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Modelling the distribution of the moss species *Hypopterygium tamarisci* (Hypopterygiaceae, Bryophyta) in Central and South America

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With 11 figures and 3 tables

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Abstract: The pleurocarpous moss *Hypopterygium tamarisci* is widely distributed in Africa, S and SE Asia, Australasia, Oceania, as well as South and Central America, where it extends into Mexico and the Caribbean. It is a species of mainly mountainous tropical and warm temperate areas. The present study focuses on the actual and the potential distributions of *H. tamarisci* in the New World south of the Tropic of Cancer. It aims to find ecological conditions for this area that determine the distribution of this species by making use of species distribution modelling techniques. We use a data set from verified herbarium specimens and a set of collection records downloaded from the GBIF (Global Biodiversity Information Facility) database. The potential distribution models of *H. tamarisci* were developed with Maxent (Phillips et al. 2006) based on the collection datasets and a set of uncorrelated bioclimatic and edaphic variables. The predicted distribution of the species matches the actual collecting localities very well. A maximum temperature below 29°C in the warmest month is the most important ecological variable that determines the presence of *H. tamarisci*. Second most important variable is the precipitation in the warmest quarter, for which *H. tamarisci* shows an increasing probability of presence under wetter conditions. The models predict the potential occurrence of the species in the Guiana Highlands, where the species does not occur. Several explanations for this mismatch are being discussed, but a satisfactory explanation is wanting.

Keywords: Autecology, bioclimatic variables, Caribbean, Central America, distribution modelling, edaphic variables, Guiana Highlands; *Hypopterygium tamarisci*, South America.

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Introduction

The genus *Hypopterygium* Brid. comprises 7 to 9 species (Kruijer & Blöcher 2007; Shaw et al. 2008) and is the largest genus of the small pleurocarpous moss family Hypopterygiaceae Mitt. The mainly pantropical to warm-temperate species *Hypopterygium tamarisci* (Sw.) Brid. ex Müll.Hal. is the most widespread species of both the genus and the family and is indigenous in the New World, Africa, Asia, Australasia, and Oceania (Pfeiffer et al. 2000; Kruijer 2002), which reflects a Gondwanan origin. The species has been introduced to Europe (Kruijer 1997, 2002, and references therein; Stech & Pfeiffer 2006).

Hypopterygium tamarisci occurs in dry to wet forests, where it grows in moist or wet places, most frequently near streams or in partially to fully shaded habitats (Kruijer 2002). The beautiful plants (gametophores) are dendroids, fans, or intermediate forms and grow in terrestrial, epilithic, epiphytic, or epixylic colonies on various substrates with various angles of inclination. The altitudinal distribution varies from 600–3160 m in the Neotropics and 0–4160 m in the Palaeotropics to 0–1550 m in (warm-)temperate areas (here including SE Brazil and adjacent areas; Kruijer 2002). Although *H. tamarisci* is widely distributed in the Tropics to warm-temperate areas of the world, it is not evenly distributed in these areas. Being predominantly a species of forests in humid climates, it is, of course, absent from deserts and semi-arid areas, with the occasional exception of a few caves and other moist, sheltered environments in arid parts of eastern Australia (Downing et al. 1997, Kruijer 2002). The species, however, is also mainly absent from tropical lowlands (e.g., Amazon basin, Congo basin) and few tropical highlands that seem to fall within distribution area of the species (e.g., Guiana Highlands, highlands of Central and NE Brazil; Kruijer 2002).

The species show great morphological variability. Truly dendroid (umbellate) plants are probably confined to horizontal substrates and true fans to nearly vertical substrates, whereas intermediate forms occur on substrates with other angles of inclination. Regional and some ecological variation is especially observed in life form, size, costa length, and number and morphology of the axillary hairs. Much variation was observed to occur in sexuality (Pfeiffer et al. 2000, Kruijer 2002). Monoicous plants predominate, but dioicous ones are common. Herbarium specimens may contain both monoicous and dioicous gametophores (occasionally both even attached). In monoicous material, the frequency of unisexual (male, female) and bisexual gametoecia varies considerably between specimens and gametophores.

