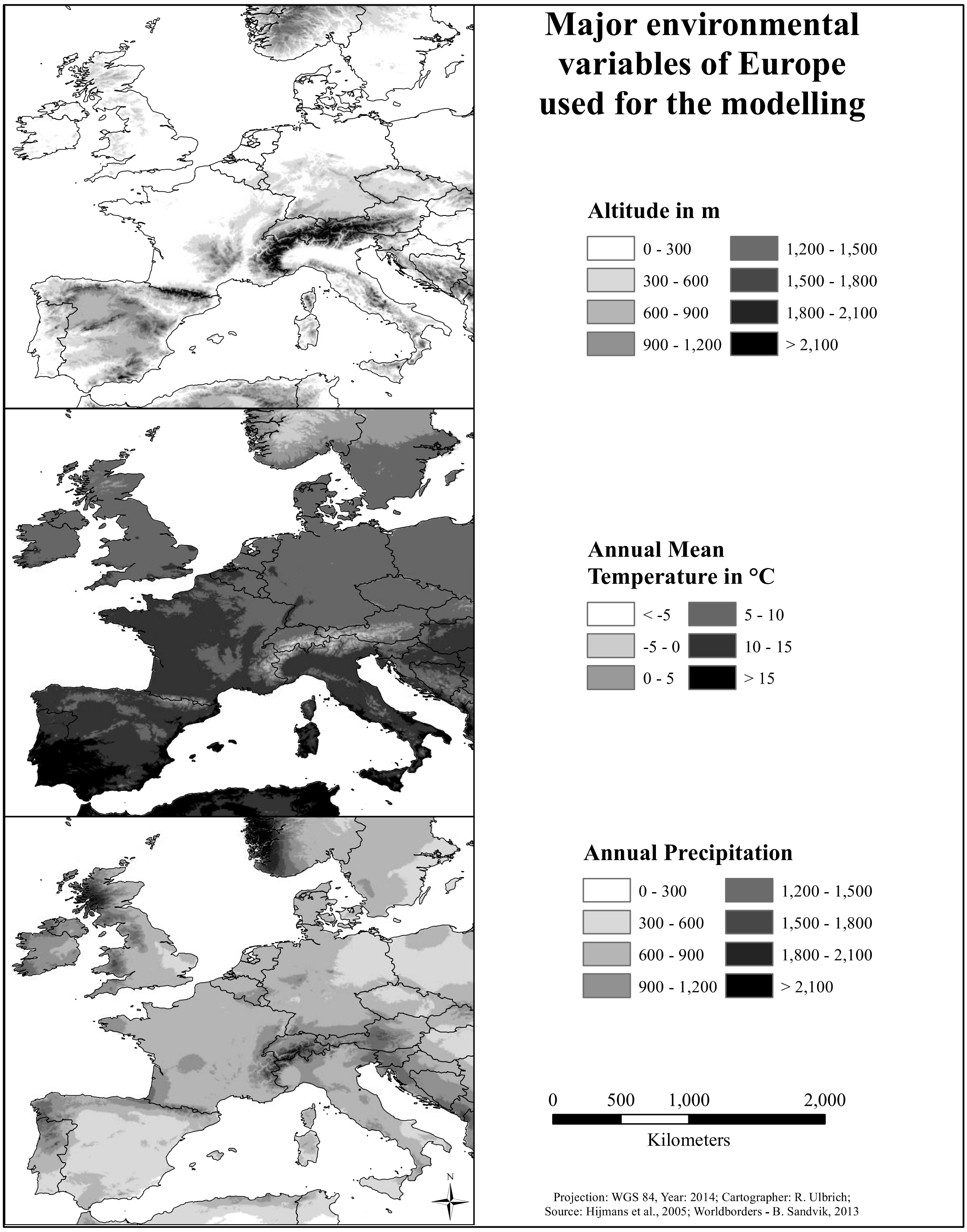


Figure 3.2 Altitude, Annual Mean Temperature and Annual Precipitation of Europe used during the modelling. Darker colours represent higher values.

A variety of soils have formed in Europe. The most common soil type in the study region are the Cambisols, which are younger soils and can be found under different vegetation. They are known to have high productivity due to their highly weathered mineral content, especially in loess areas like Austria, central to south Germany, south west France, large parts of Italy, and Switzerland. Under the moist and cool temperate forest areas in north East Germany, north, central and south west France and Switzerland are Albeluvisol soils, which are acidic and accumulate clay in subsoil. Eastern Europe like Poland and the Czech Republic have sandy Arenosols which accumulate organic material in the top horizon and have a low weathering rate, but frequent erosions (FAO/IIASA/ISRIC/ ISSCAS/JRC, 2012).

In the dry areas of Spain are Calcisols, which accumulate secondary calcium carbonate, and Regosols, which are weakly developed mineral soils (also in the mountain ranges of Portugal). More organic rich, darker soils like Umbrisols are located in north western Spain and northern Portugal. In well-drained areas like Denmark, northern Germany, Scotland and southern Sweden are Podzols or Luvisols, which have a high clay accumulation and base saturation (France, Germany, parts of Great Britain, northern Italy, Netherlands, Poland, Portugal) (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012).

3.1.2.2 Namibia

The host region “Namibia” included in this study Namibia and parts of Angola, Botswana, South Africa, Zambia and Zimbabwe (Figure 3.4). The extent of the host region “Namibia” is listed in Table 3.1.

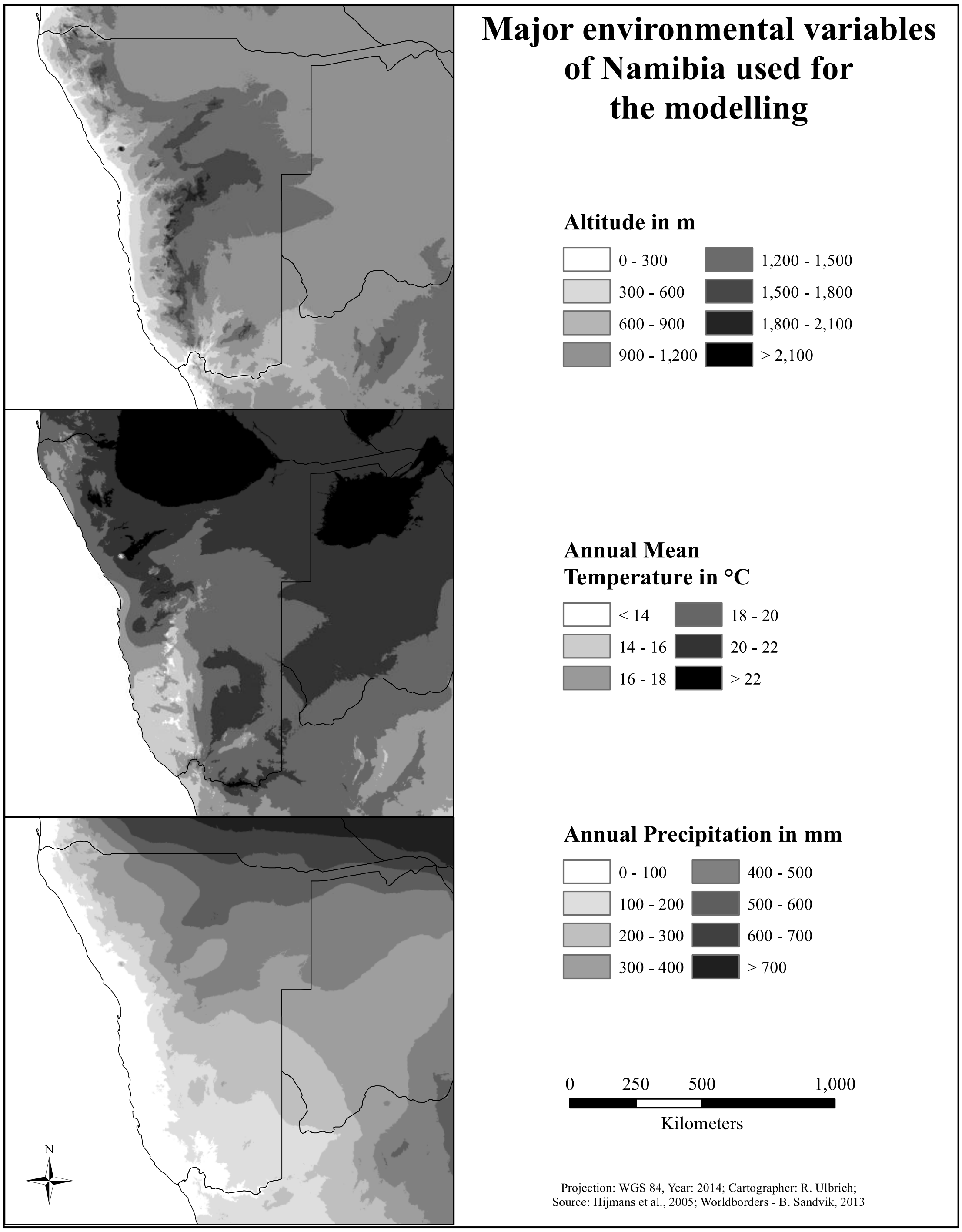
Namibia is situated in the arid and tropical climate zone. The rainfall increases from less than 50 mm per year along the coast and the southern boundary up to 600 mm in the north eastern part, the Zambezi region (Hijmans et al., 2005; Mannheimer & Curtis, 2005). The lowest average temperatures per year of 14 to 16 °C are found in the Sperrgebiet (south western Namibia) while the central and south eastern part of Namibia have an average temperature of 18 to 20 °C and the northern part towards the Angolan border has the highest average temperature of 22 °C per year (Hijmans et al., 2005).

The average altitude of northern and south eastern Namibia is around 1,000 m high with highlands up to 2,000 m in central Namibia; the coast strip reaches from 0 to 500 m (Hijmans et al., 2005).

The coastal areas of Namibia belong to the Namib Desert and have only few, highly adapted species such as succulents or grasses (Mendelsohn, Jarvis, Roberts, & Robertson, 2002). The southern part is mainly shrubland and savanna and northern regions acacia tree and shrub savanna. The northern-most regions of the southern Angolan boarder are dominated by broadleaved woodlands (Mendelsohn et al., 2002).

Ephemeral rivers transvere Namibia beginning in the eastern part of Namibia dring high rainfalls and flowing to the Atlantic for a few, if any, days a year or not at all in some years (Mannheimer & Curtis, 2005; Joubert, 2008). The floodwaters carry huge amounts of silt and organic matter, during most of the year, the “dry river” supports native vegetation in the riverbed and aids in the establishment of riparian “green belts” (Joubert, 2008).

Namibia has a diversity of rock and soil types. Arenosols with a small amount of organic matter are located in the Namib Sand Sea (south coast) and eastern parts of the country. Leptosols range from the north coast to central and southern Namibia; these soils are unsuitable for crops but allow the grazing of cattle (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). The fertile regions in northern Namibia consist mainly of Cambisols, which have a good nutrient- and water-holding capacity (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012).



Projection: WGS 84, Year: 2014; Cartographer: R. Ulbrich;
Source: Hijmans et al., 2005; Worldborders - B. Sandvik, 2013

Figure 3.3 Altitude, Annual Mean Temperature and Annual Precipitation of Namibia used during the modelling. Darker colours represent higher values.

Table 3.1 The extent of each region used in the modelling. Values of longitudes and latitudes are in decimal degrees.

Region	North	South	West	East	Approximate area in km^2
Europe	62°	35°	-11°	20°	12,500,000
Namibia	-16°	-30°	11°	18°	1,800,000
Northern America	51°	6°	-127°	-65°	3,100,000

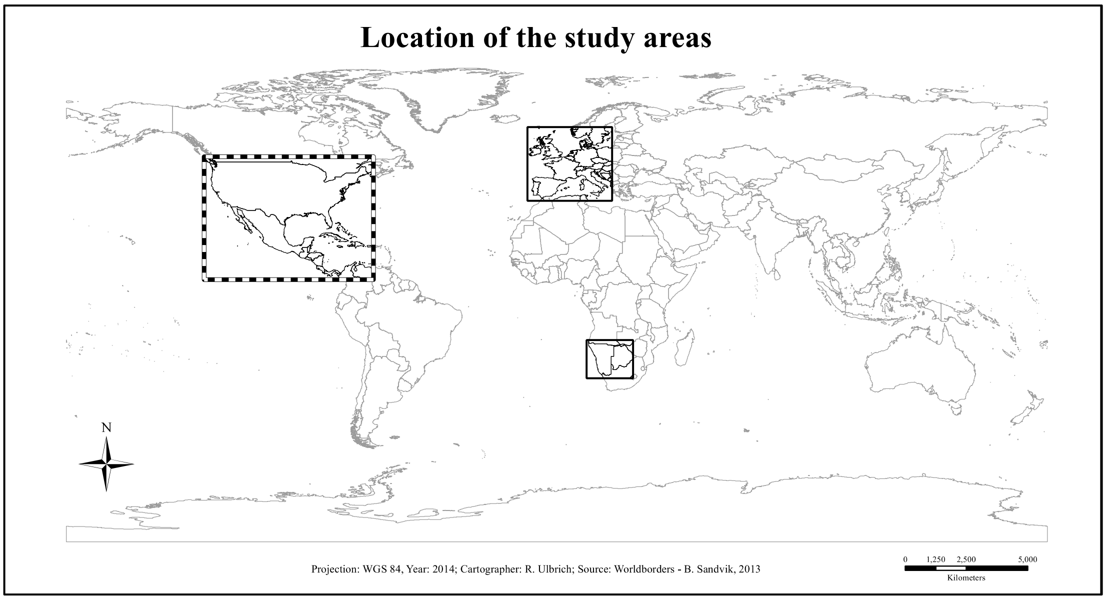


Figure 3.4 The location of the donor region (dashed line) and host regions (solid line).

3.2 Species Occurrence Points

Most of the occurrence points were obtained from the Global Biodiversity Information Facility database (www.gbif.org). Furthermore, data from the National Herbarium of Namibia (WIND), the Tree Atlas of Namibia (Curtis & Mannheimer, 2009), the database FLORKART, the Federal Environmental Ministry of Germany and the network of phytodiversity of Germany (Datenbank FLORKART, BfN, NetPhyD, 2013) were used.

Due to the few records of *Leucaena leucocephala* in the National Herbarium of Namibia, road counts were also used to supplement these data. During several trips in Namibia the number of specimens along the road were recorded per kilometre and the road was tracked with a GPS (Garmin GPSmap 60CSx).

The initial raw data of all occurrence points were checked for duplications, missing longitude/latitude data with R 3.1.0 (R Core Team, 2014) (see appendix A2) and geographic accuracy. Only points with accuracy better than 10 km were taken.

The remaining points were rarefied to reduce over fitting during the modelling process due to sample bias (Veloz 2009; Hijimans, 2012; Boria, Olson, Goodman, & Anderson, 2014). Therefore, the function "spatially rarefy occurrence data" in the SDM toolbox v1.0b (Brown, 2014) was used inside ArcGIS Map 10.2.2 (ESRI, 2014) with different distances between the initial points. The final distances are listed in Table 3.2. The function reduced the occurrence points according to number and distance in a certain area.

Table 3.2 The distances used to reduce the occurrence data of all four species in donor and host region.

Species	Northern America	Europe	Namibia
Leucaena leucocephala	40 km	-	3 km
Prosopis spp	20 km	-	30 km
Prunus serotina	50 km	25 km	-
Robinia pseudoacacia	30 km	30 km	-

Preliminary test runs showed that different distances were needed to reduce sample bias, gain the maximum number of occurrence points and have an equalized dispersal of occurrence points. For instances, the occurrence points for

Leucaena leucocephala in Namibia were originally in distances of less than 1 km which led to highly over fitting around those points. Different distances were need because the amount and the distribution of occurrence points between the species differed drastically. A unique approach would lead to over fitting of Maxent results and predict a distribution narrow to the dense occurrence points.

Furthermore, a distance of more than 920 m (environmental data was obtained in a resolution of 30 arc seconds which equals 920 m at the equator) was needed otherwise occurrence points in the same grid cell would be erase in the default setting of Maxent to avoid duplications.

The occurrence data of each species were saved in a comma-separated-value format and in the order: species, longitude, latitude (compare Phillips, 2011). The coordinate values were in degrees, the coordination system WGS 84.

3.3 Environmental Data

The environmental variables used in this study were obtained in the highest free available resolution and used in different previous and related studies (Hijmans et al., 2005; Pearson, 2007; Parolo, Rossi, & Ferrarini, 2008; De Cauwer et al., 2014). The quality of the climate variables differed because of the various amount of weather stations in each area (Hijmans et al., 2005). While a high amount of weather stations were located in North America, Europe and Namibia had fewer stations with larger distances between the locations (Hijmans et al., 2005).

In cases where the precipitation seasonality coefficient of variation values exceeded 100 % O`Donnell and Ignizio (2012) determined that the variance of precipitation throughout the year exceeded the average precipitation. Explanations for this may be that there were precipitation anomalies or errors from the original climate data (O`Donnell & Ignizio, 2012).

The environmental background data were obtained from the WorldClim website v1.4 (www.worldclim.org; Hijmans et al., 2005) and the Harmonized World Soil Database (HWSD) v1.21 (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). A total of 19 bioclim variables and the altitude data from WorldClim as well as twelve soil variables were included for the modelling. The climate data covered the "current" situation, which meant the time period 1950 to 2000.

The HWSD offers a raster file, a soil attribute database and a soil attribute database metadata. From the second one the "HWSD_SMU" and the "HWSD_DATA" tables were extracted for the further process. At first, the raster file needed to be exported as ".grd" raster file from the "HWSD_SMU" table the "MU_GLOBAL" column was exported and saved as ".dbf" file.

Afterwards, the raster file was joined with the new "HWSD_SMU.dbf" table. Therefore, the "Value" field of the raster (which represents a unique number for each grid cell) and the "MU_GLOBAL" column were used as unique identifier. The new raster was exported again to save the new attributes. For each region the fixed extent (see Table 3.1) was extracted.

From the initial attribute table ("HWSD_DATA") the twelve target attributes plus the "MU_GLOBAL" column were extracted for each region. In most cases HWSD linked more than one soil unit to a map unit. Therefore, the method by De Cauwer, Muys, Revermann, and Trabucco (2014) was used and the map unit was associated with the dominant soil unit only. Finally, each soil characteristic had to be in a single raster file. This was done with the "Lookup" function.

All 32 variables had a resolution of 30 arc seconds, which are around 920 m at the equator. The raster datasets had to be in "ASCII" format and with the same cell size to make them accessible for Maxent. The same cell size was ensured with the function "Resample". Afterwards, from the remaining environmental variables the extent of the three regions (see Table 3.1) was clipped with ArcMap 10.2.2.

Table 3.3 List of all environmental variables and processed data included in the test runs with acronym and meaning.

Acronym	Meaning
alt	Altitude
bio_1	Annual Mean Temperature
bio_2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
bio_3	Isothermally (BIO2/BIO7)(*100)
bio_4	Temperature Seasonality (standard deviation)
bio_5	Max Temperature of Warmest Month
bio_6	Min Temperature of Coldest Month
bio_7	Temperature Annual Range (BIO5 – BIO6)
bio_8	Mean Temperature of Wettest Quarter
bio_9	Mean Temperature of Driest Quarter
bio_10	Mean Temperature of Warmest Quarter
bio_11	Mean Temperature of Coldest Quarter
bio_12	Annual Precipitation
bio_13	Precipitation of Wettest Month
bio_14	Precipitation of Driest Month
bio_15	Precipitation Seasonality (Coefficient of Variation)

Acronym	Meaning
bio_16	Precipitation of Wettest Quarter
bio_17	Precipitation of Driest Quarter
bio_18	Precipitation of Warmest Quarter
bio_19	Precipitation of Coldest Quarter
awc	Available Water Storage Capacity
bs	Base Saturation
caco3	Calcium Carbonate Content of Topsoil
cec	Cation Exchange Capacity
clay	Clay Fraction of Topsoil
drain	Type of Drainage
gravel	Gravel Fraction of Topsoil
HWSD	Harmonized World Soil Database
HWSD_DATA	Table containing all Soil Mapping Unit attributes of the Harmonized World Soil Database
HWSD_SMU	Harmonized World Soil Database Soil Mapping Unit
MU_GLOBAL	Global Mapping Unit established by the Harmonized World Soil Database
oc	Organic Carbon of Topsoil
pH	pH of Topsoil
refdep	Reference Soil Depth
sand	Sand Fraction of Topsoil
silt	Silt Fraction of Topsoil

The total number of environmental variables was reduced to the ten most important environmental variables of each species with the help of several test runs. This was done to reduce the amount of correlated variables, which can lead to over fitting

(Baldwin, 2009; Elith et al., 2011; Phillips, 2011). The decision was made according to the jack-knife tests and permutation importance calculated by Maxent for model with all environmental variables. The jack-knife test measured the training gain obtained with and without any environmental variable and resulted in an indication of the importance. The permutation importance defines how each variable contributes to the model (Phillips, 2011).

All menu sequences for the named processing steps can be found in appendix A3.

3.4 Species Distribution Modelling with Maxent

3.4.1 Concept of Maxent

Maxent is a machine learning software for modelling species distributions from presence-only data (Elith, Phillips, Hastie, Dudík, En Chee, & Yates, 2011). The term “Maxent” (sometimes named “MaxEnt” but during this study the term “Maxent” will be used) stands for “Maximum entropy”.

Maximum entropy modelling means the estimation of the most uniform distribution of occurrence points compared to background points according to the environmental values of the occurrence points (Phillips & Dudík, 2008; Baldwin, 2009; Elith et al., 2011). The deterministic algorithm gives the maximum entropy probability distribution, which predicts if the model fits the location data better than would a uniform distribution. Therefore, Maxent minimizes the relative entropy between the probability density from the occurrence point data and the background samples in a defined covariate area (Elith et al., 2011). Due to the missing absence data, Maxent randomly chooses 10,000 background samples from the study area, a collection of points associated with the environmental variables (Elith et al., 2011).

Preliminary test runs showed that for all *Prunus serotina* models and the *Robinia pseudoacacia* models in Europe a bias field or mask data as background sample area was needed. Maxent calculates the distribution of maximum entropy relative to the background points of the study area which means that the selection of background points or the area from which it chooses the points has a significant impact (Elith et al., 2011). In case of biased occurrence points Maxent can lead to false predictions. A strategy by Phillips and Dudík (2008) is to replace the uniform background data by a random sample of background points out of the occurrence point distribution. The result is that background data and occurrence points become biased in the same way as the used occurrence points

With the function “Sample by Buffered Local Adaptive Convex-Hull” those bias files were calculated in SDM toolbox v1.0b. Due to the different distributed occurrence points as well as the amounts for each species test runs showed that different buffer distances were needed. A buffer distance of 100 km in Northern America and 50 km in Europe showed the best results for *Prunus serotina*, for *Robinia pseudoacacia* a buffer distance of 75 km was used.