However, molecular evidence based on *trnL* intron (Pfeiffer et al. 2000) or *trnL* intron and ITS2 (Stech et al. 2002) sequences showed that the regional forms are grouped in a single, well-supported clade, albeit that in most molecular phylogenetic reconstructions *H. discolor* Mitt. is included in the *H. tamarisci* clade. Pfeiffer et al. (2000) concluded that the observed molecular differences between the regional forms of *H. tamarisci* can be considered as 'normal' variation within a single species and proposed an artificial classification in seven informal regional variants to classify the morphological variability of the species. This classification was adopted by Kruijer (2002) and is followed here.

Subject of this paper is *H. tamarisci* in the New World, represented by Pfeiffer et al.'s (2000) 'New World' variant, the only representative of the species that occurs there. The paper focuses on the actual and the potential distributions of *H. tamarisci* in the New World and aims to find ecological conditions that determine its distribution in the New World south of the Tropic of Cancer (23.5°N).

Based on the material examined by Kruijer (2002) and additional specimens examined for this study, *H. tamarisci* occurs in there in southern North America (Mexico: Vera Cruz, Chiapas), Central America (Guatemala; Costa Rica; Panama), the Caribbean (Cuba; Jamaica; Haiti; Dominican Republic; Martinique), and South America (Colombia; Venezuela; Ecuador; Peru; Bolivia; Paraguay; Brazil: Minas Geraïs, Rio de Janeiro, São Paolo, Paraná, Santa Catarina, Rio Grande do Sul; Uruguay; Argentina: Salta, Tucumán, Buenos Aires; Chile: Chiloé). Sharp et al. (1994) reported the species also from the Mexican States Hidalgo, Oaxaca, Puebla, San Luis Potosí, and Tamaulipas, and Kindberg (1901) and Britton (1913) from Puerto Rico. The species is not known from the Lesser Antilles (except Martinique), the Guyanas, the Guiana Highlands and Llanos in Venezuela and Colombia, the lowlands of the Amazon basin, the highlands of Central and NE Brazil, and the Gran Chaco (Kruijer 2002).

According to Kruijer (2002), *H. tamarisci* occurs in the New World in various forest types, varying from subtropical rainforest to open upper montane rainforest and from broad-leaved forest to coniferous forests. The altitudinal distribution varies from 600–1950 m in Central America and the Caribbean to 700–3160 m in the Andes and 20–1350 m in SE Brazil and adjacent areas. The observed morphological variation in specimens of *H. tamarisci* from the New World, e.g., in size of the plants, was not correlated with ecological factors obtained from label information. Plant size, however, show some correlation with geography. Plants up to 4.5 cm tall occur throughout the distribution area in the Americas, whereas plants of 4.5–5.5 cm tall occur frequently in the Caribbean, the Andes, and SE Brazil and adjacent areas, and are less common in Central America. Most striking is the variability in capsule size. Small and large capsules, respectively up to 1.0 mm long and 0.8 mm wide or longer than 1.0 mm long and 0.8 mm wide, may be present in a single specimen, but the majority of the fruiting plants, from throughout the distribution area, have small capsules. Plants with large capsules, however, are most frequently found in the Andes and SE Brazil and adjacent areas.

To predict the potential distribution of *H. tamarisci* we use species distribution models (SDMs). Species distribution modelling has attracted much research attention over the last decade (for a comprehensive overview see Araújo & Guisan 2006, Peterson 2006, Elith & Leathwick 2009) and has in a few occasions been used to model the distribution of mosses (Sérgio et al. 2007). SDMs predict the potential distribution of a species by interpolating identified relationships between presence/absence or presence-only data of a species on one hand and environmental predictors on the other hand across an area of interest (Elith et al. 2006). The accuracy of an SDM, therefore, highly depends on the environmental predictors that are used to model a species' distribution or habitat suitability and should capture the ecological niche of a species. From the suite of different available applications, Maxent (Sérgio et al. 2007, Elith et al. 2006, Phillips et al. 2006) stands out, because it also performs a

jackknife analysis of variable importance. With this tool it is possible to identify which environmental variables contribute most to the predicted distribution of a species. Simultaneously, Maxent produces response curves that plot the probability of presence against the range of values of an individual environmental predictor. Identification of the most important predictors, and the analysis of the relations between the predictors and (predicted) habitat suitability, allows the description of the autecology of a species (defined here as the biological relationship between a species and its environment). Using this methodology we analyse the autecology of *H. tamarisci* and attempt to explain why this species is missing from certain regions.