Test runs for *Leucaena leucocephala* and *Prosopis* spp with bias files showed that biased sample of background points will not improve the results.

3.4.2 Maxent Settings

Most of the default parameters from Maxent 3.3.3k (Phillips, Anderson, & Schapire, 2006) were used, though the “Maximum iterations” were increased to 5,000 to ensure that the algorithm has adequate time for convergence, which reduced the possibility of over- or under-prediction (Young et al., 2011).

For each model, ten replications with the default “Crossvalidate” were completed. In each replication, Maxent divided the sample data into replicated folds and each fold in a turn is used as the test data (Phillips, Anderson, & Schapire, 2006).

During each model, jackknife tests were done to measure the importance of each environmental variable used during the model run. Jackknife tests were also done to select the ten most important environmental variables, which contributed the most per model.

During each run response curves were created and a jack-knife test was performed by Maxent to measure the variable importance.

3.4.3 Maxent Models

This study will use a similar approach to the study of Nuñez and Medley (2011), which was conduct on different distribution ranges of *Pine* spp across the world. Nuñez and Medley (2011) used occurrence points and environmental conditions of the donor area North America and different climate as well as environmental settings. But this study will tested novel methods of species distribution modelling. New models were created out of the existing occurrence record data and the environmental conditions most favoured by the plants’ in the donor and host regions.

During this study three different models were calculated:

The model “Donor” projected the ten most important environmental variables (according to the jackknife test in Maxent) and the species occurrence points from Northern America to the host region (Namibia or Europe).

The model “Host 1” used the same ten most important environmental variables of Northern America but with the data and occurrence points from the host region.

The third model, "Host 2", was calculated with the ten most important variables and the occurrence points of the host region. In the proceeding results and discussion sections the models will be named according to the species (*Leucaena leucocephala* – LL; *Prosopis* spp – PSPP; *Prunus serotina* – PS; *Robinia pseudoacacia* – RP). For example, the donor model for *Leucaena leucocephala* would be referred to as "Donor LL".

A 10 percentile training presence threshold was applied for all model outputs to represent the limits of species distribution (De Cauwer et al., 2014) in order to account for the lowest 10 % model probability that was previously shown to fall outside the suitable region of the species (Holcombe, Stohlgren, & Jarnevich, 2010; Radosavljevic & Anderson, 2014).

3.4.4 Model Evaluation

The model evaluation was done with the Area under the receiver operating characteristic curve (AUC). AUC is the predictive accuracy, which measures the probability of a random presence site being ranked above a random absence site.

The AUC values range from random selection (0.5) to models with a perfect predictive ability (1.0), meaning the model can distinguish perfectly between locations where the species is absent or present (Pearson, 2007). For example, if the probability to select a record at random from the set of presences is 0.7, it means the predicted value (AUC = 0.7) is greater than a record selected at random from the set of absences (0.5).

Fielding and Bell (1997), Phillips, Anderson and Schapire (2006), and Pearson (2007) support that the main advantage of AUC is that it evaluates all threshold scenarios and, thus, allow the provision of a single measure of model performance independent from a specifically chosen of threshold scenario.

3.4.5 Response Curves

Maxent computed two sets of response curves: 1) the prediction changes of each environmental variable while holding all other variables at their average sample value and 2) univariate models using only the chosen corresponding environmental variable. The first set of response curves had the potential to give misleading information if variables were correlated (Phillips, 2011); therefore, the second set of response curves (univariate models) were used to gain more information about the environmental setting of each species.

The curves show the dependence of predictive suitability both on the selected environmental variable and on dependencies induced by correlation between the selected and other variables (Phillips, 2011).

The three response curves of the most important variable of each model are shown in the result section whereas the remaining response curves are in the appendices (A4 to A7).

4 Results

4.1 General Results

The final occurrence points isolated after cleaning the occurrence data were used for the modelling are listed in Table 4.1.

Table 4.1 Occurrence points of all four species in all three regions in comparison between the initial amount and the final rarefied data points.

Species	**Northern America**		**Europe**		**Namibia**	
	Initial	Final	Initial	Final	Initial	Final
Leucaena leucocephala	507	153	-	-	69	32
Prosopis spp	634	320	-	-	107	57
Prunus serotina	512	153	32,845	520	-	-
Robinia pseudoacacia	333	157	15,372	566	-	-

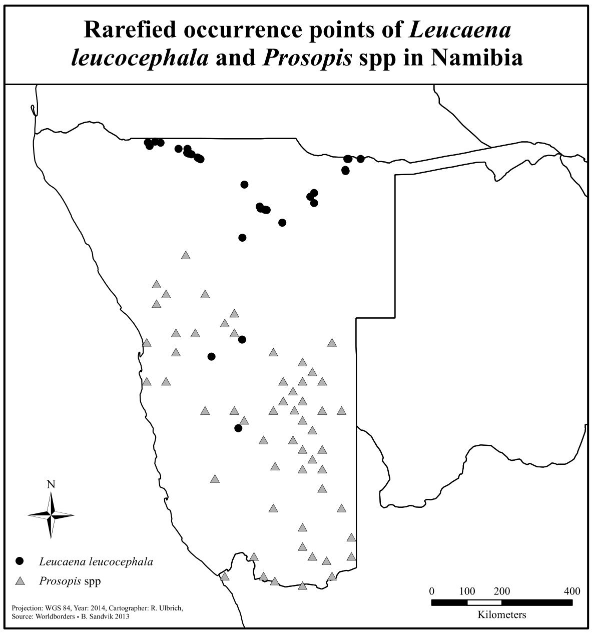


Figure 4.1 Occurrence points of *Leucaena leucocephala* and *Prosopis* spp in Namibia used during the modelling.

The 32 *Leucaena leucocephala* specimens were mainly concentrated in the northern part of Namibia, only three points were found in the central parts (Figure 4.1).

The 57 *Prosopis* spp records were mainly in the central and south eastern part of Namibia.

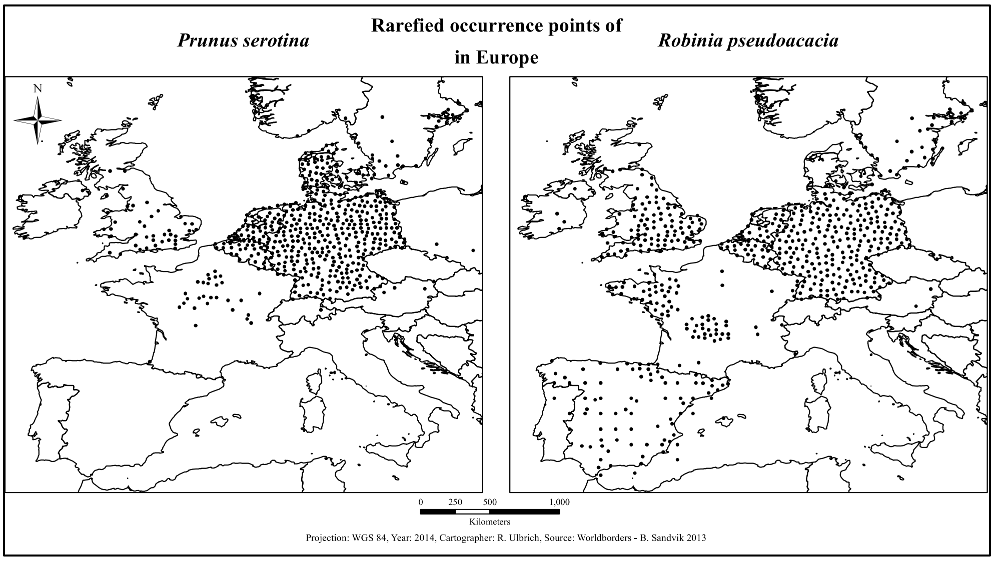


Figure 4.2 Occurrence points of *Prunus serotina* and *Robinia pseudoacacia* in Europe used during the modelling.

Most of the 520 *Prunus serotina* and 566 *Robinia pseudoacacia* records were found in Belgium, Denmark, Germany, and the Netherlands (Figure 4.2). In southern Great Britain, France, and Spain several occurrence points of *Robinia pseudoacacia* were located as well. The rarefied occurrence points for all four species in Northern America can be found under each species section in chapter 2.2 Study Species.

All 12 models had an Area under the curve (AUC) value higher than random (0.5) (Table 4.2). While the values for *Leucaena leucocephala* and *Prosopis* spp indicated good distinctions the values for *Prunus serotina* and *Robinia pseudoacacia* were closer to random pseudo-absence site. The model “Donor RP” showed an exception with an AUC value of 0.891, which implies a fairly good prediction of the model.

Table 4.2 AUC values for all four species and environmental settings.

Species	Acronym	Donor	Host 1	Host 2
Leucaena leucocephala	LL	0.942	0.94	0.944
Prosopis spp	PSPP	0.92	0.882	0.883
Prunus serotina	PS	0.681	0.629	0.632
Robinia pseudoacacia	RP	0.891	0.629	0.644

4.2 *Leucaena leucocephala*

The three most important environmental variables for *Leucaena leucocephala* in model “Donor LL” were mean temperature of coldest quarter (23.3 %), precipitation of wettest month (12.5 %) and mean temperature of driest quarter (11.3 %) (Figure 4.3 and Table 4.3). The second model, “Host 1 LL”, calculated annual mean temperature (22.1 %), precipitation of warmest quarter (20.9 %) and altitude (20.1 %) as the most important variables, whereas mean temperature of driest quarter showed no importance for the model at all (0 %).

In the third model, “Host 2 LL”, the variables mean temperature of warmest quarter, annual precipitation and precipitation of driest month replaced minimum temperature of coldest month, mean temperature of driest quarter and precipitation of wettest quarter; and formed the ten most important environmental variables for this model. The most important variable was temperature seasonality with 24.6 %, followed by altitude (19.9 %) and annual precipitation (13.3 %).

Table 4.3 The permutation importance in percentage for the most important environmental variables of *Leucaena leucocephala* for all three models. The most important values are in bold.

Environmental variables	Explanation	Donor LL	Host 1 LL	Host 2 LL
alt	Altitude	5.1	20.1	19.9
bio_1	Annual Mean Temperature	8.9	**22.1**	8.2
bio_4	Temperature Seasonality	11.1	14.2	**24.6**
bio_6	Min. Temp. of Coldest Month	9.2	0.4	-
bio_9	Mean Temp. of Driest Quarter	11.3	0	-
bio_10	Mean Temp. of Warmest Quarter	-	-	3.5
bio_11	Mean Temp. of Coldest Quarter	**23.3**	1.3	1.6
bio_12	Annual Precipitation	-	-	13.3
bio_13	Precipitation of Wettest Month	12.5	10.6	12.1
bio_14	Precipitation of Driest Month	-	-	0
bio_15	Precipitation Seasonality	6	9.5	6.2
bio_16	Precipitation of Wettest Quarter	9.3	0.9	-
bio_18	Precipitation of Warmest Quarter	3.4	20.9	10.7

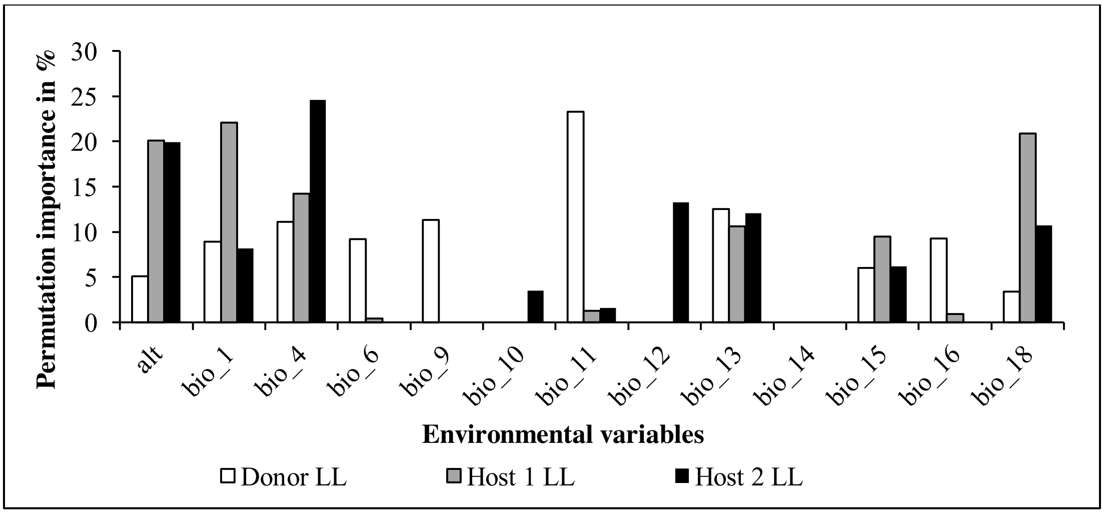


Figure 4.3 Comparison of the permutation importance of environmental variables between the models “Donor LL”, “Host 1 LL” and “Host 2 LL”.

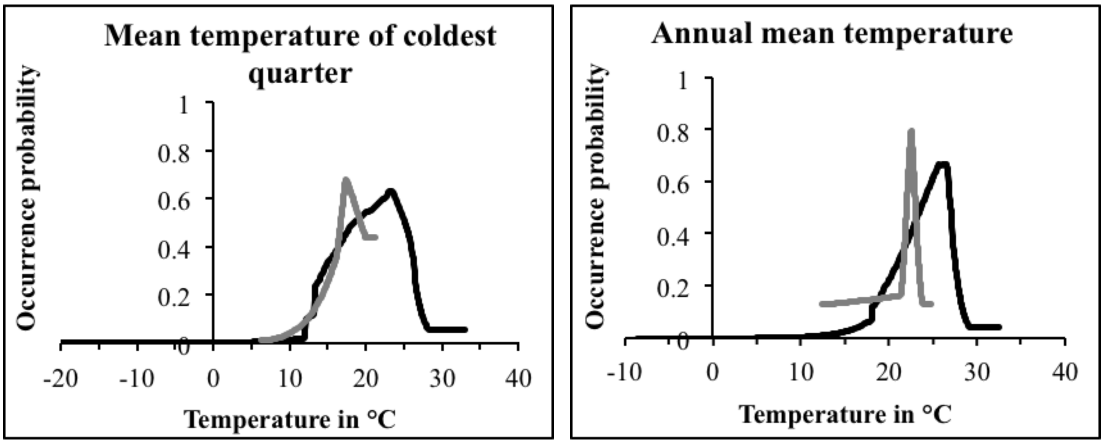


Figure 4.4 Response curves of "mean temperature of coldest quarter" and "annual mean temperature" for model "Donor" (black) and "Host 1" (grey) on the probability of occurrence for *Leucaena leucocephala*.

The response curves for the most important variables in Model "Donor LL" and "Host 1 LL" calculated an almost similar picture (Figure 4.4). While the maximum values were next to each other, the response curves of "Donor LL" spread through a lower temperature range and have a lower occurrence probability.

The curve of "Donor LL" for the annual mean temperature rose earlier (at around 16 °C) and decreased after the lowest point of "Host 1 LL" (25 °C).

Other variables such as altitude proposed a high occurrence probability in very low-altitude areas ("Donor LL") while the response curve of "Host 1 LL" showed the optimum at 1,000 m and above. The minimum temperature for the coldest month for "Donor LL" had a maximum occurrence probability of 0.6 at 14 °C, "Host 1 LL", rather, had its maximum occurrence probability at 7 °C and slightly higher. Similarly, the mean temperature for driest quarter of "Host 1 LL" (17 °C) was below "Donor LL" (24 °C) and covered almost the same temperature range.

The precipitation for the wettest month showed two different curves. "Host 1 LL" reached the maximum occurrence probability of 0.7 at 120 mm while "Donor LL" only reached is highest probability of 0.6 by 180 mm.

Both models showed higher occurrence probability with an increasing precipitation seasonality. The regions' curves exceeded the 100 % and had a maximum occurrence probability of 0.6. The precipitation from the wettest and warmest quarter showed a constant occurrence probability of 0.6 from 500 mm onwards for "Donor LL" while "Host 1 LL" reached the turning point of 0.7 at 320 mm.

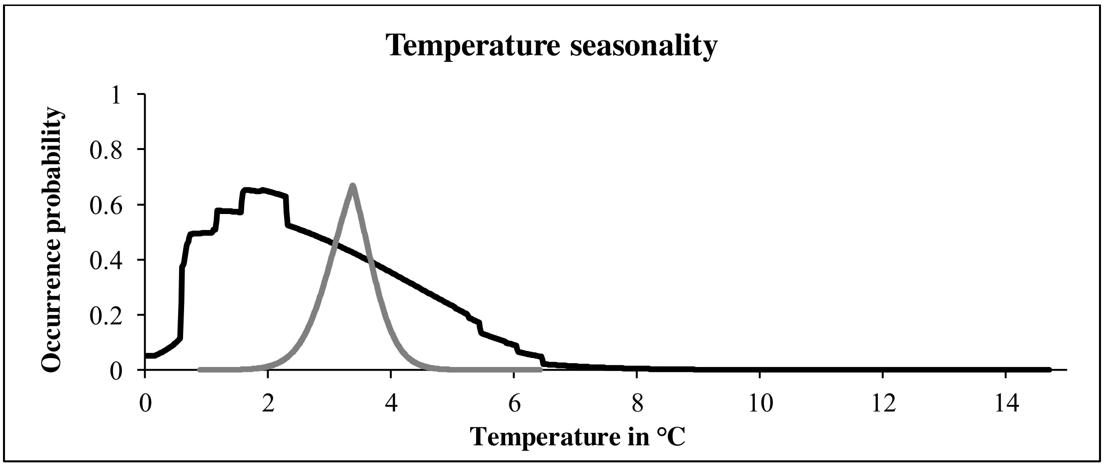


Figure 4.5 Response curve of "temperature seasonality" for model "Donor" (black) and "Host 1" (grey) on the probability of occurrence for *Leucaena leucocephala*.

The temperature seasonality exemplified the yearly temperature variation as based on the standard deviation of the twelve mean monthly temperature values. Temperature seasonality contributed the most to "Host 2 LL" which had the same response curve as model "Host 1 LL". The response curve of "Donor LL" ranged from 0 to14 °C but from 6 °C onwards the occurrence probability was almost 0 %. The highest point was below 2 °C in comparison to almost double for "Host 1 LL", below 4 °C.

The mean temperature from the warmest quarter for "Host 2 LL" ranged from 15 °C to 32 °C with the highest occurrence probability of 0.6 at 25 °C. The annual precipitation of "Host 2 LL" ranged up to 900 mm with the highest probability of 0.7 at 520 mm. The precipitation of the driest month was below 14 mm.

The model “Donor LL” calculated a widespread distribution of *Leucaena leucocephala* for the northern part of Namibia with a probability between 0.34 and 0.5 (Figure 4.6). South of the Angolan border the occurrence probability was between 0.5 and 0.6. Only the region within the western coastal areas had a higher probability over 0.6.

The comparison of both models showed that model “Host 1 LL” calculated a smaller distribution area with a higher occurrence probability (0.6 to 0.8) south of the Angolan border. The model predicted no probability of occurrence for the coastal area and eastern part of Namibia.

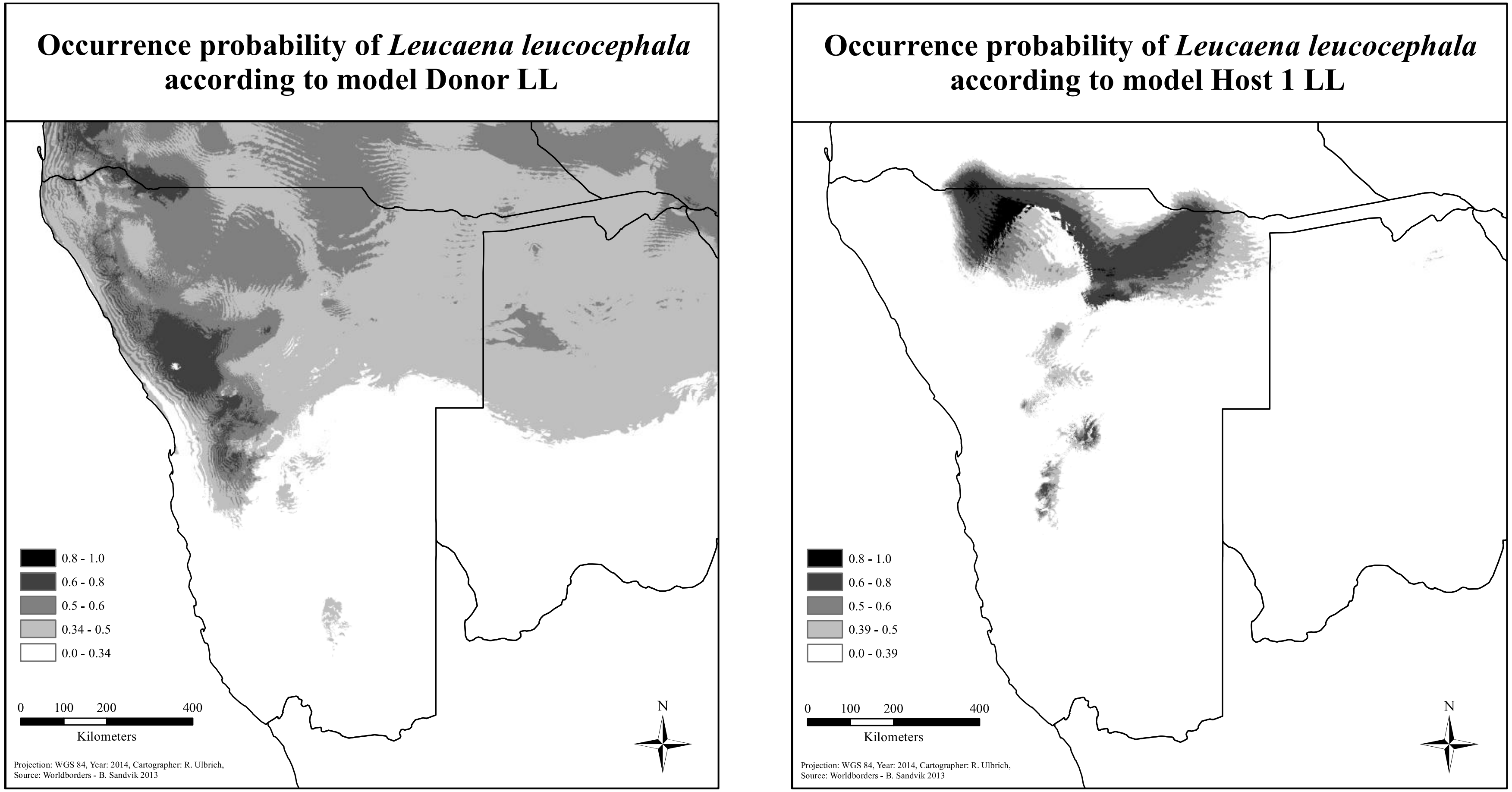


Figure 4.6 Species distribution of *Leucaena leucocephala* according to model “Donor LL” (left) and “Host 1 LL” (right). Darker areas represent higher occurrence probability; lighter areas represent lower probability. Logistic values of threshold: 0.34 (Donor) and 0.39 (Host 1).