Material and methods

Species records: We used two sets of collection records. The first set is compiled by Kruijer, based on data from 382 herbarium specimens of the 'New World' variant of *H. tamarisci*, of which 341 were examined for Kruijer's (2002) revision and 41 were identified later, that are preserved in the following institutional herbaria (abbreviations follow Holmgren et al. 1990): BM, BR, COI, F, G, GRO, HBG, L, MEL, NMW, NY, PC, RO, S, TDC, U, UPS, W, Z, and ZT. The additional material include specimens that are preserved in Frahm's personal herbarium (BONN). The co-ordinates of collecting localities were obtained using information written or printed on the labels of the specimens in combination with various sources of information, including 'The Times Atlas of the World' (mid-century edition, vols. 1–5, 1955–1959; comprehensive editions, 1967, 1992), the United States Office of Geography's 'Official Standard Names' gazetteer volumes for the various countries (1952–74, and 1999–2009 internet versions, now (Dec. 2009) to be obtained by logging on to the GEOnet Names Server (GNS) of the US National Geospatial-Intelligence Agency (earth-info.nga.mil/gns/html/index.html), Google Maps (maps.google.com) and Google Earth (earth.google.com), and various other atlases, maps (e.g., in Herzog 1916), and local internet information. In determining the co-ordinates of a collecting locality an uncertainty of 10 km was accepted; in most cases the obtained accuracy was higher. Specimens of which the collecting locality are not known have consequently been omitted from the analyses (e.g., Perrotet s.n., unknown coll. s.n.; BR, both from Martinique). This resulted in (only) 133 unique and validated records of *H. tamarisci* (Fig. 1).

The second set comprised the records of the first set supplemented with collection records downloaded from the GBIF (Global Biodiversity Information Facility) database (www.gbif.org; downloaded 2009/12/16) totalling 450 records. This data set does include some duplicates but the distribution model developed by Maxent (see below), was set to remove these records. This dataset comprises 313 unique records (Fig. 3).

Bioclimatic data: To model the distribution of *H. tamarisci*, we first defined the study area as the New World south of the Tropic of Cancer. To relate the occurrence records of *H. tamarisci* with abiotic conditions, we downloaded the 19 bioclimatic variables, and the altitudinal data from the WorldClim database at 5 arcmin (~100 km^2 at the equator) resolution (www.worldclim.org) (Hijmans et al. 2005). To this set of climate data we added the variable 'FAO07 - Length of available growing period (16 classes)' downloaded from the FAO GeoNetwork (www.fao.org/geonetwork/srv/en/main.home). Since we modelled a species that is also epiphytic/epilithic, we also included a data layer on the potential evapotranspiration (PET). We used the following equation to estimate the PET ratio: the mean annual biotemperature (°C) divided by total annual precipitation (mm); this ratio is then multiplied by an empirically derived constant of 60 (Loiselle et al. 2008). The total list of bioclimatic variables that were considered to model the distribution is given in Table 1.

To avoid problems with multicollinearity (i.e., highly correlated variables), we selected the most meaningful and uncorrelated bioclimatic variables (Pearson correlation coefficient less than 0.7 or larger than -0.7). This requirement was fulfilled for the bioclimatic variables (including altitude and potential evapotranspiration) Alt, Bio02, Bio04, Bio05, Bio12, Bio15, Bio18, and PET (Table 1).

Table 1. Abbreviations and descriptions of the 21 bioclimatic variables (19 bioclimatic variables, altitude, and potential evapotranspiration) used for modelling the distribution of *H. tamarisci*. The most meaningful and uncorrelated bioclimatic variables (see text), including altitude and potential evapotranspiration, are given in bold.

Bioclimatic variable	Description
Alt	**Altitude in m asl.**
BIO1	Annual Mean Temperature
BIO2	**Mean Diurnal Range (Mean of monthly (max temp - min temp)**
BIO3	Isothermality (P2/P7) (*100)
BIO4	**Temperature Seasonality (standard deviation *100)**
BIO5	**Max Temperature of Warmest Month**
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (P5-P6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	**Annual Precipitation**
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	**Precipitation Seasonality (Coefficient of Variation)**
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	**Precipitation of Warmest Quarter**
BIO19	Precipitation of Coldest Quarter
FAO07	Length of Available Growing Period
PET	**Potential Evapotranspiration**

Soil data: Because *H. tamarisci* also grows terrestrially, we included a set of edaphic conditions. These data were downloaded from the FAO GeoNetwork. Although the FAO data are categorical, their classes do follow a continuous scale. To prevent the use of correlated variables we used Spearman rank correlation to identify correlated variables which were subsequently omitted from the environmental data set. This was only the case for the 'FAO13 - Soil moisture storage capacity' which was correlated with 'FAO05 - Easy available water'. The selected edaphic variables are listed in Table 2.