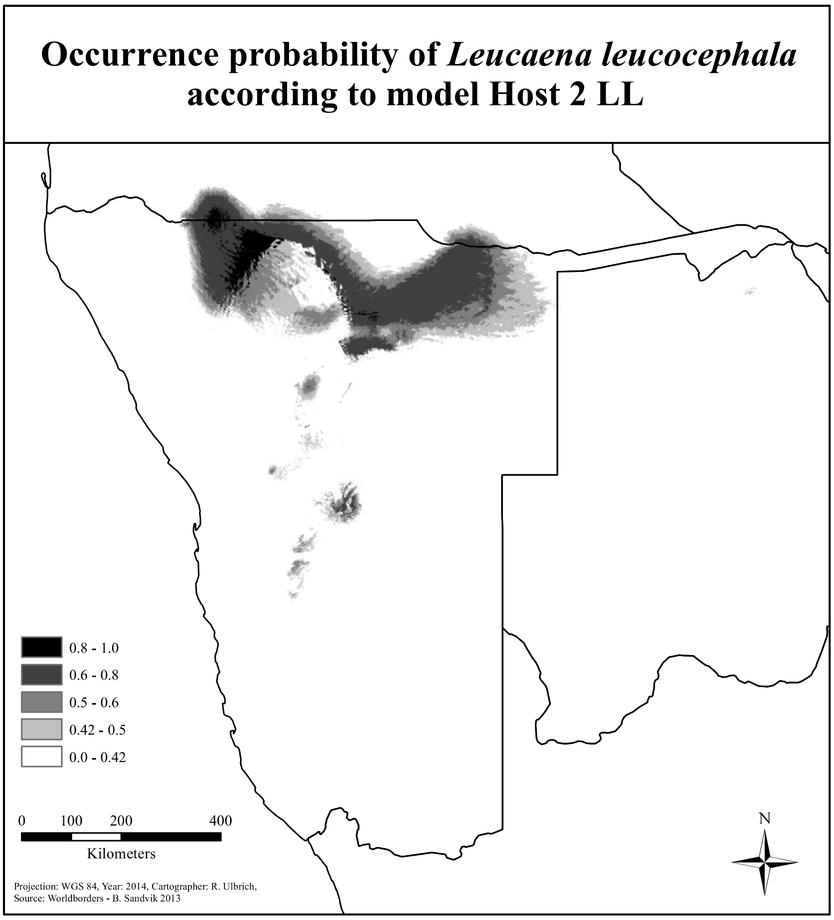


Figure 4.7 Species distribution of *Leucaena leucocephala* according to model “Host 2 LL”. Darker areas represent higher occurrence probability; lighter areas represent lower probability. Logistic value of threshold: 0.42.

The distribution map of model “Host 2 LL” (Figure 4.7) calculated a nearly similar map compared to “Host 1 LL”.

4.3 *Prosopis* spp

The most important environmental variables for *Prosopis* spp in the first model “Donor PSPP” were mean temperature of coldest quarter (29.9 %), annual precipitation (18.9 %) and mean temperature of driest quarter (15.6 %). Annual precipitation represented the most important variable for the model “Host 1 PSPP” with 51.3 % (Table 4.4 and Figure 4.8), followed by minimum temperature of coldest month (13.8 %) and temperature seasonality (9.6 %).

The variables maximum temperature warmest month, minimum temperature of coldest month, mean temperature of wettest quarter, mean temperature of coldest quarter and precipitation seasonality were replaced with altitude, mean diurnal range; precipitation of driest quarter, precipitation of warmest quarter and precipitation of coldest quarter in the third model, “Host 2 PSPP”. The most important environmental variables were annual precipitation with 59.8 %, mean diurnal range with 15.7 % and precipitation of wettest quarter with 8.6 %.

Table 4.4 The permutation importance in percentage for the most important environmental variables of *Prosopis* spp of all three models. The most important values are in bold.

Environmental variables	Explanation	Donor PSPP	Host 1 PSPP	Host 2 PSPP
alt	Altitude	-	-	2.2
bio_2	Mean Diurnal Range	-	-	15.7
bio_4	Temperature Seasonality	2.4	9.6	4.5
bio_5	Max. Temp. of Warmest Month	0.4	8.1	-
bio_6	Min. Temp. of Coldest Month	2.3	13.8	-
bio_8	Mean Temp. of Wettest Quarter	13.1	0	-
bio_9	Mean Temp. of Driest Quarter	15.6	1.1	0.8
bio_11	Mean Temp. of Coldest Quarter	**29.9**	0.8	-
bio_12	Annual Precipitation	18.9	**51.3**	**59.8**
bio_14	Precipitation of Driest Month	6.2	6.4	4.9
bio_15	Precipitation Seasonality	8.7	0.2	-
bio_16	Precipitation of Wettest Quarter	2.4	8.8	8.6
bio_17	Precipitation of Driest Quarter	-	-	1.7
bio_18	Precipitation of Warmest Quarter	-	-	0.9
bio_19	Precipitation of Coldest Quarter	-	-	1

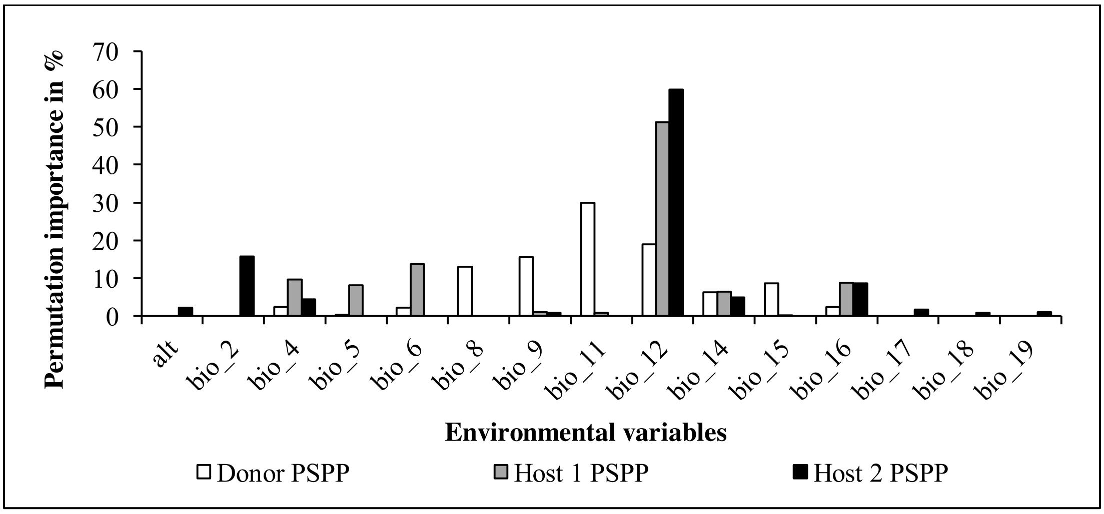


Figure 4.8 Comparison of the permutation importance of environmental variables between the models “Donor PSPP”, “Host 1 PSPP” and “Host 2 PSPP”.

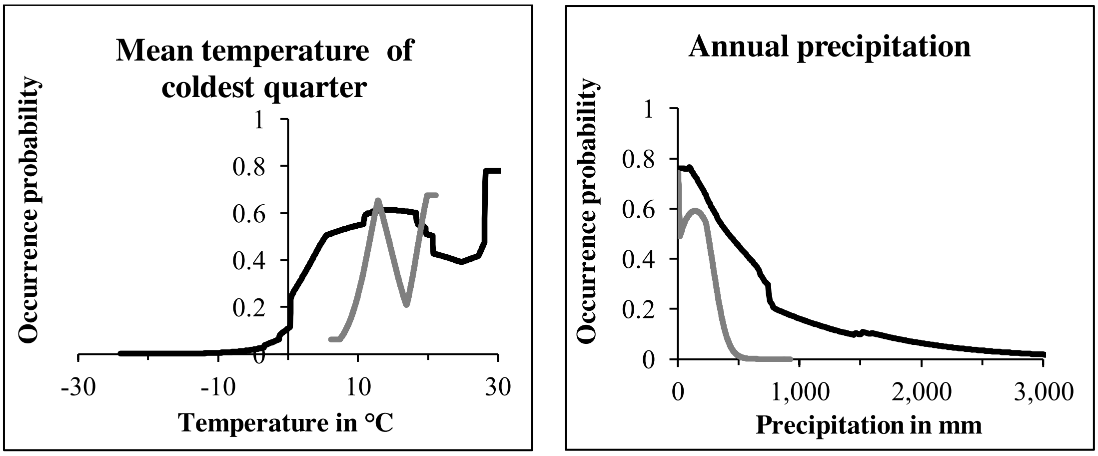


Figure 4.9 Response curves of "mean temperature of coldest quarter" and "annual precipitation" for model "Donor" (black) and "Host 1" (grey) on the probability of occurrence for *Prosopis* spp.

The curve of "Donor PSPP" for mean temperature from the coldest quarter increased rapidly around 0 °C with a maximum around 15 °C of 0.6 (Figure 4.9). The curve of "Host 1 PSPP" started with 5 °C, reached together with "Donor PSPP" the maximum of 0.6 and decrease promptly to 0.2.

The response curve of "Host 1 PSPP" for the annual precipitation displayed "Host 2 PSPP" as well. The curve started with a maximum of 0.6 occurrence probability, which decreased to 0 around 500 mm precipitation. The curve of "Donor PSPP" starts with a maximum of 0.8 as well and decreased to 0.2 at 800 mm precipitation.

The temperature seasonality of "Donor PSPP" ranged mainly between 2 and 8 °C (maximum occurrence probability: 0.6). "Host 1 PSPP" had a maximum occurrence probability of 0.6 at 1 and 6 °C. The maximum temperature for the warmest month was between 18 and 40 °C for "Host 1 PSPP" with an increase from 0.4 to almost 1.0 occurrence probability over 33 °C, the same value where the curve of "Donor PSPP" increased up to 0.8 and a maximum temperature range of 50 °C. The minimum temperature for the coldest month ranged from -10 °C to 20 °C for "Donor PSPP" with a maximum of 0.6 occurrence probability. The curve of “Host 1” was in between the values. Both models had more or less the same maximum occurrence probability (0.8) at a mean temperature of 28 °C for the wettest and driest quarter.

The precipitation for the driest month showed similar curves starting with a maximum occurrence probability of 0.7 at 0 mm precipitation and felt to non-occurrence probability with increasing precipitation. The precipitation seasonality ranged between 0 and 1.5 % while the “Donor PSPP” curve increased with higher values and the “Host 1 PSPP” curve remained stable.

Both curves of the precipitation for the wettest quarter starts with a maximum occurrence probability of 0.8 and decreased to 0.4 (“Donor PSPP”) and 0 (“Host 1 PSPP”) at 220 mm, “Donor PSPP” stayed stable on this value.

The response curve for altitude of “Host 2 PSPP” had a maximum occurrence probability at 100 and 2,100 m of 0.7 with a minimum in between of 0.4 at 1,000 m. The mean diurnal range had a peak of 0.8 occurrence probability at 18 °C. The precipitation for the driest quarter of “Host 2 PSPP” had a maximum occurrence probability of 0.6 at 2 mm and decreased to 0 at around 20 mm. The precipitation for the warmest quarter ranged up to 250 mm with the highest occurrence probability of 0.6 at 150 mm. The precipitation for the coldest quarter started with a maximum occurrence probability (0.6) and went down to 0 at around 60 mm.

The possible distribution map for *Prosopis* spp produced a low probability for most of the study region (between 0.33 and 0.5) (Figure 4.10) according to model “Donor PSPP”. The northwest part showed an increase up to 0.8. A higher probability was visible around the Orange River on the southern border to South Africa.

Model “Host 1 PSPP” calculated a high probability for the southern part of Namibia (up to 0.7) and the central coast area (up to 0.8). The north eastern part of Namibia had no occurrence probability according to model “Host 1 PSPP”. The south western part calculated a similar map to the model “Donor PSPP”.

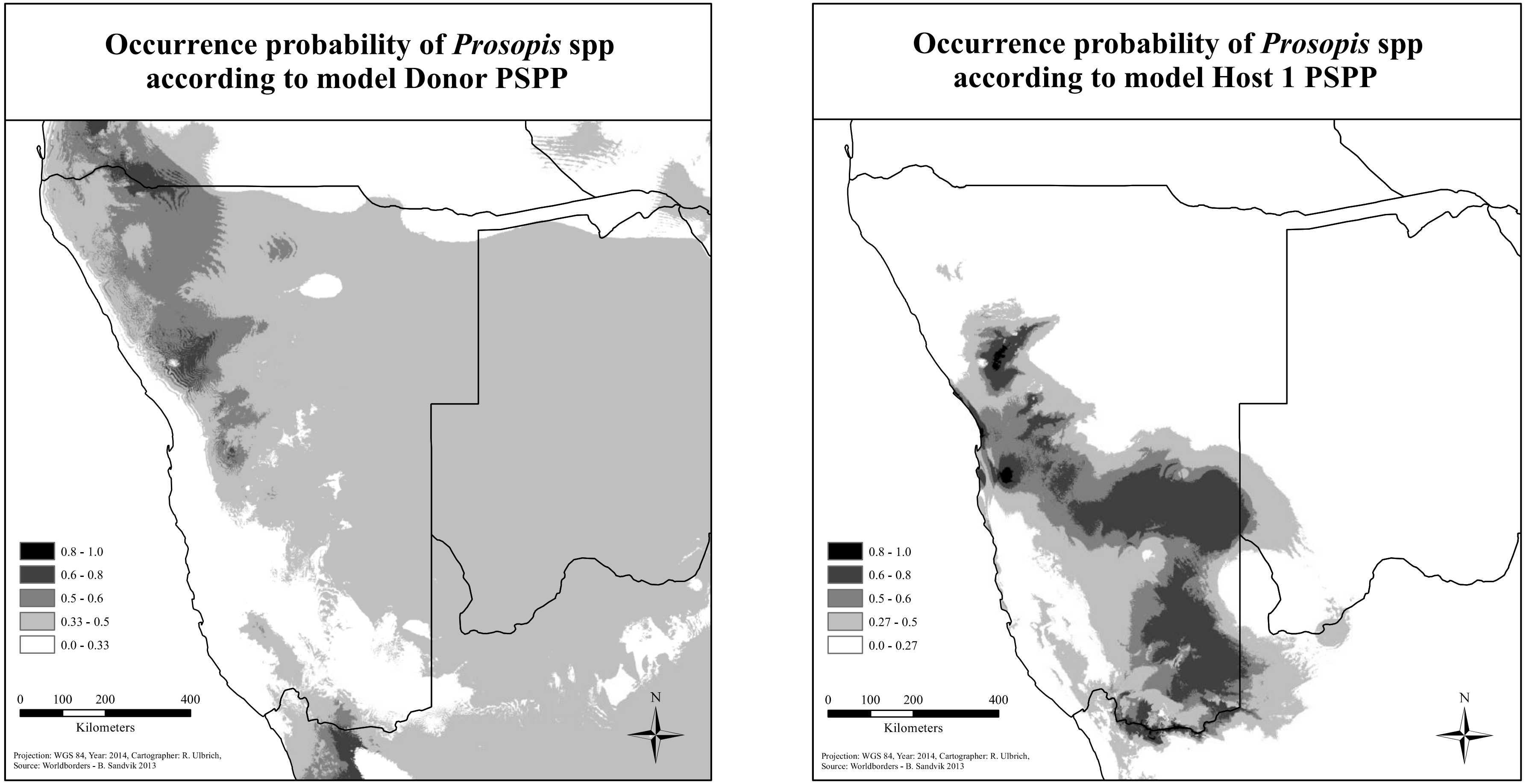


Figure 4.10 Species distribution of *Prosopis* spp according to model “Donor PSPP” (left) and “Host 1 PSPP” (right). Darker areas represent higher occurrence probability; lighter areas represent lower probability. Logistic values of threshold: 0.33 (Donor) and 0.27 (Host 1).

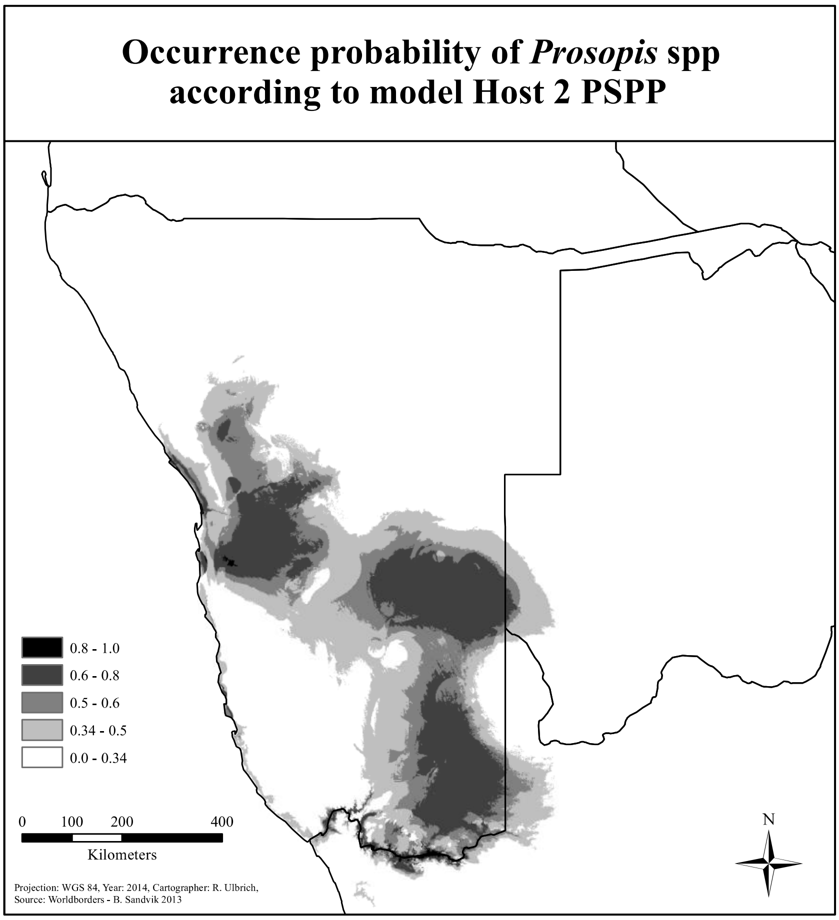


Figure 4.11 Species distribution of *Prosopis* spp according to model "Host 2 PSPP". Darker areas represent higher occurrence probability; lighter areas represent lower probability. Logistic value of threshold: 0.34.

The model "Host 2 PSPP" (Figure 4.11) showed a similar picture to model "Host 1 PSPP". The occurrence probability for the north western part was not as high as in "Host 1 PSPP" (0.5 to 0.6). It estimated no occurrence probability for the Sperrgebiet and parts of the central south of Namibia.

4.4 *Prunus serotina*

Altitude was the most important environmental variable for the model "Donor PS" (23 %) (Table 4.5 and Figure 4.12). The second and third most important variables were minimum temperature of coldest month and mean temperature of driest quarter (18.7 % and 16.3 %).

The model "Host 2 PS" replaced the variables available water storage capacity, minimum temperature of coldest month, mean temperature of driest quarter, precipitation of driest month and base saturation with annual mean temperature, mean temperature of wettest quarter, precipitation seasonality, calcium carbonate content of topsoil and clay fraction of topsoil. The most important variables for this model were annual mean temperature (34.1 %), temperature seasonality (19.2 %) and altitude (12.6 %).

Table 4.5 The permutation importance in percentage for the most important environmental variables of *Prunus serotina* of all three models. The most important values are in bold.

Environmental variables	Explanation	Donor PS	Host 1 PS	Host 2 PS
alt	Altitude	**23**	16.5	12.6
awc	Available Water Storage Capacity	2.8	5.8	-
bio_1	Annual Mean Temperature	-	-	**34.1**
bio_4	Temperature Seasonality	9.1	18.7	19.2
bio_6	Min. Temp. of Coldest Month	18.7	**23.1**	-
bio_8	Mean Temp. of Wettest Quarter	-	-	3.7
bio_9	Mean Temp. of Driest Quarter	16.3	13.8	-
bio_13	Precipitation of Wettest Month	10.8	2.7	0.5
bio_14	Precipitation of Driest Month	5.1	1.2	-
bio_15	Precipitation Seasonality	-	-	8.3

Environmental variables	Explanation	Donor PS	Host 1 PS	Host 2 PS
bio_17	Precipitation of Driest Quarter	1.9	5.4	4.7
bs	Base Saturation	8.6	4.9	-
caco3	Calcium Carbonate Content of Topsoil	-	-	3.3
clay	Clay Fraction of Topsoil	-	-	10.9
gravel	Gravel Fraction of Topsoil	3.7	7.8	2.7

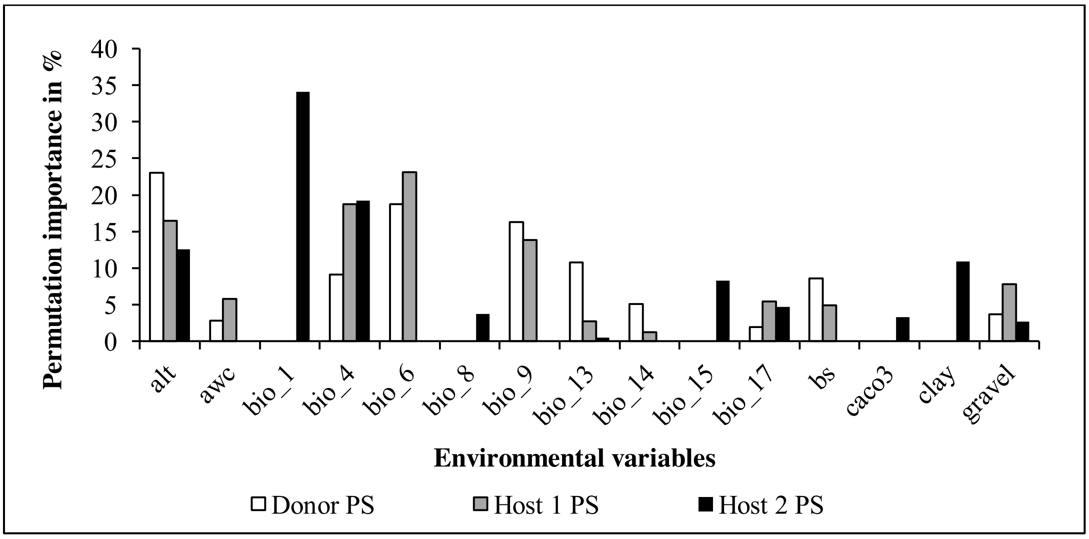


Figure 4.12 Comparison of the permutation importance of environmental variables between the models "Donor PS", "Host 1 PS" and "Host 2 PS".