In total we used 21 uncorrelated bioclimatic and edaphic variables to model the potential distribution of *H. tamarisci*. We only used grid cells which had data for all data layers, in total 239,987 grid cells. This means that the data layers were cropped to the continental extent of the FAO soil data and further excluding water bodies, rivers, glaciers, rock, shifting sand, and missing data. All data layer manipulations were performed with Manifold GIS (Manifold Net).

Maxent distribution model: From the variety of modelling techniques we selected Maxent (Phillips et al. 2006), because Maxent outperforms other applications (Elith et al. 2006), and is most robust for georeferencing errors (Graham et al. 2008). We ran two models, one with the verified collections (133 records; Kruijer's data), and one where we added the GBIF records totalling 450 records. Duplicate records from the same grid cell (two collections each in eight cells) were omitted from these two sets of unique records, by which procedure, respectively, 125 (Kruijer's) and 313 (Kruijer & GBIF's) unique records remained in the analyses.

We set Maxent to only use unique records. We used the ten times cross-validation option of Maxent (version 3.3.2) to test model accuracy. This means that the dataset is ten times partitioned into 90% training data and 10% test data. Model accuracy is measured by the Area Under the Curve (AUC) value (Fielding & Bell 1997). We report the average AUC value from 10 test datasets. AUC values higher

Table 2. Abbreviations and circumscriptions of the edaphic variables used for modelling the distribution of *H. tamarisci*.

Abbreviation of edaphic variable	Circumscription of edaphic variable
FAO01	Base saturation % (topsoil)
FAO02	Carbon/Nitrogen-Class (topsoil)
FAO03	CEC (Cation Exchange Capacity) clay (topsoil)
FAO04	CEC soil (topsoil)
FAO05	Easy available water
FAO06	Effective soil depth
FAO08	Nitrogen % (topsoil)
FAO09	Organic Carbon % (topsoil)
FAO10	Organic Carbon pool
FAO11	pH (topsoil)
FAO12	Soil Drainage Class
FAO14	Soil Production Index
FAO15	Textural Class (topsoil)

than 0.7 indicate reliable models, values higher than 0.8 good models (but see Raes & ter Steege 2007). Since our main interest is to identify the environmental parameters that determine the distribution of *H. tamarisci* and because all test AUC values were larger than 0.9 (see Results) we have chosen to use all collection records for the two final models.

Secondly, we performed a jackknife analysis to measure the importance of each variable to the two final distribution models. This analysis gives a heuristic estimate of relative contributions of the environmental variables to the Maxent model and is standard output of Maxent. Since we only make use of uncorrelated variables this measure is reliable to use. For the three environmental predictors that contribute most to the final model we also report the response curves. Response curves plot the predicted probability of presence for the range of values of a given predictor. The probabilities are calculated for the range values of one variable, with all other variables set to their average value over the set of presence localities.

Statistical analysis: Since the Maxent models predict that the Guiana Highlands harbour suitable habitat for *H. tamarisci* (see Results), being also the largest among the areas where suitable habitats are predicted and without records of the species, we decided to further explore where the cells representing the Guiana highlands were located in multivariate space of predicted presence. We defined the Guiana Highlands as the mountainous region crossing the borders of Guyana, Venezuela, and Brazil with an altitude higher than 250 m asl.

We first selected those variables that contributed at least 2.5% to the Maxent model of Kruijer; based on the jackknife procedure of Maxent. We chose for Kruijer's model because the two models did not differ much, and Kruijer's data is most reliable. To select the cells of predicted presence we first converted the continuous Maxent prediction to discrete presence-absence values by setting a threshold. We used the 10 percentile presence threshold, the Maxent value that excludes 10 percent of the presence records (Liu et al. 2005). Since we are familiar with the difficulties of accurate georeferencing, we consider this as a conservative but save threshold to use.