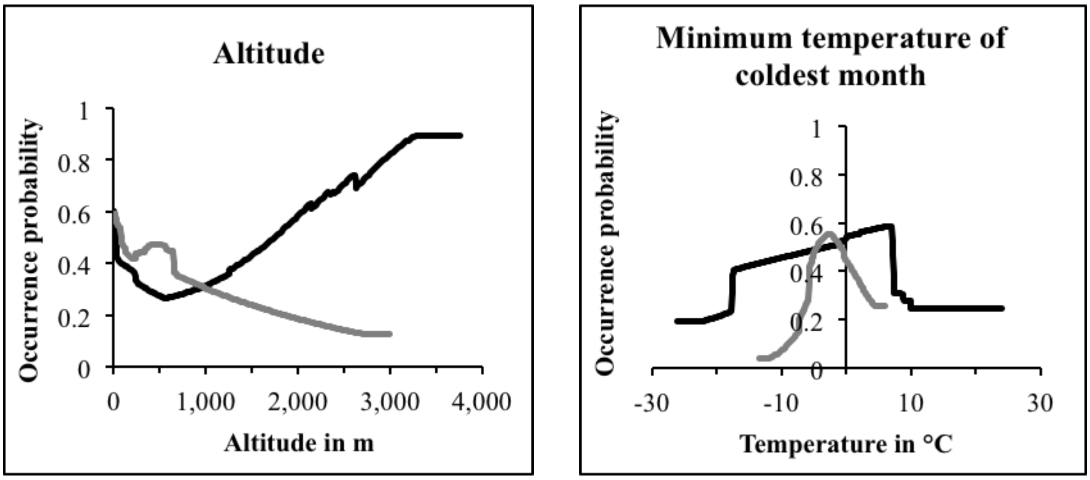


Figure 4.13 Response curves of "altitude" and "min temperature of coldest month" for model "Donor" (black) and "Host 1" (grey) on the probability of occurrence for *Prunus serotina*.

The response curves for altitude showed an almost contrary picture (Figure 4.13): While the curve of model "Donor PS" decreased from 0.4 to 0.2 (500 m) and increased again up to 1.0 occurrence probability (over 3,000 m), model "Host 1 PS" declined from 0.6 (0 m) to 0.2 at 3,000 m.

The minimum temperature for coldest month curve of "Donor PS" increased steadily from an occurrence probability of 0.4 (-20 °C) to 0.6 (8 °C) and remained at 0.2 again. The curve for "Host 1 PS" was smaller but reached the maximum of almost 0.6 earlier (-5 °C) and declined to 0.3 at 5 °C.

The available water storage capacity was similar between "Donor PS" and "Host 1 PS" with an occurrence probability of 0.5 from 0 to 6 mm/m soil unit ("Donor PS") and up to 8 mm/m soil unit for "Host 1 PS".

The temperature seasonality ranged up to 12 °C ("Donor PS") with a value between 0.4 to 0.6 occurrence probability while the curve of "Host 1 PS" was between 4 to 8 °C and reached a maximum of 0.6 occurrence probability and went down with higher temperature.

Both models had a comparable response curve for mean temperature of driest quarter whereby "Donor PS" covered a larger temperature extent (-15 to 35 °C) in comparison to "Host 1 PS" (-12 to 22 °C). "Donor PS" reached a maximum occurrence probability of 0.6 at 12 °C, "Host 1 PS" the same at 2 °C.

The highest occurrence probability for the precipitation of wettest month for "Donor PS" was between 70 and 320 mm (0.5). "Host 1 PS" reached the same value between 60 and 130 mm.

The precipitation for the driest month calculated the highest probability with 0.6 occurrence probability up to 50 mm for both models, afterwards "Host 1 PS" went down to 0.1. The curves for precipitation of driest quarter were close to each other. "Donor PS" started with a peak of 0.6 at 50 mm and decreased to 0.4 at 550 mm. "Host 1 PS" went down to 0.2 at 450 mm.

The base saturation of the topsoil showed a similar picture for both response curves, which were stable at around 0.5 occurrence probability from 0 to 100 %. The gravel fraction of the topsoil presented a stable value for "Donor PS" (0.5) up to 55 %. "Host 1 PS" decreased from 0.6 to 0.4 occurrence probability at 25 %.

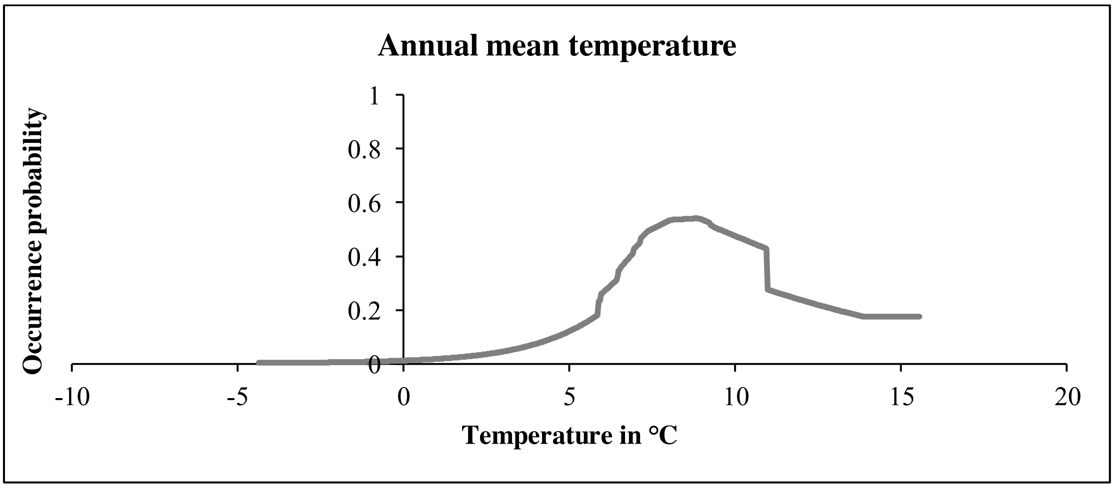


Figure 4.14 Response curves of "annual mean temperature" for model "Host 2" (grey) on the probability of occurrence for *Prunus serotina*.

The annual mean temperature was for model "Host 2 PS" the most important variable only. Lower temperatures (-5 °C) had almost no occurrence probability, which increased at 5 °C (0.2) to the maximum at 8 °C (0.6).

The mean temperature of wettest quarter was between -5 to 22 °C for "Host 2 PS" with an average occurrence probability of 0.5. The precipitation seasonality ranged between 0 to 0.5 % with a maximum occurrence probability of 0.6. The calcium carbonate content of topsoil had a stable occurrence probability of 0.5 up to 16 %. The response curve for the clay fraction of the topsoil had a steady value of 0.5 and ranged up to 60 %.

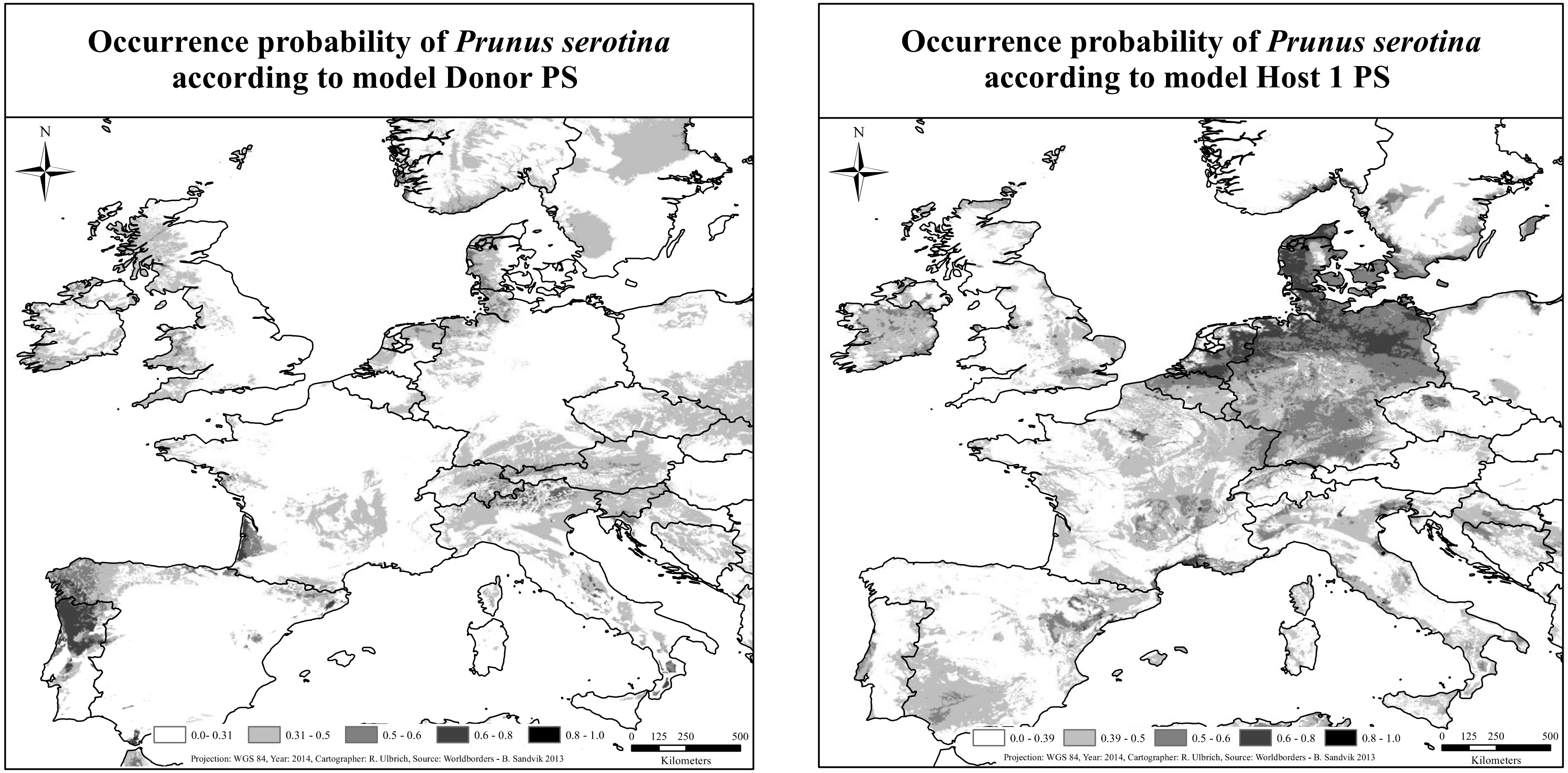


Figure 4.15 Species distribution of *Prunus serotina* according to model “Donor PS” (left) and “Host 1 PS” (right). Darker areas represent higher occurrence probability; lighter areas represent lower probability. Logistic values of threshold: 0.31 (Donor) and 0.39 (Host 1).

The model “Donor PS” calculated a small occurrence probability for *Prunus serotina* in Central Europe (Figure 4.15). The highest probability in Germany can be found in the northwest with 0.31 to 0.5 and the southern parts towards the Alps (0.31 to 0.5). The highest probability for whole Europe was calculated in the north of Portugal, a small region in south western France and the Alp region (0.6 to 0.8).

The possible distribution map of model “Host 1 PS” showed an occurrence probability of 0.39 and more for most of Europe. Especially, the northern part of Germany, the Netherlands and Denmark had a probability of 0.6 to 0.8. On the other side, the Alps had almost no occurrence probability. Model “Host 1 PS” calculated only a weak occurrence probability (0.31 to 0.5) for the southern parts of Sweden and Norway, Ireland and southwest of Spain.

The occurrence maps for the host models showed a clustered but differentiated higher occurrence probability for Germany and the neighbouring countries were most of the occurrence points were obtained. The change of occurrence probability across the border to eastern neighbouring countries of Germany might be a result of over fitting in Maxent due to the occurrence point locations.

The lower AUC value of the three models (between 0.6 and 0.7) might confirm this. The weaker performance for the host models could be a result of the clustered occurrence points used in Europe.

The third map produced a comparable picture with model “Host 1 PS” (compare Figure 4.15 and Figure 4.16). It calculated the same high occurrence probability for *Prunus serotina* in Germany and eastern France but less for the rest of Europe. While model “Host 1 PS” had a probability of 0.31 to 0.5 for the southwest of Spain, model “Host 2 PS” calculated none for most of the country.

The map of model “Donor PS” did not predict an occurrence probability for most of the actual occurrence records of *Prunus serotina* in Europe. On the other side, several regions (Ireland, southern Spain) had a predicted occurrence probability but no recorded occurrence points. This does necessarily imply that the species is absent here but, rather, that species records could be incomplete or limited from those areas and suggest a wrong depiction of the current situation.

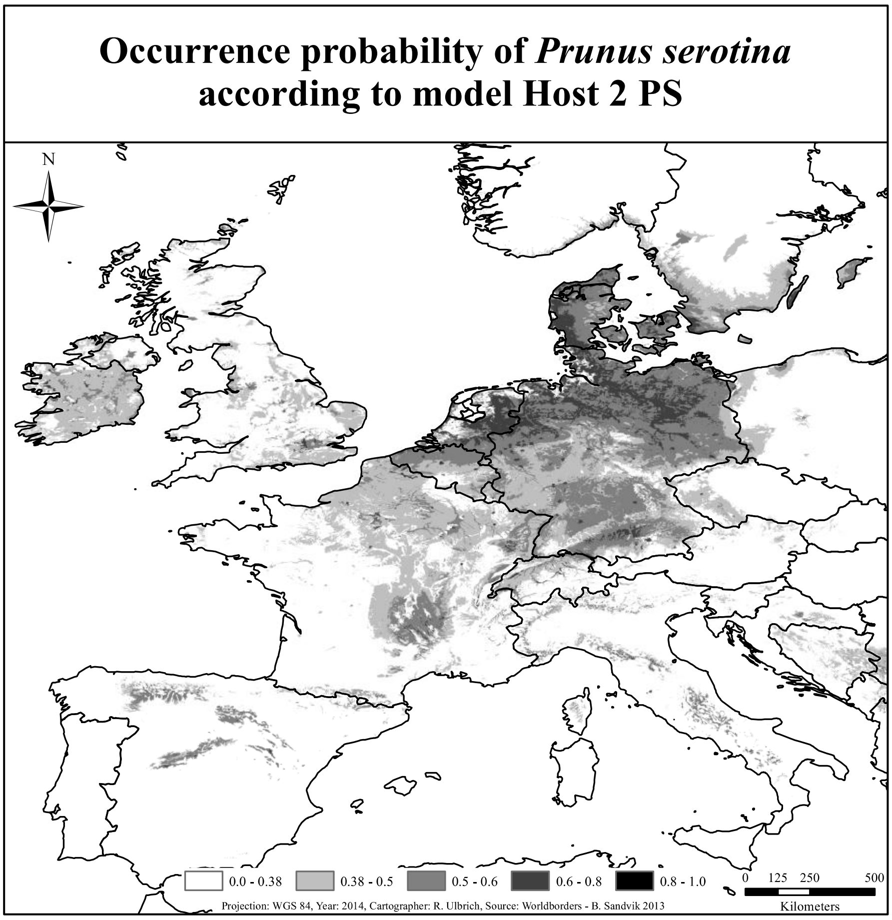


Figure 4.16 Species distribution of *Prunus serotina* according to model “Host 2 PS”. Darker areas represent higher occurrence probability; lighter areas represent lower probability. Logistic value of threshold: 0.38.

4.5 *Robinia pseudoacacia*

The model “Donor RP” identified mean temperature of coldest quarter (26.1 %), precipitation seasonality (17.1 %) and precipitation of driest month (13.3 %) as most important environmental variables (Table 4.6 and Figure 4.17). In the second model temperature seasonality represented the most important variable with 25.4 %. Altitude and precipitation of warmest quarter followed with 17.9 % and 17.2 %.

Table 4.6 The permutation importance in percentage for the most important environmental variables of *Robinia pseudoacacia* of all three models. The most important values are in bold.

Environmental variables	Explanation	Donor RP	Host 1 RP	Host 2 RP
alt	Altitude	5.9	17.2	-
bio_1	Annual Mean Temperature	-	-	11.2
bio_4	Temperature Seasonality	8.1	**25.4**	12.8
bio_5	Max. Temp. of Warmest Month	-	-	**24.4**
bio_6	Min Temp. of Coldest Month	-	-	15.2
bio_8	Mean Temp. of Wettest Quarter	5.1	4.8	-
bio_9	Mean Temp. of Driest Quarter	5.9	12.2	5.3
bio_11	Mean Temp. of Coldest Quarter	**26.1**	12.9	-
bio_13	Precipitation of Wettest Month	4.2	0.8	-
bio_14	Precipitation of Driest Month	13.3	3.6	8
bio_15	Precipitation Seasonality	17.1	1.3	6.8
bio_18	Precipitation of Warmest Quarter	12.7	17.9	10.9
bio_19	Precipitation of Coldest Quarter	1.4	3.8	-
clay	Clay Fraction of Topsoil	-	-	2.5
sand	Sand Fraction of Topsoil	-	-	2.9

Five variables were replaced in the third model, namely altitude, mean temperature of wettest quarter, mean temperature of coldest quarter, precipitation of wettest month and precipitation of coldest quarter. The new variables were annual mean temperature, maximum temperature of warmest month (which is also the most important variable with 24.4 %), minimum temperature of coldest month (second most important – 15.2 %), clay fraction of topsoil and sand fraction of topsoil. The third important variable was temperature seasonality with 12.8 %.

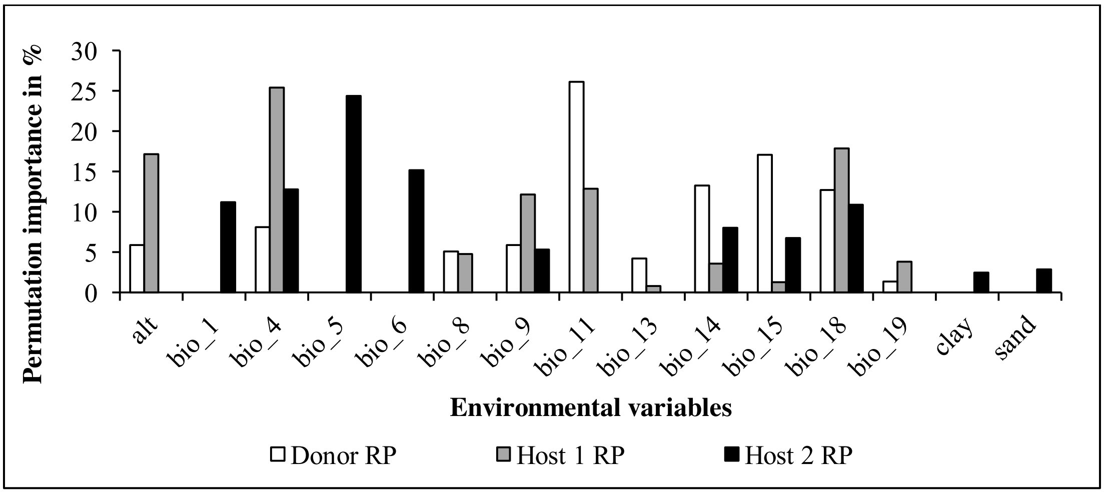


Figure 4.17 Comparison of the permutation importance of environmental variables between the models "Donor RP", "Host 1 RP" and "Host 2 RP".

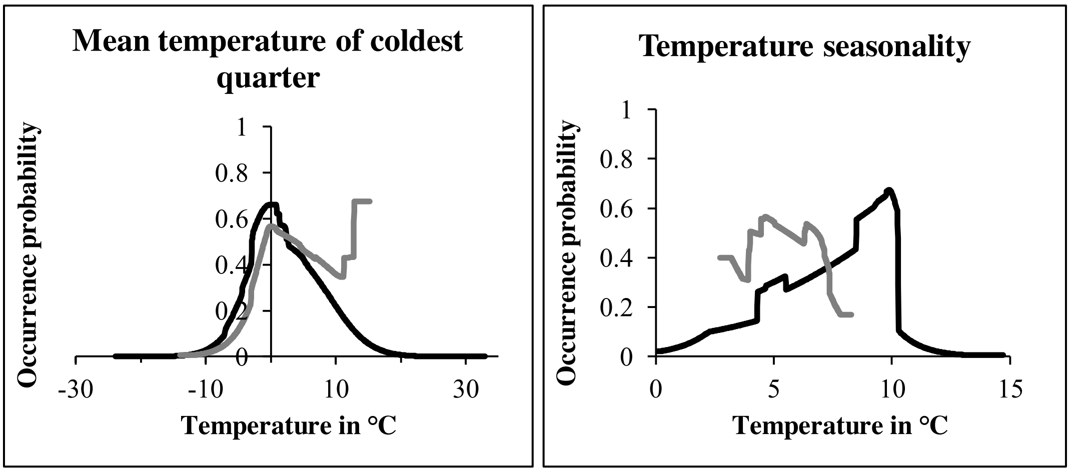


Figure 4.18 Response curves of "mean temperature coldest quarter" and "temperature seasonality" for model "Donor" (black) and "Host 1" (grey) on the probability of occurrence for *Robinia pseudoacacia*.

The response curves for mean temperature of coldest quarter of model "Donor RP" and "Host 1 RP" showed a similar picture (Figure 4.18). The occurrence probability increased from 0 (-10 °C) to 0.6 (0 °C). The maximum for “Host 1 RP” was slightly lower and the curve increased again at 10 °C to over 0.7.

The temperature seasonality showed a peak of 0.6 occurrence probability at 10 °C for “Donor RP“. “Host 1 RP” ranged between 4 and 6 °C with an occurrence probability of 0.5. The mean temperature for the wettest quarter had similar response curves for both models. The maximum occurrence probability (“Donor RP”: 0.6; “Host 1 RP”: 0.5) was around 5 and 20 °C. The mean temperature for the driest quarter had a maximum occurrence probability at 0 °C (“Donor RP”: 0.8; “Host RP” 1: 0.6). Both curves decreased afterwards.

The mean temperature for the coldest quarter had a peak at 0 °C for both models with a maximum occurrence probability of 0.6. Lower and higher temperatures showed a lower occurrence probability in both cases.