Subsequently, we performed a PCA (Principal Component Analysis) on the values of the seven most contributing variables of those gridcells for which *H. tamarisci* is predicted to be present based on Kruijer's dataset. Finally, we plotted the predicted presence localities on PC axes 1 and 2 and within this multivariate space we highlighted those gridcells that represent the Guiana Highlands and those that represent the actual 125 unique collection localities.

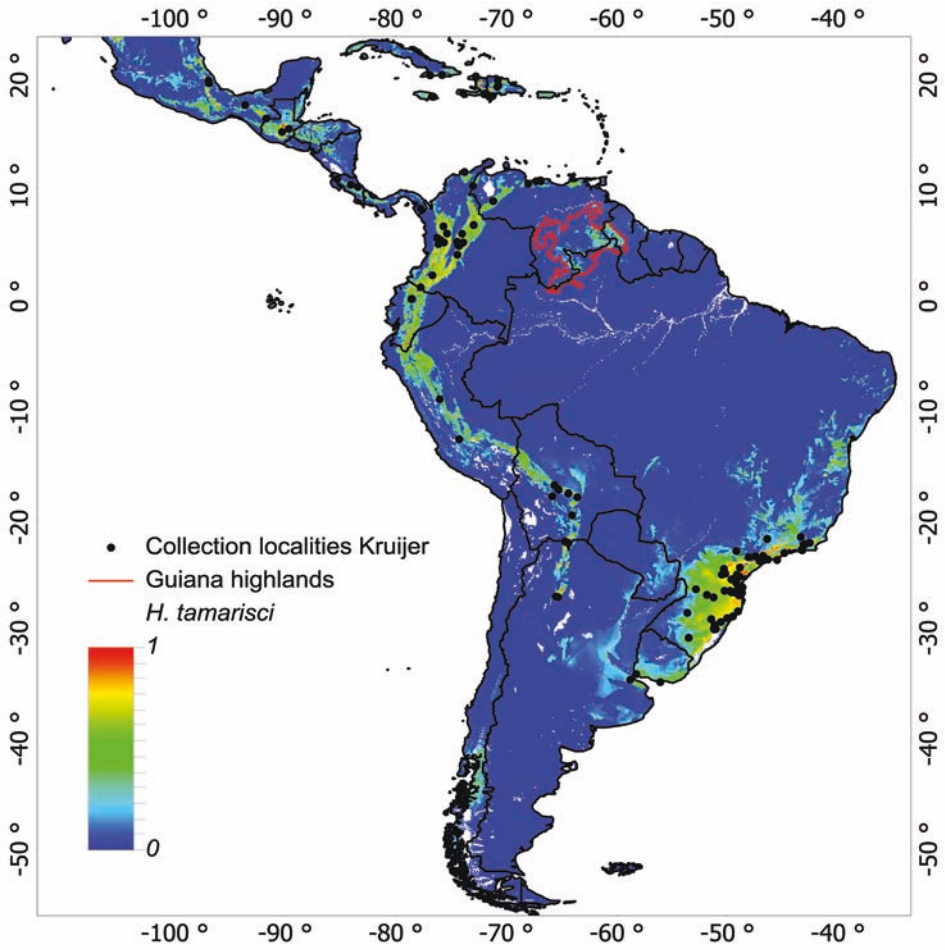


Fig. 1. Maxent distribution model for *H. tamarisci* based on 125 records from specimens identified by Kruijer (see text). Probability of presence increases from dark blue (0) to red (1). Most areas in red are obscured by the black dots representing the collection localities. The red demarcation line indicates the Guiana Highlands (above 250 m asl).

Results

Both models predict the presence localities very well. The mean AUC values based on 10 times cross-validated Maxent models based on 125 (Kruijer's) and 313 (Kruijer & GBIF's) unique records were 0.921 and 0.933, respectively. Fig. 1 shows the predicted Maxent distribution of *H. tamarisci* based on Kruijer's verified data. Model values close to 1 indicate high probability of presence. Fig. 2 shows predicted presence of the thresholded model with the predicted presence areas in grey. Similarly, the results for the model based on all 313 records are presented in Figs 3 and 4, respectively.

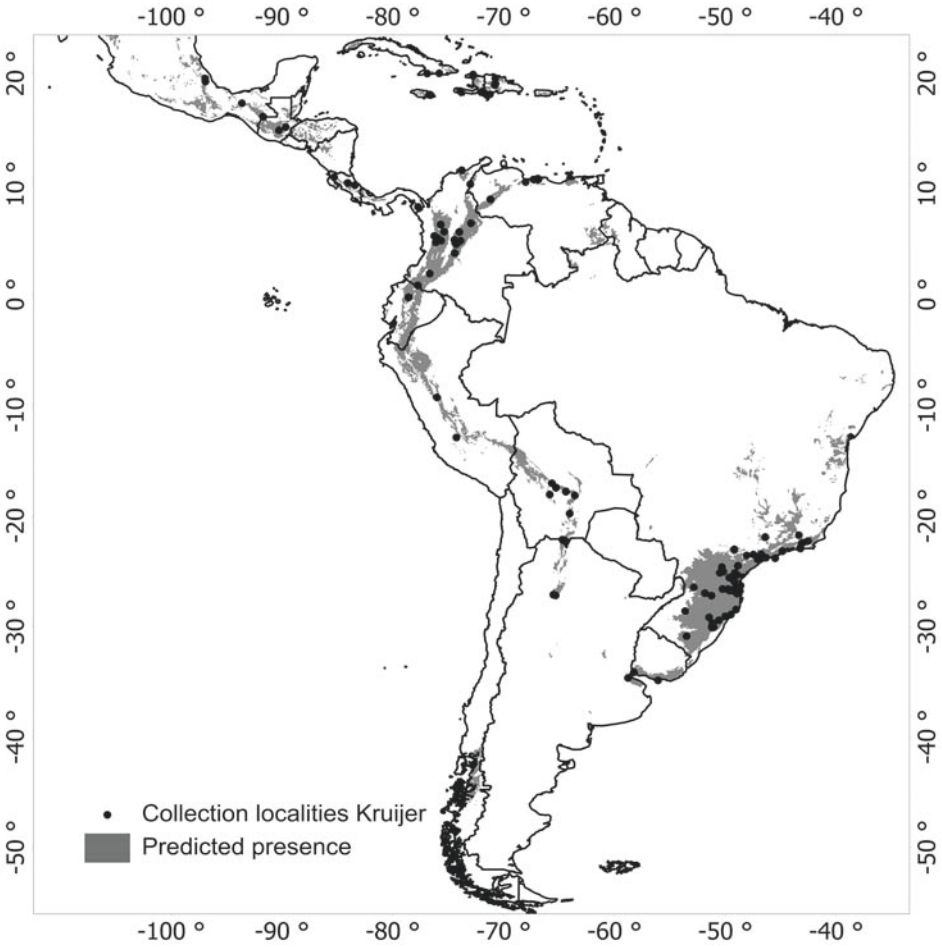


Fig. 2. Thresholded Maxent distribution model for *H. tamarisci* based on 125 records from specimens identified by Kruijer (see text). Grey areas indicate predicted presence.

The average percentages contribution and corresponding ranks for the 21 variables of the two series of 10 times cross-validated Maxent models are given in Table 3. Bio05, the maximum temperature in the warmest month, is identified as the most important variable by both models. The largest difference between the two series of models was that the model based on the combined datasets (313 records) identified altitude (Alt) as secondly most important variable (Table 3). For the model based on Kruijer's data the second most important variable was Bio18, precipitation of warmest quarter; followed by Bio12, annual precipitation. Bio18 and Bio12 have position 3 and 4 in the ranking for the model based on all records (Table 3). Because we not fully trust the georeferencing of the GBIF records that were added to this dataset, we show the environmental data and response curves for environmental variables Bio05