“Donor RP” and “Host 1 RP” had the highest occurrence probability of 0.6 and 0.8 for a precipitation between 0 and 100 mm in the wettest month. The precipitation of driest month produced a stable value of 0.5 for “Donor RP” from 10 to 350 mm, whereas “Host 1 RP” had a peak of 0.6 at 40 mm.

The precipitation seasonality calculated the highest occurrence probability for “Donor RP” (0.9) at 6 % and for “Host 1 RP” (0.6) at 13 %. Both curves decreased after the peak, the curve of “Donor RP” exceeded the 100 %.

Both models had an occurrence probability of 0.6 for 150 to 320 mm precipitation during the warmest and coldest quarter. The “Donor RP” value remained stable from around 0.3 onwards.

The maximum temperature of warmest month was the most important environmental variable for model "Host 2 RP" only (Figure 4.19). The curve increased from almost no occurrence probability (0 °C) to 0.6 at 20 °C and declined to 0.3 (40 °C).

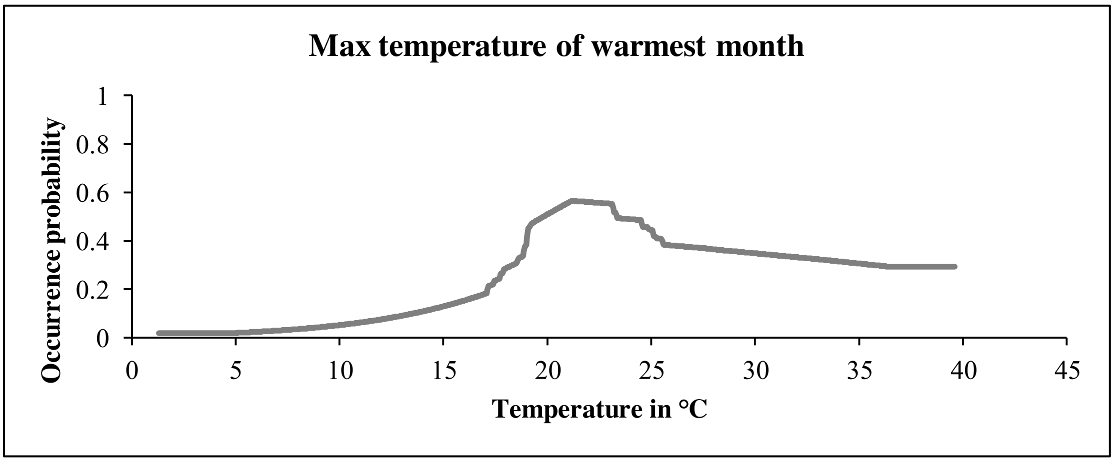


Figure 4.19 Response curves of "max temperature of warmest month" for model "Host 2" (grey) on the probability of occurrence for *Robinia pseudoacacia*.

"Host 2 RP" produced a peak of 0.6 occurrence probability for an annual mean temperature of 8 °C, decreased up to 0.4 (17 °C). The maximum temperature warmest month showed the highest occurrence probability (0.6) at 22 °C. The curve ranged from 0 to 40 °C. The minimum temperature for the coldest month ranged from -17 to 12 °C and had a peak of 0.6 occurrence probability at -4 °C. The clay and sand fraction of topsoil predicted a more or less stable occurrence probability of 0.5 from 0 to 50 and 100 %.

The distribution map of *Robinia pseudoacacia* (Figure 4.20) according to model "Donor RP" calculated a low occurrence probability for most parts of Europe (0.24 to 0.5). Belgium, parts of France, Spain and Great Britain showed exceptions (0.5 to 0.8). Most parts of Germany show a low probability (0.24 to 0.5).

The possible distribution of *Robinia pseudoacacia* was more widespread in the model "Host 1 RP". In comparison to "Donor RP" the probability was increased in

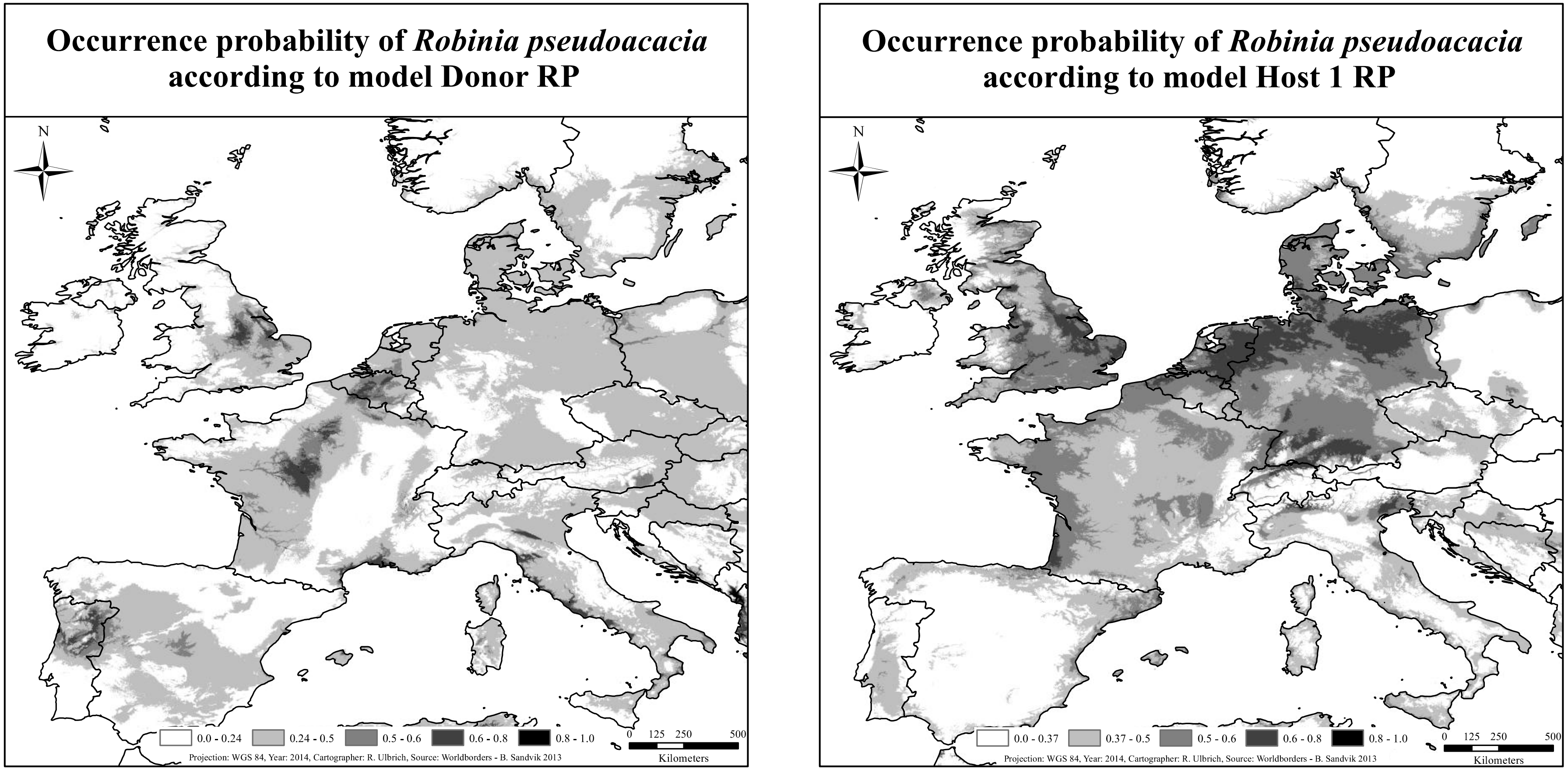
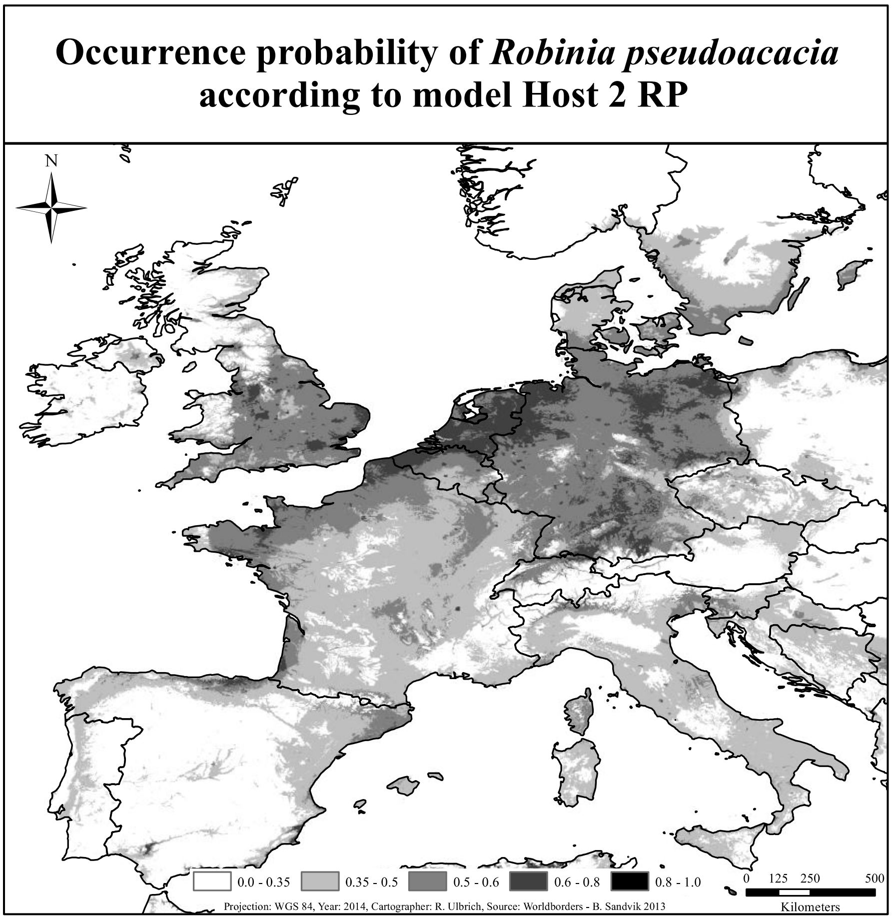


Figure 4.20 Species distribution of *Robinia pseudoacacia* according to model “Donor RP” (left) and “Host 1 RP” (right). Darker areas represent higher occurrence probability; lighter areas represent lower probability. Logistic values of threshold: 0.24 (Donor) and 0.37 (Host 1).

the Netherlands (up to 0.8), most parts of France (0.37 to 0.6), Great Britain (0.5 to 0.8), the southern parts of Norway and Sweden (0.37 to 0.6), Denmark (0.5 to 0.6),and Germany (0.5 to 0.8). Germany had a higher probability in the northern and southern parts (0.8) compared to the central part (0.37 to 0.5).

The third map, model “Host 2 RP”, estimated a more similar distribution to model “Host 1 RP” (Figure 4.21). Differences were visible in Germany where parts in the central north, east and south vary from “Host 1 RP” (0.6). Further changes could be found on the southern coast of Norway, central France and the eastern part of Great Britain.


Occurrence probability of *Robinia pseudoacacia* according to model Host 2 RP

Projection: WGS 84, Year: 2014, Cartographer: R. Ulbrich, Source: Worldborders - B. Sandvik 2013

Figure 4.21 Species distribution of *Robinia pseudoacacia* according to model “Host 2 RP”. Darker areas represent higher occurrence probability; lighter areas represent lower probability. Logistic value of threshold: 0.35.

5 Discussion

5.1 General Discussion

The number of occurrence points used in this study was reliable and comparable with other studies which suggest at least 30 points per species (Phillips & Dudík, 2008; Baldwin, 2009). Still, though the number of records did not imply the spread or bias of the points, which will be discussed in each of the following sections.

In the Namibian host region, the sampled tree species (*Leucaena leucocephala* and *Prosopis* spp) had limited numbers of occurrence points and a narrow regional spread (compare with occurrence points in Figure 4.1). Similarly, occurrence points of the European species *Prunus serotina* and *Robinia pseudoacacia* were biased towards Germany, Belgium and the Netherlands. In all four cases an over fitting of the Maxent output was likely (Phillips, Anderson & Schapire, 2006; Phillips & Dudík, 2008, Elith et al., 2011).

Following previously tested methods, this study reduced occurrence points to minimize the bias in distribution (Brown, 2014). Although the occurrence points were reduced (see Table 4.1) a clustering of occurrence points was still visible and higher occurrence probabilities were calculated by Maxent around these points. The results showed a higher equal distance between the occurrence points is needed while having a high number of occurrence points.

For European models the corporation of further local or national herbaria, research stations or databases should be considered to obtain more reliable points from different nations and include the whole environmental conditions of the species in this area which was also suggested by Elith et al. (2006) and Phillips & Dudík (2008).

The scale of Namibian models should be reconsidered as well. For instance a larger area including South Africa and Botswana with reliable occurrence points of the two species could improve the host models which is suggested by Elith et al. (2006; 2011).

The clustering or bias of occurrence points affected the AUC values since the predictive accuracy is negatively influenced by the comparison of presence data with the background environment (Fielding & Bell, 1997; Hirzel, Hausser, Chessel, & Perrin, 2002; Pearson, 2007).

While evaluating of models according to the AUC value seems to be the only method for presence-only data models (Raes & ter Steege, 2007), the creation of pseudo-absences or use of thresholds would allow other evaluation methods (Raes & ter Steege, 2007; Baldwin, 2009; Liu, White, & Newell, 2011). In most cases, Kappa index according to omission and commission error was calculated and compared (Mingyang et al., 2008; Evangelista et al., 2009; Jarnevich & Reynolds, 2011) or a Pearson correlation coefficient according to the correlation between a model prediction and a presence/absence in test data (e.g. in Mingyang et al., 2008; Phillips & Dudík, 2008; Václavík & Meentemeyer, 2009). For this study, only presence data was used, therefore no other evaluation methods than AUC could be used.

Václavík and Meentemeyer (2012) discussed the difficulties of modelling invasive species in different stages of the invasion. Similar issues can be found in this study, especially for the Namibian species where few records were found and the time between introduction and data collection was short. This will be discussed in more detail in each of the following species section.

The earlier mentioned time gap between introduction and rapid spread of invasive alien species might influence the results of the models as well. Also it is obvious that the climate of Germany or Hawaii (areas were studies about time gap and invasive alien species were conducted by Kowarik (1995) and Daehler (2009)) is not directly comparable to that of Namibia and, thus, time gaps cannot be estimated; however, further research could explore the possible time lag of *Leucaena leucocephala* and *Prosopis* spp dispersal in Namibia.

The soil data showed biased results for the modelling in Namibia along state and regional borders, which might be a result of the data compilation. The HWSD dataset was produced with regional and national soil collections, which might create the bias in areas with weak data collections (FAO/IIASA/ISRIC/ISSCAS/JRC, 2012). For these reasons the soil variables were excluded for *Leucaena leucocephala* and *Prosopis* spp.

In most cases the response curves of the donor models expanded across wider environmental ranges than the host models. This may imply that occurrence points of species in the donor region covered a larger ecological niche than in the host area. This was validated with the environmental data. In the following section the range of the two most important environmental variables in host and donor region of each species will be listed.

The mean temperature from the coldest quarter was one of the most important variables for *Leucaena leucocephala*. The variable extended from 10 to 18 °C in

Namibia (host) in comparison to -17 to 26 °C in Northern America (donor). Another important variable for *Leucaena leucocephala* was the annual mean temperature, which ranged from 15 to 22 °C in Namibia and from 0 to 27 °C in Northern America. In both cases the range of the host region (Namibia) was smaller and inside the range of the donor region. It implies that *Leucaena leucocephala* did not cover it's full potential distribution range in Namibia and might be able to expand in future time.

The two most important variables of *Prosopis* spp were the mean temperature of coldest quarter (listed above) and the annual precipitation. The latter ranged from 33 to 780 mm in Namibia (host) and 165 to 2,571 mm in Northern America (donor). Again, the suitable range for the invasive alien species lied in between the donor region or even lower for the annual precipitation. The latter might imply a much smaller need of precipitation per year than the species obtained in its native range.

Altitude and the minimum temperature of the coldest month were the most important variables for *Prunus serotina*. The first variable ranged from 0 to 1,711 m in Europe (host) and up to 2,525 m in Northern America. The second variable, the minimum temperature of the coldest month, extended -12 to 6 °C in Europe and -25 to 21 °C in Northern America. According to the models and the ranges in the donor region, *Prunus serotina* would be able to reach higher altitudes in Europe in comparison to the actual distribution. The second environmental variable, minimum temperature of coldest month, showed that the species covered only a portion of the full range in comparison to the donor region which allows potential further spread as well.

The mean temperature of coldest quarter, -9 to 11 °C in Europe (host) and -17 to 26 °C in Northern America (donor), and the temperature seasonality, which ranged from 0 to 6 °C in Europe (host) and 1 to 11 °C in Northern America (donor), were the two most important variables for *Robinia pseudoacacia* during the modelling. In both cases, the invasive alien species range was smaller but close to the range of the donor region. It implied the species did not cover it's full potential yet in the host region and might spread in future.

5.2 *Leucaena leucocephala*

Most of the occurrence points of *Leucaena leucocephala* were obtained via road counts (27 out of 32) which was the only suitable option to gain points in Namibia due to the few records from the National Herbarium of Namibia (3). Phillips and Dudík (2008) as well as others (Phillips, Anderson, & Schapire, 2006; Elith et al., 2011) notified that the sampling bias due to road counts could lead to over fitting in Maxent. The distribution maps of "Host 1 LL" and "Host 2 LL" showed the highest occurrence probability around the main locations of records, which could imply an over fitting in those areas.

Considering the host maps would only imply a regional pressure of the species in northern areas of Namibia, the collected records inside the country and the projection by "Donor LL" showed that this did not reflect the potential distribution of *Leucaena leucocephala*. The limited regional occurrence of the species might be influenced by the time passed after the first introduction. No literature about the time and place of introduction to Namibia were found, only for South Africa in the 19th century (Macdonald, Kruger, & Ferrar; 1986; Henderson, 2001).

The distribution and dispersal through the Directorate of Forestry nurseries is likely as the species has been sold since 1992 (Joubert, 2008) and planted around several compounds. Furthermore, the species was not listed in Erkkilä and Siiskonen (1992) who had insights in the forestry archives of Namibia and analysed the period from 1850 to 1990. They listed several other invasive alien species including *Prosopis* spp, which supported a recent introduction of the species and a lack of sufficient time for dispersal. Therefore, the expansion of the species according to model “Donor LL” could be more possible and account for the limited occurrence area of the host models.

The AUC values of all three models of *Leucaena leucocephala* were above 0.94 occurrence probability implying a fairly good model prediction. As mentioned above the distribution maps showed a different picture. Phillips (2011) mentioned that AUC values tend to be higher for species with narrow ranges in relation to the described study area by the environmental data. Furthermore, AUC does not consider how well a model was calibrated (Elith et al., 2011).

The response curves for each environmental variable showed differences between “Donor LL” and “Host 1 LL” not only in the shape of the curve but also in the covered areas. In most cases, the curves of “Donor LL” covered a broader range of values than the “Host 1 LL” curve, suggesting that the occurrence points of “Donor LL” cover a broader range of climate conditions and have a larger ecological niche than the host occurrence points. Furthermore, the occurrence points in Namibia seemed to be located in almost the same climate situation as in the donor region.

The annual mean temperature showed that optimum for “Donor LL” and especially for “Host LL 1” was below the suggested range descripted in Orwa et al., 2009. The response curve of altitude may be formed in this way (“Host LL 1”) because most of the species records in Namibia were located in altitudes over 1,000 m with only several occurrence points found in lower altitudes. This may also explain the high contribution of the variable to the models “Host 1 LL” and “Host 2 LL”.

The annual precipitation of “Host 2 LL” was below the descripted range of Orwa et al., 2009; this difference may be a result of the limited occurrence points and the low precipitation rate in Namibia. Nevertheless, a comparison with the annual rainfall data from Northern America showed that most of the occurrence points of *Leucaena leucocephala* were in areas with more than 1,000 mm precipitation per year (maximum of the response curve during the modelling, see appendix A4) (Hijmans et al., 2005). This implies that the species prefers areas with higher rainfall than in Namibia but seems to be able to cope with the low precipitation rate.

5.3 *Prosopis* spp

The occurrence points of *Prosopis* spp were obtained from GBIF and National Herbarium of Namibia and covered a widespread area of Namibia.

The models “Host 1 PSPP” and “Host 2 PSPP” predicted a high occurrence probability around the actual locations of the species, which could be a result of over fitting through the modelling because areas without occurrence points seems to have less to no occurrence probability. In most cases, the response curves of model “Donor PSPP” cover a wider climatic range than the host models, which could explain the larger potential occurrence area by model “Donor PSPP” for Namibia. Most of the response curves of host models predicted similar shapes or fragments when compared to model “Donor PSPP” which may suggest a smaller potential occurrence areas of the species in the host region.

The expansive range of environmental variables from Northern America was not found in Namibia which might be caused by the study area extent, which was limited to Namibia and parts of neighbouring countries, and caused a different geographical as well as climatic setting. The regional scale excluded other occurrence areas such as in South Africa (Brown et al., 1985; Bromillow, 2010), which might allow a wider environmental range in the host region.

Similarities of predicted occurrence probability were found in the south western area of Namibia (Sperrgebiet) where all models showed a comparable area with no occurrence probability for the *Prosopis* spp and in the Kunene area with higher probability.

The smaller occurrence area of the host models could be due to the contradiction between the different climate settings in Namibia and Northern America while the response curves produced surprisingly similarities.

Another aspect for this contradiction could be the time gap between introduction and rapid spread of the invasive species in Namibia. Several authors showed *Prosopis* spp was introduced, first noticed or sown in Namibia not even 120 years ago (Brown, Macdonald, & Brown, 1985; Macdonald, Kruger, & Ferrar, 1986; Erkkilä & Siiskonen, 1992; Smit, 2005). The dispersal area increased from Windhoek and Okahandja (Brown, Macdonald, & Brown, 1985; Macdonald, Kruger, & Ferrar, 1986) to Rehoboth and the Swakop River (Erkkilä & Siiskonen, 1992) as well as large parts of south eastern Namibia (Smit, 2005).

Taking this lag of dispersal time and time gap from introduction to invasion into account the possible distribution according to model “Donor PSPP” might be a possible future scenario.

This could be investigated with an approach by studies of Hoffman et al. (2008) as well as Jarnevich and Reynolds (2011). They mapped the possible distribution of different invasive alien tree species in North America along rivers. Such a study might be an interesting future consideration of modelling the spread of *Prosopis* spp along rivers in Namibia.