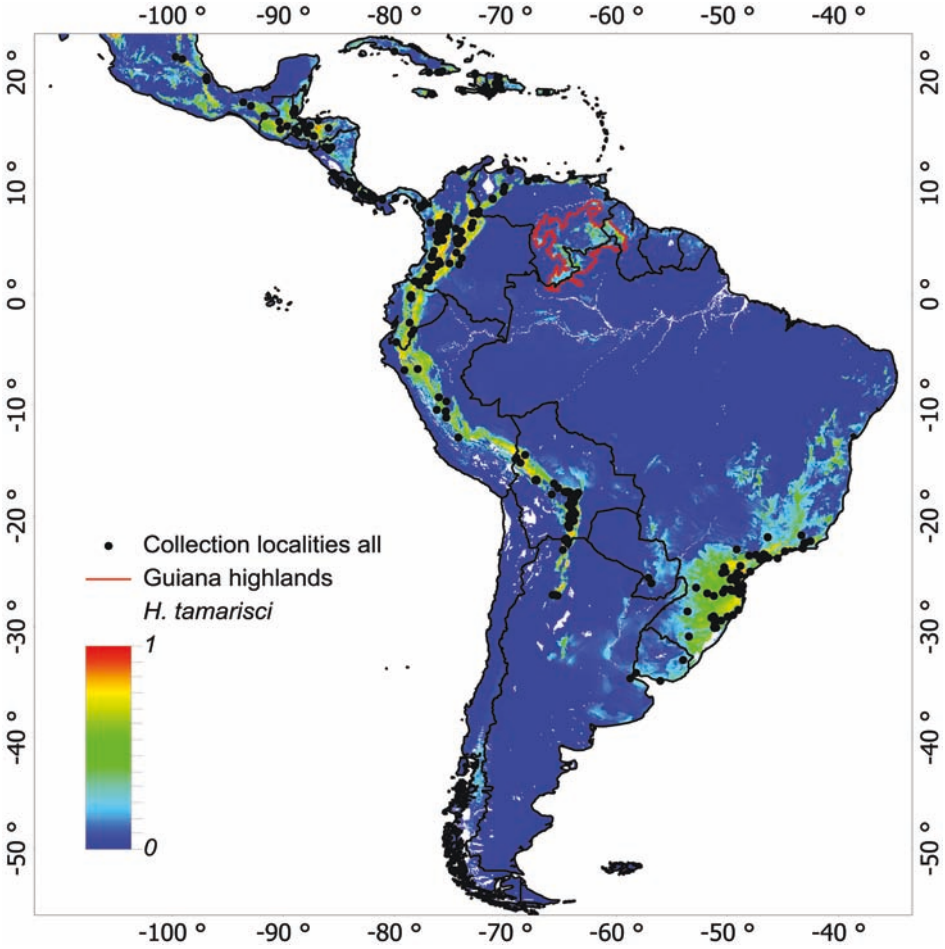


Fig. 3. Maxent distribution model for *H. tamarisci* based on 313 records from Kruijer and GBIF (see text). Probability of presence increases from dark blue (0) to red (1). Most areas in red are obscured by the black dots representing the collection localities. The red demarcation line indicates the Guiana Highlands (above 250 m asl).

(Figs 5 & 6), Bio18 (Figs 7 & 8), and Bio12 (Figs 9 & 10) based on Kruijer's verified data. The response curve for the 'Maximum Temperature in the Warmest Month' (Bio05) shows that the probability of presence drops when temperatures exceed 29°C in the warmest month (Fig. 6). These areas largely represent the lowland regions of the continent (Fig. 5). The response curve for the 'Precipitation in the Warmest Quarter' shows an increasing probability of presence with wetter conditions (Fig.8). *H. tamarisci* is largely absent from the dryer regions (Fig. 7). The response curve for 'Annual Precipitation' (Fig.10) shows an optimum range between 750–3000 mm precipitation annually. The geographic distibution of annual precipitation is shown in Fig. 9.