Although the AUC values of all three models were above 0.882 implying a good prediction for potential distribution, the distribution maps showed a more clustered picture. The contradiction between AUC output and the clustered maps maybe a result of the narrow environmental range of the used occurrence points (Phillips, 2011).

The host models showed that *Prosopis* spp might grow in higher altitudes in Namibia (up to 2,400 m) compared to the numbers of Orwa et al (2009) (up to 1,500 m). According to the response curves, precipitation is a limiting factor for the occurrence of *Prosopis* spp. On the other hand, the area in Namibia with higher annual precipitation (north eastern area) had no occurrence probability but was also an area without any recorded occurrence points. This might be a result of the previous mentioned over fitting of Maxent due to the occurrence points in the host area.

5.4 *Prunus serotina*

A large portion of occurrence points for *Prunus serotina* were located in Germany and the neighbouring countries (Belgium, Denmark, Netherlands), which are also the locations where *Prunus serotina* was introduced to Europe in the 19th century (Klotz, 2007; Kowarik, 1999 in Seitz & Nehring, 2013).

A difference in the ecological niche covered in donor and host region could not be supported with the response curves of the variables which means that the ecological niches are the same for donor and host region. Another possibility could be the correlation of variables and over fitting from the donor region, which results in highly specified occurrence areas for the projection.

The slightly different occurrence maps of the host models might be due to one or more environmental variables that were used in model "Host 1 PS" but not in model "Host 2 PS". Similarly, the minimum temperature for the coldest month and mean temperature of driest quarter were both notated as high permutation importance for model "Donor PS" and "Host 1 PS". They were both not used in "Host 2 PS".

The species was introduced during the 19th century for forestry purpose (Starfinger, 2010), which implied the more extensive dispersal and possible spread compared to former introduction as an ornamental plant in the 17th century (Klotz, 2007). According to Kowarik (1995), the time lag between introduction of a species and its invasion *Prunus serotina* could be in the actual stage of invasion. In the beginning of the rapid spread invasive alien species have a more clustered distribution. This could also explain the clustered occurrence of the species to regions of former intentional introduction areas (Belgium, Germany, Netherlands).

The response curves of "Donor PS" and host models showed no huge differences except for altitude. In most cases the host models had a similar forms but smaller ranges.

The maximum altitude of 2,000 m by Starfinger (2010) was reflected in the host models but different for the "Donor PS" model which might contribute to the low occurrence probability in lower areas of Europe for the model “Donor PS” (Alps region, Pyrenees mountains).

Although *Prunus serotina* might grow on a wide range of soil conditions (clay, loam and sand) (Gilman & Watson, 1994; Starfinger, 2010; Seitz & Nehring, 2013) the soil characteristics were only important for model “Host 2 PS”. However, the sandy and poor soil condition proclaimed by Seitz & Nehring, (2013) were still represented in the results with higher occurrence probabilities in the northern and sandy parts of Germany.

5.5 *Robinia pseudoacacia*

The occurrence records of *Robinia pseudoacacia* were more spread over Europe with a higher concentration in Germany and the neighbouring countries. All three models predicted a widespread occurrence of the species in Europe. “Donor RP” predicted a map that had an occurrence probability, although with low chance, for almost all areas with actual records in Europe. The host models calculated higher occurrence probability in areas with higher numbers of records, supporting the need for more unique distributed occurrence points in future studies. Spain, which had few records, obtained almost no areas with a likely occurrence. It might be due to the low number in comparison to other parts of Europe.

Around 200 years ago, *Robinia pseudoacacia* was introduced to several German regions (Starfinger & Kowarik, 2010; Seitz & Nehring, 2013). Taking the time lag between introduction and invasion of Kowarik (1995) into account the species might be in the process of invasion. He proposed a higher invasion success of the species in subcontinental or submediterranean climate as compared to regions with oceanic influence (Kowarik, 1995). A change in climate allowed a longer growing period due to the increasing heat, which meant a more favourable climate for *Robinia pseudoacacia* in the 19th century (Kowarik, 1995).

The high AUC value for the donor model and the distribution map were in agreement, giving a fairly good projection of occurrence probabilities for *Robinia pseudoacacia* in Europe. The occurrence probability was mainly low (below 0.5) but covered most of the actual known occurrence locations of the species. The lower AUC values for the host models might be a result of the low spread occurrence records.

The response curves of the models showed similarities while the host models had smaller ranges than model “Donor RP”. The high importance of maximum temperature for the warmest month and minimum temperature coldest month in model “Host 2 RP” suggests a higher influence of weather extremes on plant distributionin the host area compared to the donor area.

The response curve of altitude predicted a similar occurrence range of 1,500 m seen by different authors (Orwa et al., 2009; Starfinger & Kowarik, 2010). Nevertheless, inline with the response curves, the species seems to grow in higher altitudes (up to 4,000 m).

6. Conclusions and Recommendations

The study showed the potential use of Maxent in projecting the potential distribution of selected invasive alien species to Europe and Namibia as well as limitations. The three calculated models used occurrence records from donor and host regions as well as a set of different variables namely current climate and different soil characteristics.

The output of the Maxent models produced distribution maps with different quality meaning not all maps could be taken as face values. The accuracy of the final maps was highly dependent on the number of occurrence points as the major part, quality and quantity of environmental data, and the extent of the study area.

Models of *Prunus serotina* and *Robinia pseudoacacia* showed that projections from donor to host areas might not accurately represent the actual and potential distribution of invasive alien species. On the other hand, projections form the donor region towards Namibia showed a higher possible distribution than host models in Namibia only. In both areas, the clustered (European species) or limited amount (Namibian species) of occurrence points were seen as the cause which led to over fitting and underestimating of the distribution range with Maxent. Furthermore, the method use for reducing occurrence points augmented the issues of underestimation because of the limited reduction in occurrence point bias. As expressed by Kowarik (1995), time lags between introduction and invasion can alter the accurate predictions in models. Given the low focus on invasive alien species in Namibia, the donor models for Namibian species might give a useful prediction of the future spread and threat of *Leucaena leucocephala* and *Prosopis* spp.

The different behaviour of alien species (high adaptation, opportunistic, high reproduction and invasion time) compared to native species made it necessary to obtain occurrence records for both areas and calculate donor and host models as well as a constant monitoring and update of such models.

The limited amount of occurrence points of Namibian species (especially for *Leucaena leucocephala*) decreased the informative value of the distribution map, which alone would lead to false conclusions and underestimate the potential threat of the species. The occurrence points for *Prunus serotina* were highly clustered which lead to over fitting as well. A lower number of records in Germany, Belgium and Netherlands might help or/and additional records from neighbouring countries such as Austria, Czech Republic, Poland and Switzerland.

The study extent of Namibia might have affected the over fitting of Namibian species and, thus, future model prediction should include states like South Africa, Botswana and others.

The AUC values reflected an acceptable model of *Robinia pseudoacacia* although the occurrence points were regional clustered (Belgium, Germany, Netherlands). Even though the AUC was decided to be the most accurate evaluation method for this kind of study the use of AUC implied the discussed advantages and disadvantages. Future studies should consider the use of absence points and would be able to use other evaluation methods additionally.

The response curves of each model might be another helpful tool to compare the distribution of the species in donor and host areas. While smaller ranges of response curves in host models might be caused by the location of occurrence points it could give a hint to which suitable areas are not yet infested. The comparison might show possible changes in preferred climate conditions as well. The knowledge will improve the identification of vulnerable areas and management of invasive alien species. It allows managers of vulnerable areas (for example national parks, nature reserves) and conservationists to allocate time and effort where it is needed and avoid a more resources intense generalized approach, which cover larger areas and include non-vulnerable regions as well.

The response curves showed that occurrence records in the host areas did not cover the exact range as points from the donor region. The number of occurrence points and their location may explain this misfit. Therefore, a high quality and unique range of occurrence points in both, donor and host areas are needed.

While Germany had different organizations and institutes such as the Federal Agency of Nature Conservation and FLORKART, which focus on monitoring and recording of invasive alien plants, Namibian invasive alien species are seriously understudied and under recorded. Some alien species such as *Prosopis* spp and *Opuntia* spp Mill. were included in the Tree Atlas of Namibia but the actual records in the Herbarium of Namibia are not enough for distribution modelling.

The distribution models cannot compensate for the lack of occurrence points in an area, but rather a combination of donor and host models can establish a proper assessment of the potential threats of invasive alien species. To ensure reliable models, a variety of sources, a widespread amount of occurrence points, and high quality of environmental variables are essential.

Therefore, the regular monitoring and update of Maxent models with new and actual occurrence points for invasive alien species in Germany and Namibia should be considered. Models including the riparian spread of *Prosopis* spp in Namibia might be another method of monitoring and predicting the future spread of those species to vulnerable areas.

All four species, *Leucaena leucocephala*, *Prosopis* spp, *Prunus serotina* and *Robinia pseudoacacia* are invasive alien species in Germany or Namibia. While both countries are aware of alien species in their regions methods or action plans to fulfil the precautionary approach are limited. Most programs and management methods dealing with invasive alien species are done when the problem is already there and outcompete native flora and fauna while using resources or change the soil composition and endanger highly adapted local species.

The monitoring of invasive alien species will not only raises awareness about the actual distribution and spread of such species but would allow the use of new prediction methods such as species distribution modelling. The combination of ground truthing (accurate occurrence points in the field) and software calibration as well as development will allow more accurate models of potential distribution ranges invasive alien species without having the species in the host region already.

Species distribution modelling with Maxent and presence-only data is a promising method and simple tool for the management and monitoring of invasive alien species not just in Germany but especially in Namibia.

References

Alpert, P., Bone, E., & Holzapfel, C. (2000). Invasiveness, invisibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics, 3*(1), 52-66.

Baldwin, R. A. (2009). Use of maximum entropy modelling in wildlife research. *Entropy, 11,* 854-866. doi:10.3390/e11040854

Başnou, C. (2006). Robinia pseudoacacia. Retrieved from http://www.europe-aliens.org/pdf/Robinia_pseudoacacia.pdf

Bethune, S., Griffin, M., & Joubert, D. (2004). *Consultancy report on information collected regarding Invasive alien species in Namibia for the SABSP (Southern Africa Biodiversity Support Programme)*. Windhoek, Namibia: MET.

Boria, R. A., Olson, L. E., Goodman, S. M., & Anderson R. A. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modeling, 275*, 73-77.

Boyer, D. C., & Boyer, H. J. (1988). The status of alien invasive plants in the major rivers of the Namib Naukluft Park. *Madoqua, 16*(1), 51-58.

Brand, K., & Matthew, S. (2004). *Africa invaded – the growing danger of invasive alien species*. Cape Town, South Africa: Global Invasive Species Programme.

Brandes, D. (2000). Neophyten in Deutschland: Ihre standörtliche Einnischung und die Bedrohung der indigenen Flora. In H. Opitz & C. Mayr (Eds.), *Was macht der Halsbandsittich in der Thujahecke?* (pp. 44-54). Germany: NABU.

Bromillow, C. (2001). *Problem plants of South Africa* (2nd ed.). Pretoria, South Africa: BRIZA.

Bromillow, C. (2010). *Problem plants of South Africa* (3rd ed.). Pretoria, South Africa: BRIZA.

Brown, C. J., Macdonald, I. A. W., & Brown, S. E. (1985). *Invasive alien organism in South West Africa/Namibia*. Pretoria, South Africa: CSIR.

Brown, J. L. (2014). SDMtoolbox (version 1.0b) [Computer software]. Retrieved from http://sdmtoolbox.org

De Cauwer, V., Muys, B., Revermann, R., & Trabucco, A. (2014). Potential, realised, future distribution and environmental suitability for *Pterocarpus angolensis* DC in southern Africa. *Forest Ecology and Management, 315*, 211-226.

Chenje, M., & Mohamed-Katerere, J. (2006). Invasive alien species. In *Africa Environment Outlook 2: Our Environment, Our Wealth* (pp. 331-349). Nairobi, Kenya: UNEP.

Curtis, B. A., & Mannheimer, C. A. (2005). *Tree Atlas of Namibia*. Windhoek, Namibia: National Botanical Research Institute.

Datenbank FLORKART, BfN, & NetPhyD (2013). *Datenbank FLORKART der floristischen Kartierung Deutschlands*. Bonn, Germany: Bundesamt für Naturschutz und Netzwerk Phytodiversität Deutschland.

Daehler, C. C. (2009). Short lag times for invasive tropical plants: Evidence from experimental plantings in Hawai'i. *PLoS ONE, 4*(2), 1-5. doi: 10.1371/ journal.pone.0004462

Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., … Zimmermann, N. E. (2006). Novel methods improve prediction of species distributions from occurrence data. *Ecography, 29,* 129-151.

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions, 17,* 43-57.

Erkkilä, A., & Siiskonen, H. (1992). *Forestry in Namibia 1850-1990*. Finland: University of Joensuu.

ESRI (2014). ArcGIS (version 10.2.2) [Computer software]. NY: Environmental Systems Research Institute.

European Environment Agency (2007). *European forest types. Categories and types for sustainable forest management reporting and policy* (2nd ed.). Copenhagen, Denmark.

Evangelista, P. H., Stohlgren, T. J., Morisette, J. T., & Kumar, S. (2009). Mapping invasive tamarisk (*Tamarix*): A comparison of single-scene and time-series analyses of remotely sensed data. *Remote Sensing*, *1,* 519-533. doi: 10.3390/rs1030519

FAO/IIASA/ISRIC/ISSCAS/JRC (2012). *Harmonized World Soil Database (version 1.2)*. FAO, Rome, Italy and IIASA, Laxenburg, Austria. Retrieved from http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/

Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation, 24*(1), 38-49.

Genovesi, P., & Shine, C. (2003). *European strategy on invasive alien species*. Strasbourg, France: Council of Europe.

Gilman, E. F., & Watson, D. G. (1994a). *Prosopis glandulosa. Fact Sheet ST-502*. Florida: Environmental Horticulture Department.

Gilman, E. F., & Watson, D. G. (1994b). *Prunus serotina. Fact Sheet ST-516*. Florida: Environmental Horticulture Department.

Gilman, E. F., & Watson, D. G. (1994c). *Robinia pseudoacacia. Fact Sheet ST-570*. Florida: Environmental Horticulture Department.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters, 8,* 993-1009.

Guisan, A., Zimmermann, N. E., Elith, J., Graham, C. H., Phillips, S., & Peterson, A. T. (2007). What matters for predicting the occurrences of trees: Techniques, data, or species' characteristics? *Ecological Monographs, 77*(4). 615-630.

Henderson, L. (2001). *Alien weeds and invasive plants. A complete guide to declared weeds and invaders in South Africa*. Cape Town, South Africa: Paarl Printers.

Hijmans, R. J. (2012). Cross-validation of species distribution models: Removing spatial sorting bias and calibration with a null model. *Ecology, 93*, 679–688.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very High resolution interpolated climate surface for global land areas. *International Journal of Climatology, 25*, 1965-1978.

Hoffman, J. D., Narumalani, S., Mishra, D. R. Merani, P., & Wilson, R. G. (2008). Predicting potential occurrence and spread of invasive plant species along the North Platte River, Nebraska. *Invasive Plant Science and Management, 1*(4), 359-367.

Holcombe, T. R., Stohlgren, T. J., & Jarnevich, C. S. (2010). From points to forecasts: Predicting invasive species habitat suitability in the near term. *Diversity, 2,* 738-767. doi: 10.3390/d2050738

Jarnevich, C. S., & Reynolds, L. V. (2011). Challenges of predicting the potential distribution of a slow-spreading invader: A habitat suitability map for an invasive riparian tree. *Biological Invasions*, 13, 153–163. doi: 10.1007/s10530-010-9798-4

Jaryan, V., Datta, A., Uniyal, S. K., Kumar, A., Gupta, R. C., & Singh, R. D. (2013). Modelling potential distribution of *Sapium sebiferum:* An invasive tree species in western Himalaya. *Current Science, 105*(9), 1282-1288.

Jeschke, J. M., & Strayer, D. L. (2008). Usefulness of bioclimatic models for studying climate change and invasive species. *New York Academy of Sciences, 1134,* 1-24. doi: 10.1196/annals.1439.002

Jiménez-Valverde, A., Peterson, A. T., Soberón, J., Overton, J. M., Aragón, P., & Lobo, J. M. (2011). Use of niche models in invasive species risk assessments. *Biological Invasions, 13*. 2785–2797. doi: 10.1007/s10530-011-9963-4

Joubert, D. F. (2008). Invasive plants in Namibian subtropical and riparian woodlands. In R. K. Kohli, S. Jose, H. P. Singh & D. R. Batish (Eds.), *Invasive Plants and Forest Ecosystems* (pp. 379-407). CRC Press.

Kaiser, M. (E d.) (2001). *Die Welt in der wir leben*. Munich, Germany: Wolfgang Kunth.

Kleinbauer, I., Dullinger, S., Klingenstein, F., May, R., Nehring, S., & Essl, F. (2010). *Ausbreitungspotenzial ausgewählter neophytischer Gefäßpflanzen unter Klimawandel in Deutschland und Österreich*. Bonn, Germany: Bundesamt für Naturschutz.

Klingenstein, F., Kornacker, P. M., Martens, H., & Schippmann, U. (2005). *Gebietsfremde Arten: Positionspapier des Bundesamtes für Naturschutz (BfN-Skripten 128)*. Bonn, Germany: BMU.

Klotz, S. (2007). Prunus serotina. Retrieved from http://www.europe-aliens.org/pdf/Prunus_serotina.pdf

Kowarik, I. (1995). Time lags in biological invasions with regard to the success and failure of alien species. In P. Pyšek, K. Prach, M. Rejmanek & M. Wade (Eds.) *Plant Invasions* (pp. 15-38). SPB Academic Publishing.

Liu, C., White, M., & Newell, G. (2011). Measuring and comparing the accuracy of species distribution models with presence-absence data. *Ecography, 34,* 232-243. doi: 10.1111/j.1600-0587.2010.06354.x

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). *100 of the world's worst invasive alien species: A selection from the global invasive species database*. New Zealand: Holland Printing.

Macdonald, I. A., Kruger, F. J., & Ferrar, A. A. (1986). *The ecology and management of biological invasion in South Africa*. Cape Town, South Africa: Oxford University Press.

Mack, R. N., Simberloff, D., Mark Lonsdale, W., Evans, H., Clout, M., & Bazzaz, F. (2000). Biotic invasions: Causes, epidemiology, global consequences and control. *Issues in Ecology, 5,* 1-20.

Mannheimer, C. A., & Curtis, B. A. (Eds.) (2005). *Le Roux and Müller's field guide to the trees & shrubs of Namibia*. Windhoek: Macmillan Education Namibia.

Mendelsohn, J., Jarvis, A., Roberts, C., & Robertson T. (2002). *Atlas of Namibia: A portrait of the land and its people*. Cape Town, South Africa: New Africa Books.

Mingyang, L., Yunwei, J., Kumar, S., & Stohlgren, T. J. (2008). Modeling potential habitats for alien species *Dreissena polymorpha* in continental USA. *Acta Ecologica Sinica, 28*(9), 4253-4258

Nuñez, M. A., & Medley, K. A. (2011). Pine invasions: Climate predicts invasion success; something else predicts failure. *Diversity and Distributions, 17*, 703-713.

O'Donnell, M. S., & Ignizio, D. A. (2012). *Bioclimatic predictors for supporting ecological applications in the conterminous United States*. Reston, VA: U.S. Geological Survey.

Orwa C., Mutua, A., Kindt, R., Jamnadass, R., & Simons, A. (2009). *Agroforestree database: A tree reference and selection guide* (version 4.0). Retrieved from http://www.worldagroforestry.org/resources/databases/agroforestree

Parolo, G., Rossi, G., & Ferrarini, A. (2008). Toward improved species niche modelling: *Arnica Montana* in the Alps as a case study. *Journal of Applied Ecology, 45,* 1410-1418. doi: 10.1111/j.1365-2664.2008.01516.x

Pasiecznik, N. M., Harris, P. J. C., & Smith, S. J. (2004). *Identifying tropical* Prosopis *species: A field guide*. Coventry, UK: HDRA.

Pearson, R. G. (2007). *Species' distribution modeling for conservation educators and practitioners*. American Museum of Natural History.

Perrings, C. (2005) *Biological invasions and poverty*. Tempe: Arizona State University.

Phillips, S. J. (2011). A brief tutorial on Maxent. Retrieved from http://www.cs.princeton.edu/~schapire/maxent/tutorial/tutorial.doc

Phillips, S. J., & Dudík, M. (2008). Modeling of species distribution with Maxent: New extensions and a comprehensive evaluation. *Ecography, 31,* 161-175.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modelling of species geographic distributions. *Ecological Modelling, 190*, 231-259.

Phillips, S. J., Dudík, M., & Schapire, R. E. (2004). *Proceedings of the Twenty-First International Conference on Machine Learning: A maximum entropy approach to species distribution modelling*. 655-662

Pimentel, D., Lach, L., Zuniga, R., & Morrison, D. (2005). Environmental and economic costs of nonindigenous species in the United States. *BioScience, 50*(1), 53-65.

Pimentel, D., McNair, S., Janecka, J., Wightman, J. Simmonds, C., O'Connell, C., … Tsomondo, T. (2001). Economic and environmental threats of alien plant, animal, and microbe invasion. *Agriculture, Ecosystems and Environment, 84*, 1-20.

R Core Team (2014). R: A language and environment for statistical computing (version 3.1.0) [Computer software]. Vienna, Austria R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distribution: Complexity, overfitting and evaluation. *Journal of Biogeography, 41*, 629-643. doi:10.1111/jbi.12227

Raes, N., & ter Steege, H. (2007). A null-model for significance testing of presence-only species distribution models. *Ecography, 30*, 727-736.

Rupprecht, F., Oldeland, J., & Finckh, M. (2011). Modelling potential distribution of the threatened tree species *Juniperus oxycedrus*: How to evaluate the predictions of different modelling approaches? *Journal of Vegetation Science, 22,* 647-659.

Seitz, B., & Nehring, S. (2013). *Naturschutzfachliche Invasivitätsbewertung* Prunus serotina – *Späte Traubenkirsche*. Bonn, Germany: Bundesamt für Naturschutz.

Shine, C., Williams, N., & Gündling, L. (2000) *A guide to designing legal and institutional frameworks on alien invasive species*. Gland, Switzerland and Cambridge, United Kingdom: IUCN.

Smit, P. (2005). *Geo-ecology and environmental change: An applied approach to manage* Prosopis-*invaded landscapes in Namibia*. Windhoek, Namibia: UNAM.

Smit, P., & Steenkamp, C. (2003). Namibia. In I. A. W. Macdonald, J. K. Reaser, C. Bright, L. E. Neville, G. W. Howard, S. J. Murphy & G. Preston (Eds.), *Invasive alien species in southern Africa: National reports & directory of resources* (pp. 40-44). Cape Town, South Africa: Global Invasive Species Programme.

Starfinger, U. (2010). *NOBANIS – Invasive Alien Species Fact Sheet – Prunus serotina*. Retrieved from www.nobanis.org

Thuiller, W., Midgley, G. F., Hughes, G. O., Bomhard, B., Drew, G., Rutherford, M. C., & Woodward, F. I. (2006). Endemic species and ecosystem sensitivity to climate change in Namibia. *Global Change Biology, 12,* 759-776. doi: 10.1111/j.1365-2486.2006.01140.x

USDA NRFC (2014). *Prunus serotina*. Retrieved from http://plants.usda.gov/core/profile?symbol=PRSE2

Václavík, T., & Meentemeyer, R. K. (2009). Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions? *Ecological Modelling, 220,* 3248-3258.

Van Wyk, B., & Van Wyk, P. (2011). *Field guide to trees of southern Africa* (15th ed.). Cape Town, South Africa: Struik Nature.

Veloz, S. D. (2009). Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography, 36*, 2290-2299.

Weber, E. (2003). *Invasive plant species of the world: A reference guide to environmental weeds*. Germany: University of Potsdam.

Wells, M. J., Balsinhas, A. A., Joffe, H., Engelbrecht, V. M., Harding, G., & Stirton, C. H. (1986). *A catalogue of problem plants in southern Africa incorporating the national weed list of South Africa*. Pretoria, South Africa: Botanical Research Institute.

Wilson, P. D., Downey, P. O. Leishman, M., Gallagher, R., Hughes, L., & O`Donnell, J. (2009). Weeds in a warmer world: predicting the impact of climate change on Australia’s alien plant species using MaxEnt. *Plant Protection Quarterly, 24*(3), 84-87.

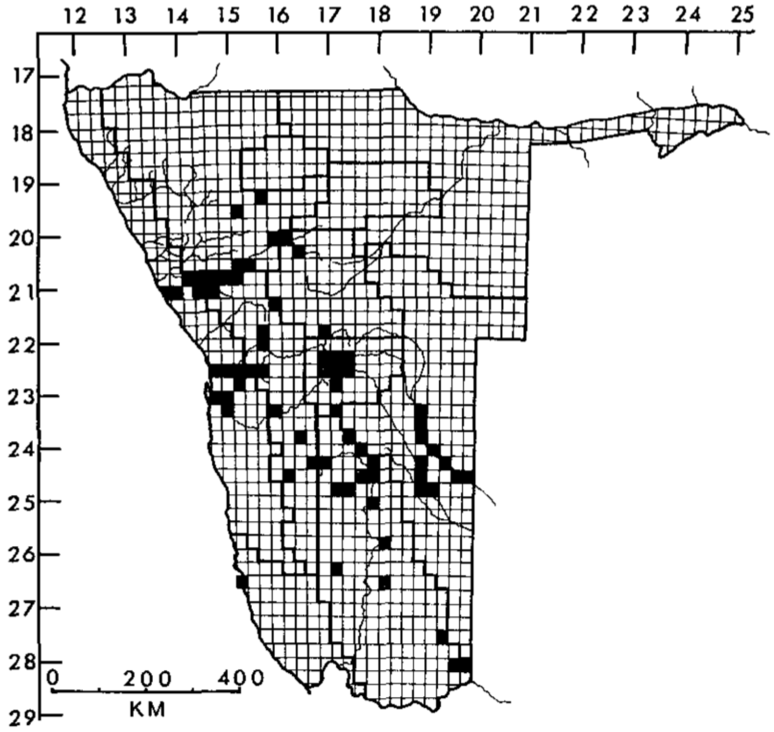
De Wit, M. P., Crookes, D. J., & Van Wilgen, B. W. (2001). Conflicts of interest in Environmental management: Estimating the costs and benefits of a tree invasion. *Biological Invasions, 3*, 167-178.

Young, N., Carter, L., & Evangelista, P. (2011). A MaxEnt Model v3.3.3e tutorial (ArcGIS v10). Retrieved from http://ibis.colostate.edu/WebContent/WS/ColoradoView/TutorialsDownloads/A_Maxent_Model_v7.pdf

Zentralverband Gartenbau e.V. (2008). Umgang mit invasiven Arten: Empfehlungen für Gärtner, Planer und Verwender.

Appendices

A1: Map of *Prosopis* spp in Namibia from Brown, Macdonald, & Brown, 1985.



A2: Menu sequences in ArcGIS 10.2.2 in the order they were descripted in the methodology section.

1) Export of raster file to different raster format:

- Right click on layer > Data > Export Data

2) Joining table with raster file:

- Right click on raster file > Join and Relates > Join, keep only matching records

3) Clipping certain extend of an area:

- ArcToolbox > Data Management Tools > Raster > Raster Processing > Clip

4) Separating raster files according to certain attributes:

- ArcToolbox > 3D Analyst Tools > Raster Reclass > Lookup > Lookup field, e.g. pH

5) Resampling to ensure the same raster cell size:

- ArcGIS Map 10.2.2: ArcToolbox > Data Management Tools > Raster > Raster Processing > Resample
- Environments Settings > Processing Extent and Raster Analysis

6) Sample by buffered local adaptive convex-hull:

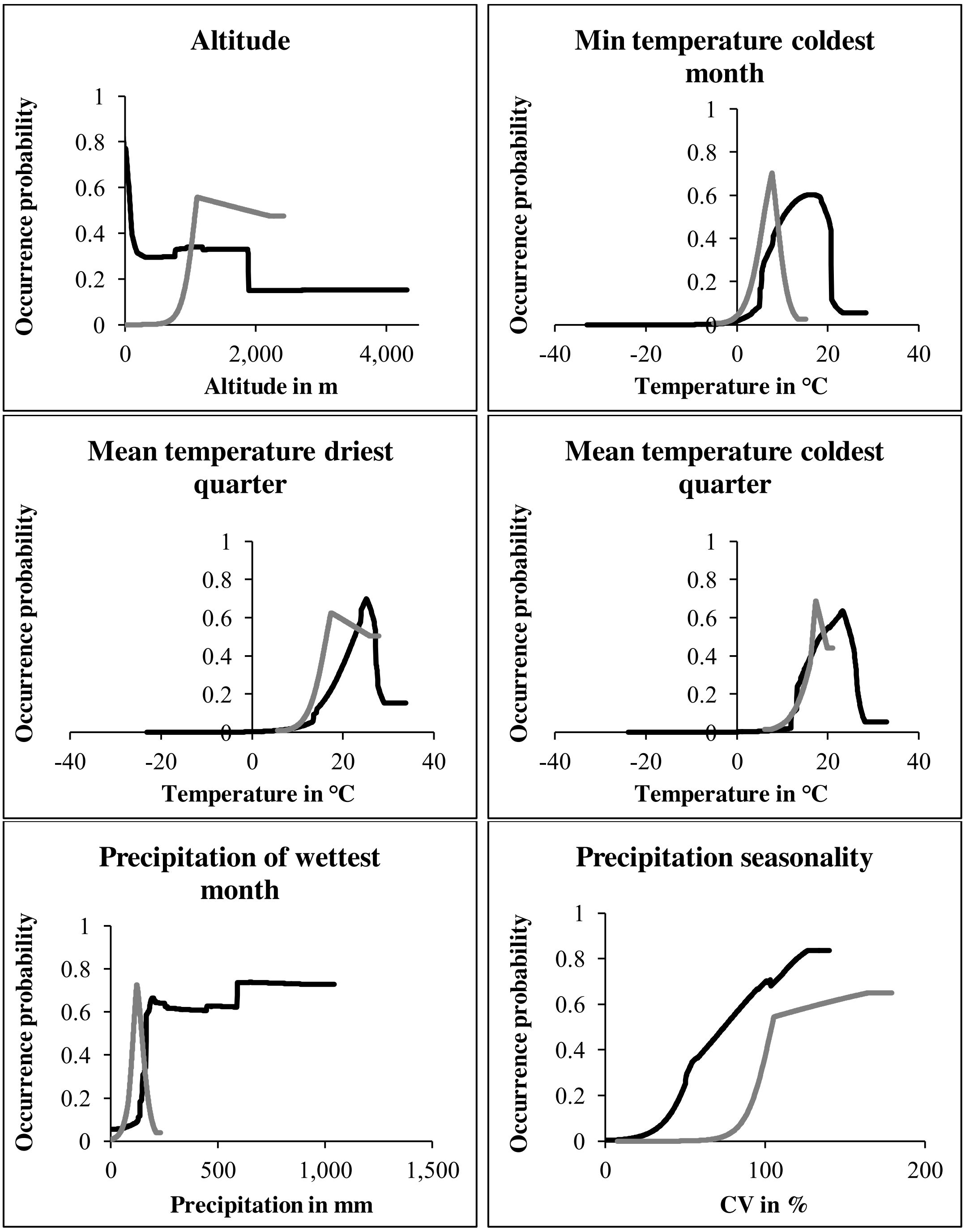
- Arc Toolbox > SDM Toolbox v1.0b > SDM Tools > Background Selection via Bias Files > Sample by Buffered Local Adaptive Convex-Hull

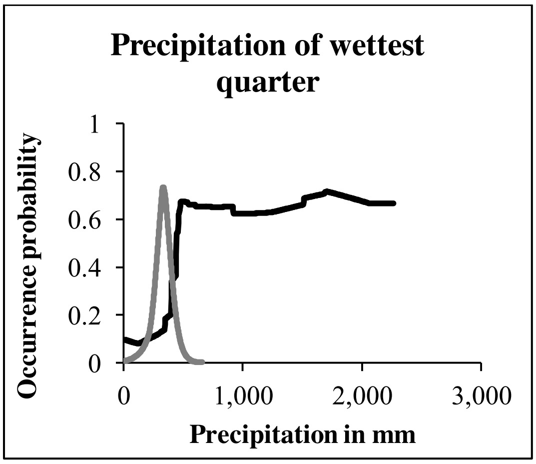
A3: Command lines to remove duplicated or false occurrence points in R.

```
#species table in ".csv" format with three columns: species, longitude and latitude

#loading the table “example”
example <- read.csv("~/path/to/file/example.csv)

#getting amount of duplicated records in columns longitude and latitude
duplicates <- duplicated(example [, c(‘longitude’, ‘latitude’)])
sum(duplicates)

#removing duplicates from table
example <- example[!duplicates,]

#removing points were longitude or latitude is 0
lonzero = subset(example, longitude==0)
example <- example[!lonzero,]

latzero = subset(example, latitude==0)
example <- example[!latzero,]

#removing points without any geographic reference (lon or lat is ‘NA’)
example <- subset(example, !is.na(longitude) & !is.na(latitude)

#save data
write.csv (example, file=”/path/to/file/example.csv”)
```

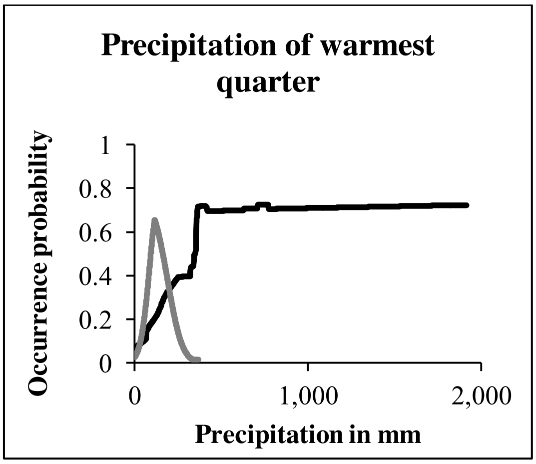
A4: Response curves for models of *Leucaena leucocephala*.

Model “Donor LL” (black) and “Host 1 LL” (grey):



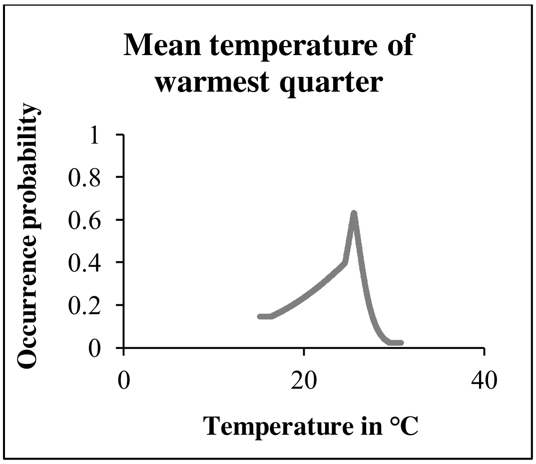


Precipitation of wettest quarter

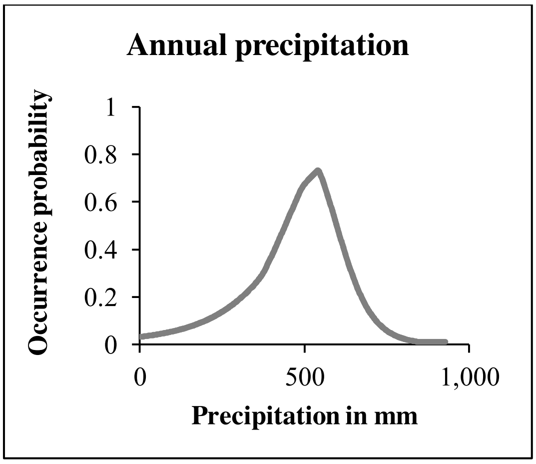


Precipitation of warmest quarter

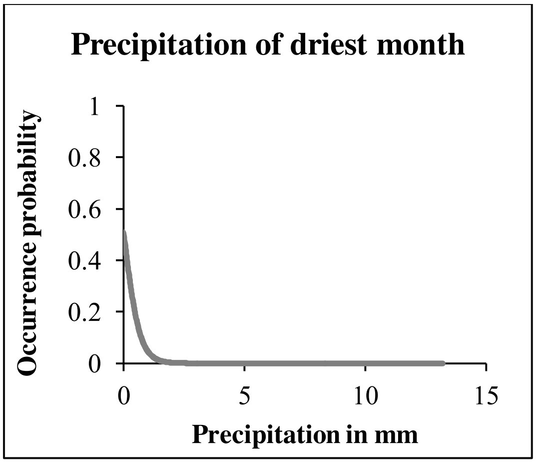
Model “Host 2 LL”:



Mean temperature of warmest quarter



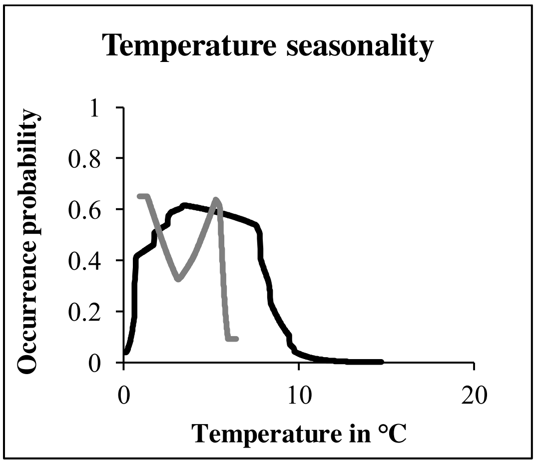
Annual precipitation

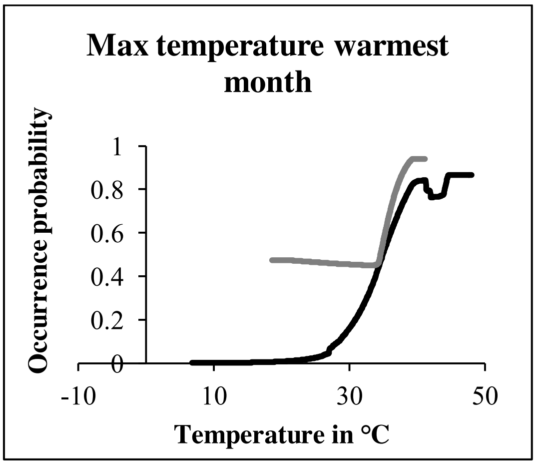


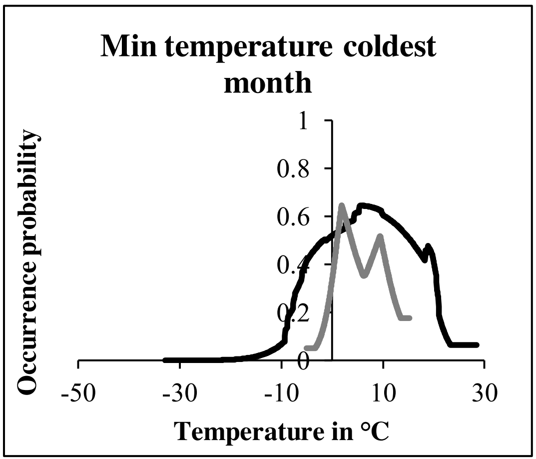
Precipitation of driest month

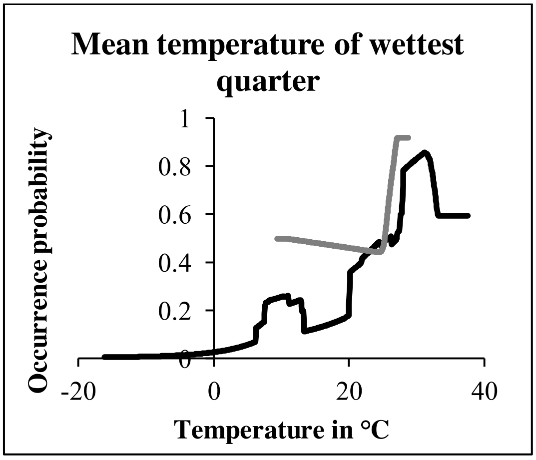
A5: Response curves for models of *Prosopis* spp.

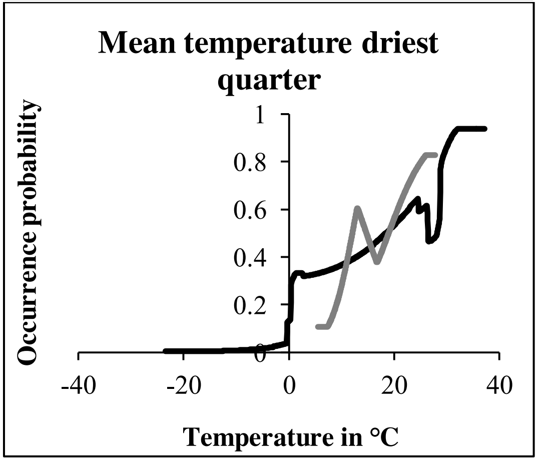
Model “Donor PSPP” (black) and “Host 1 PSPP” (grey):

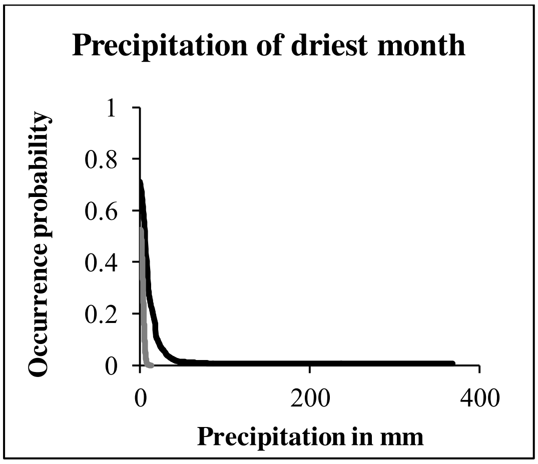


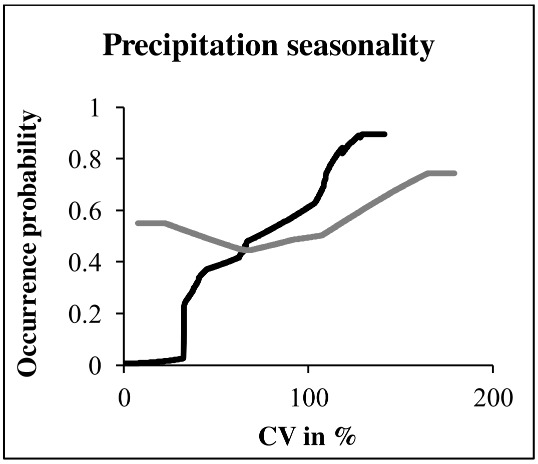


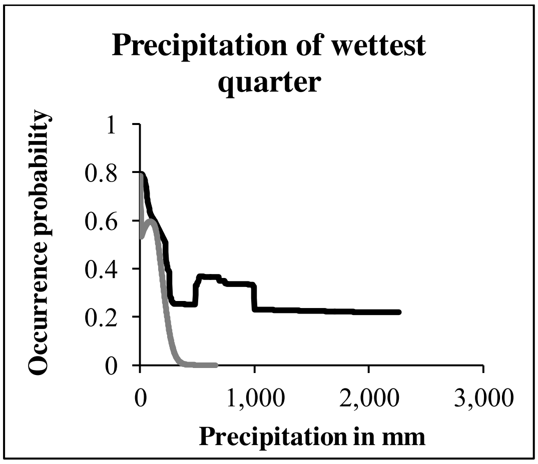




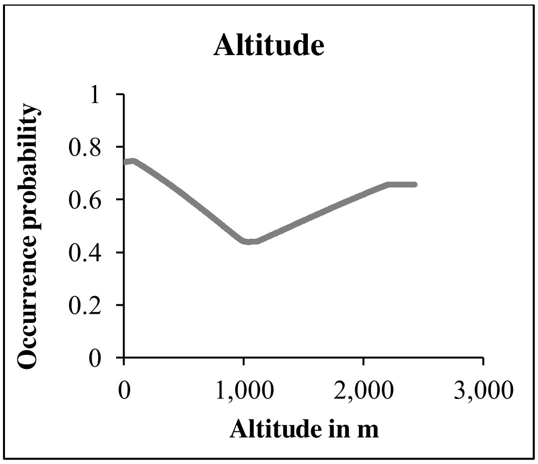


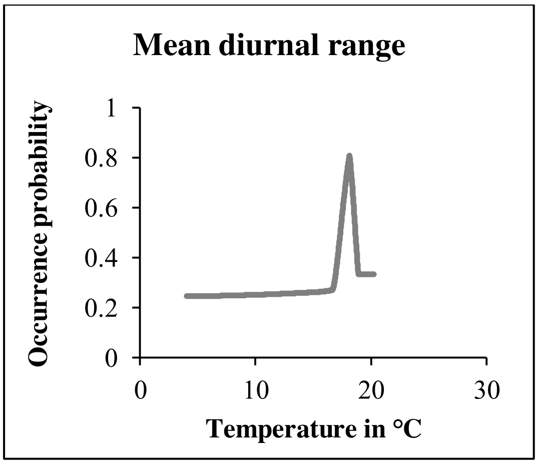


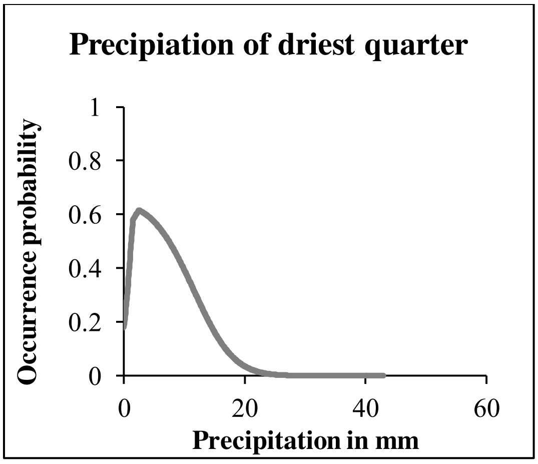


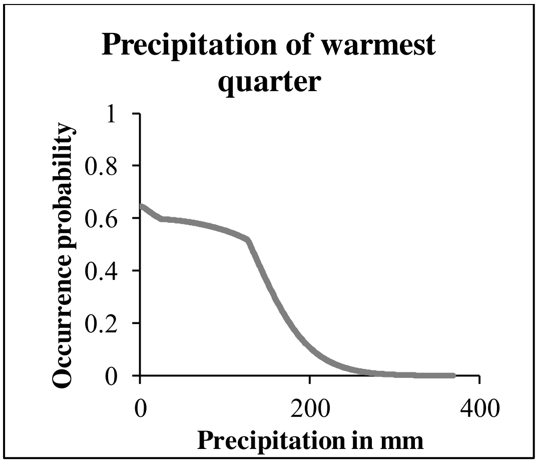


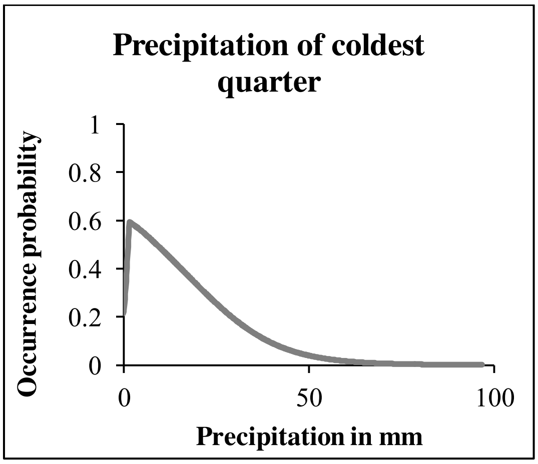
Model “Host 2 PSPP”:





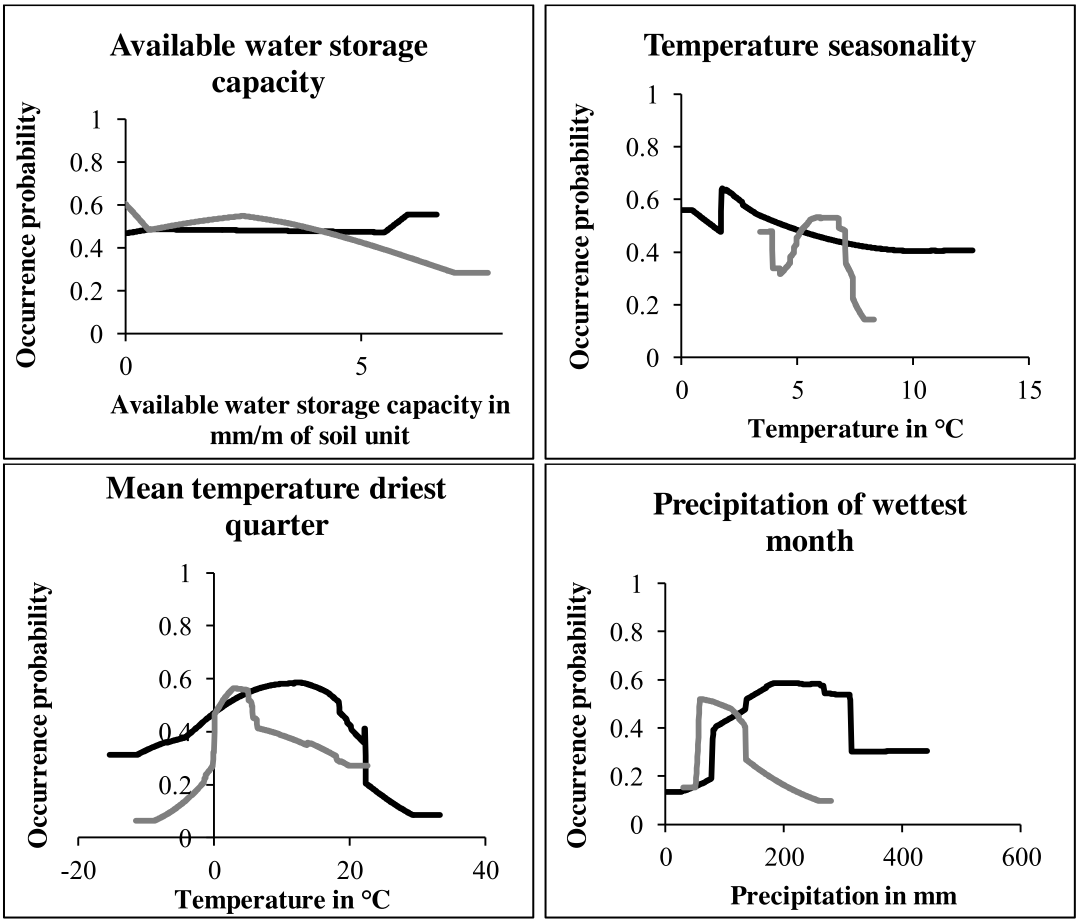


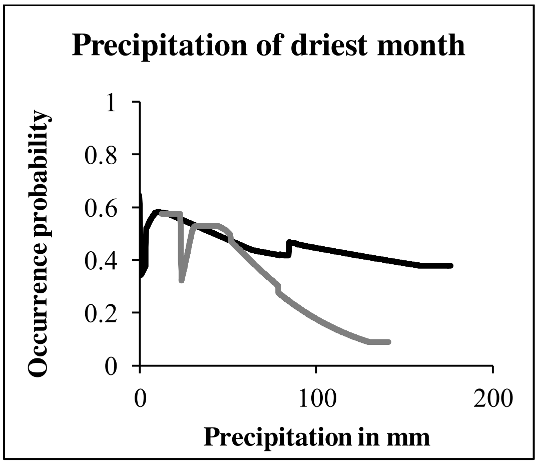


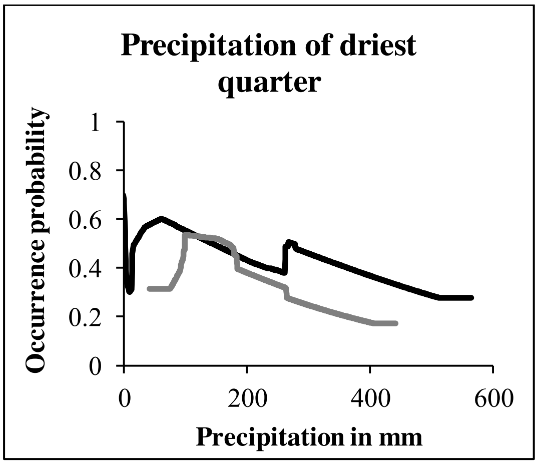


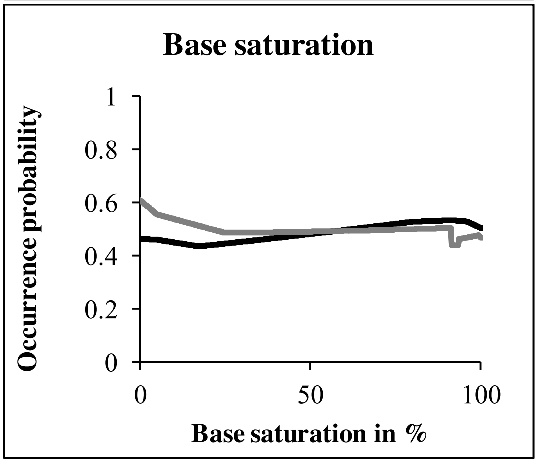
A6: Response curves for models of *Prunus serotina*.

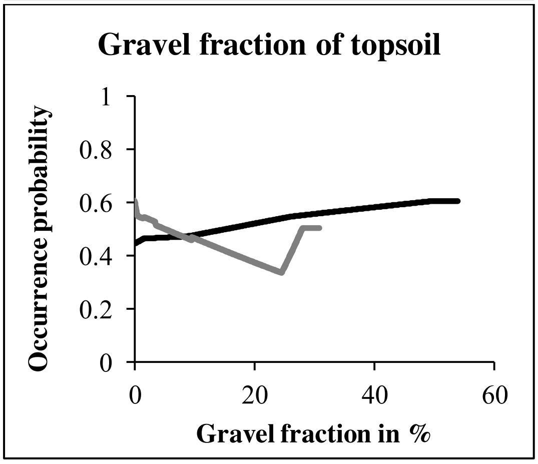
Model “Donor PS” (black) and “Host 1 PS” (grey):



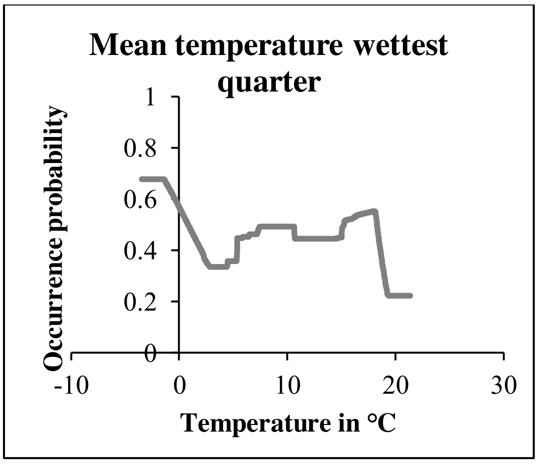

Precipitation of driest month

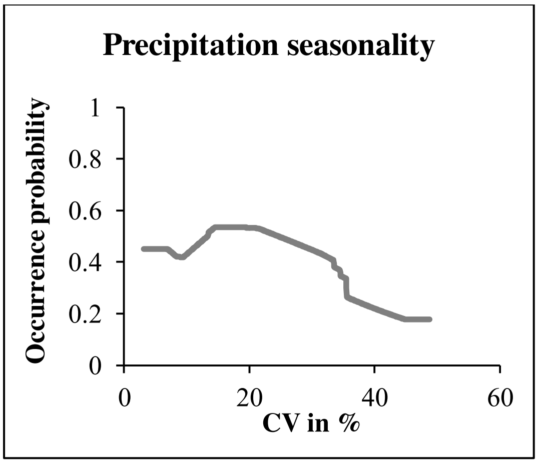

Precipitation of driest quarter

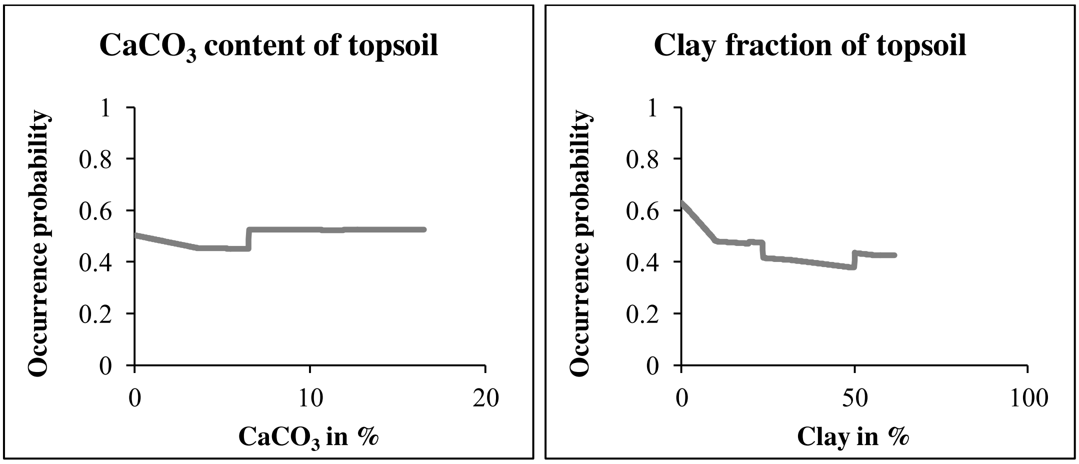

Base saturation


Gravel fraction of topsoil

Model “Host 2 PS”:

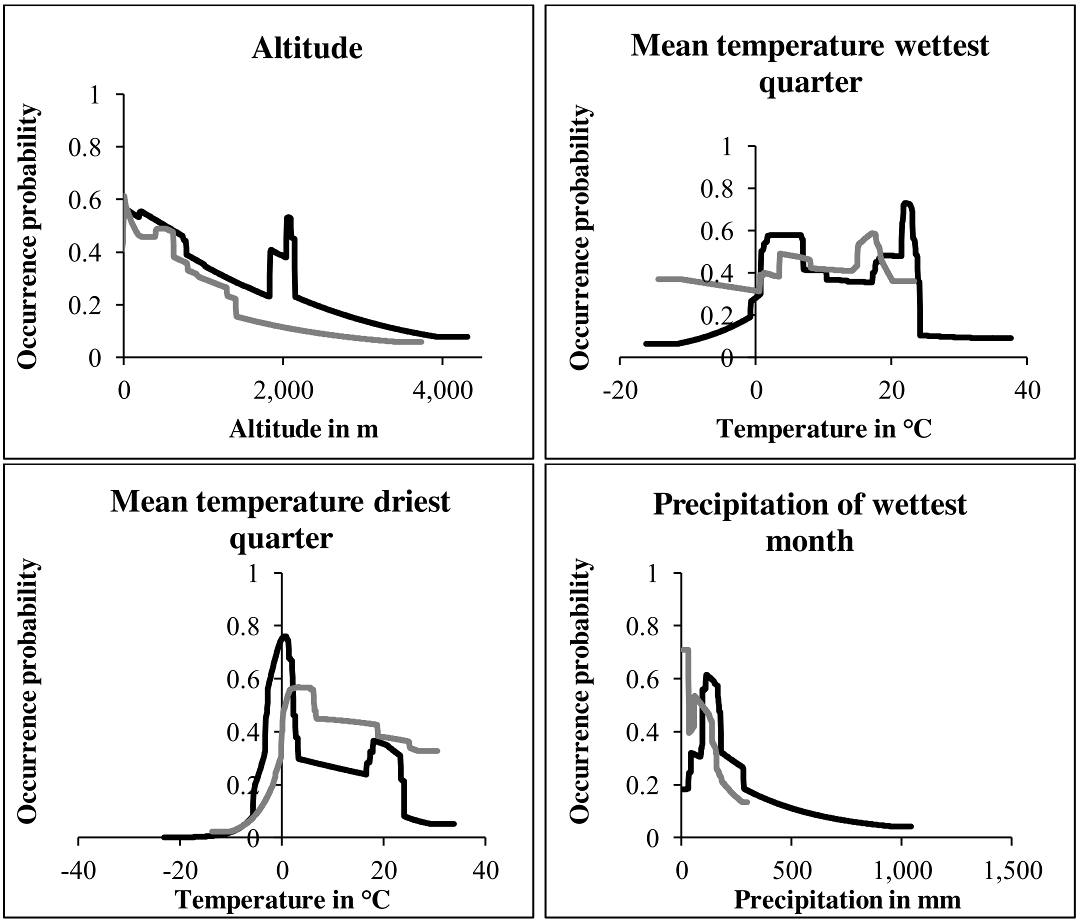

Mean temperature wettest quarter

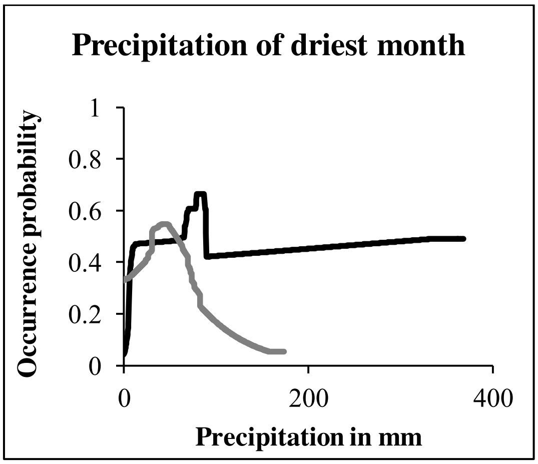

Precipitation seasonality

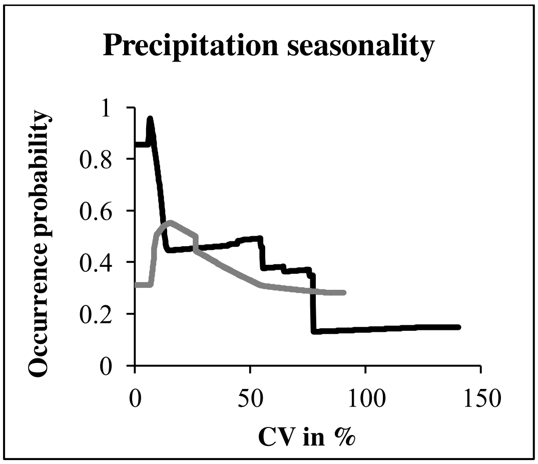


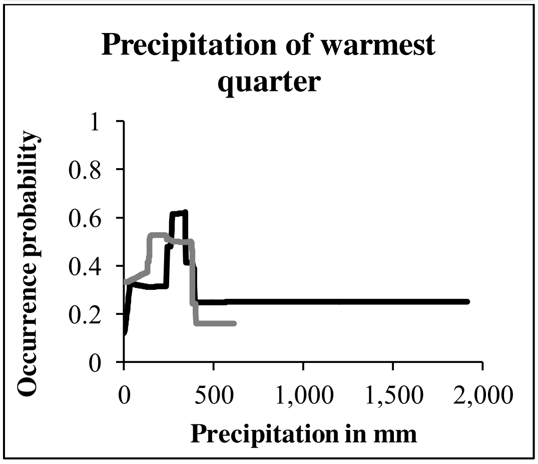
A7: Response curves for models of *Robinia pseudoacacia*.

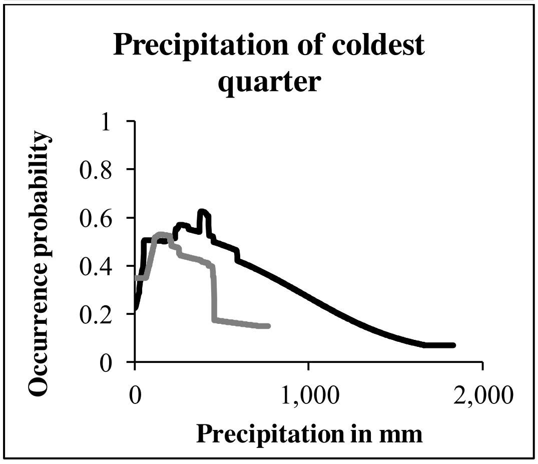
Model “Donor RP” (black) and “Host 1 RP” (grey):



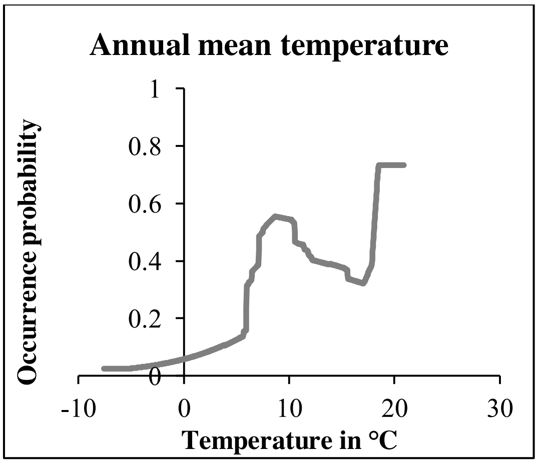


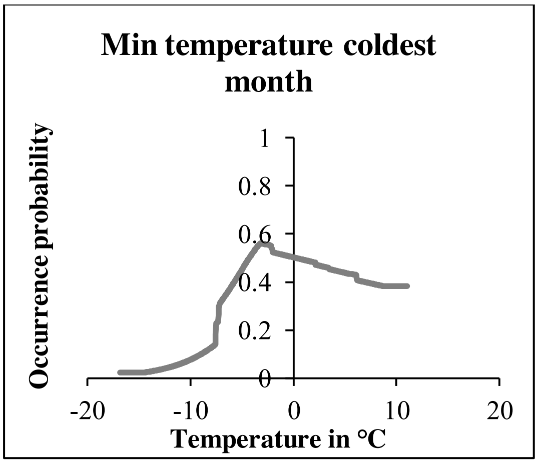


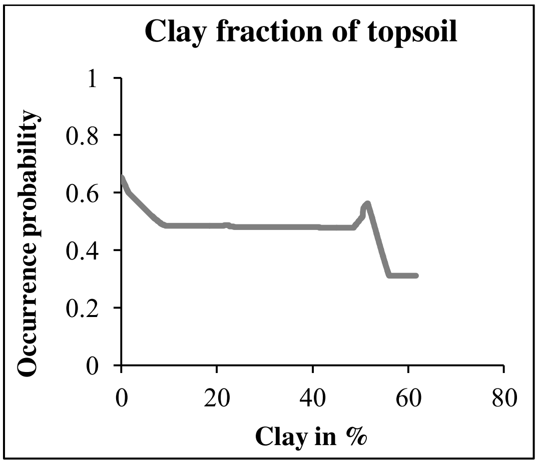


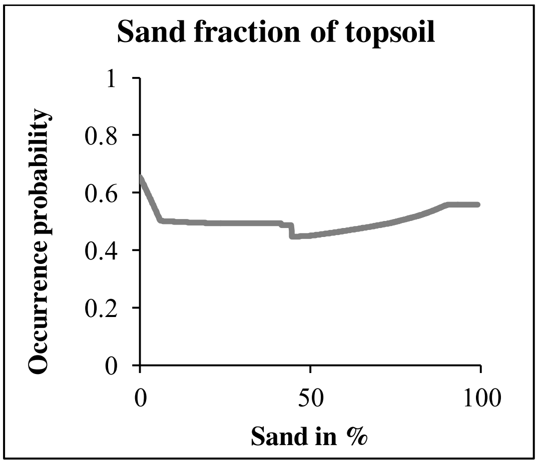


Model “Host 2 RP”:






Clay fraction of topsoil
Occurrence probability
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
Clay in %


Sand fraction of topsoil
Occurrence probability
1
0.8
0.6
0.4
0.2
0
0
50
100
Sand in %