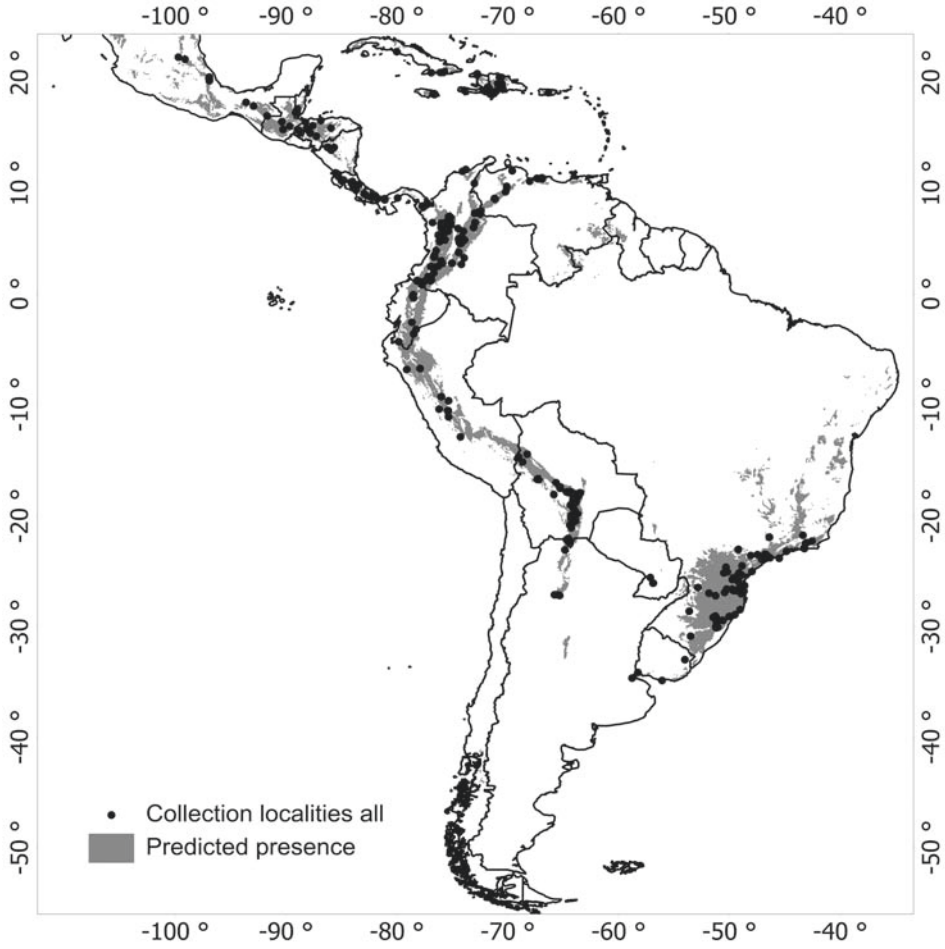


Fig. 4. Maxent distribution model for *H. tamarisci* based on 313 records from Kruijer and GBIF (see text). Grey areas indicate predicted presence.

Principal Component Analysis: Like for the response curves we conducted the multivariate PCA analysis on the model based on Kruijer's verified data. The results of the PCA of the seven variables that contributed more than 2.5% to the Maxent model is given in Fig. 11. PC axes 1 and 2 explained 29.2% and 24.9% of the total variance, respectively. It is evident that the ecological niche dimensions of the Guiana Highlands for these seven variables do not differ from the area for which *H. tamarisci* was predicted to be present (red outline, Fig. 1). The grid cells representing the Guiana Highlands are close to the middle of the cloud (Fig. 11). We also plotted the collection localities to show that these cover the full dimensions of multivariate space (Fig. 11).

Table 3. Average rank and relative contribution of the 21 environmental variables to the 10 times cross-validated Maxent models based on 125 (Kruijer's) and 313 (Kruijer & GBIF's) unique records (duplicate records from the same grid cell omitted).

Variable	125 records		313 records	
	rank	% contribution	rank	% contribution
Bio05	1	43.9	1	29.3
Bio18	2	16.4	3	20.9
Bio12	3	10.6	4	6.2
FAO06	4	4.8	5	3.5
FAO08	5	4.5	19	0.3
Alt	6	2.9	2	24
Bio02	7	2.6	8	2.5
Bio04	8	1.9	12	0.7
Bio15	9	1.6	9	1.8
FAO09	10	1.5	10	1.0
PET	11	1.4	7	2.6
FAO14	12	1.3	20	0.2
FAO05	13	1.2	16	0.5
FAO10	14	1.0	17	0.5
FAO11	15	1.0	18	0.4
FAO04	16	0.9	6	2.7
FAO02	17	0.8	15	0.6
FAO01	18	0.8	13	0.7
FAO03	19	0.6	21	0.1
FAO15	20	0.2	11	0.8
FAO12	21	0.1	14	0.7

Discussion and conclusions

Explained presence and absence: The distribution of *Hypopterygium tamarisci* in the New World is overall well explained by both models (Figs 1–4), and the underlying bioclimatic and edaphic variables (Tables 1–2). The most important variable is the maximum temperature in the warmest month (Bio5; Figs 5–6), which contributes 43.9% to the full Maxent model based on Kruijer's 125 unique records, followed by the precipitation of the warmest quarter (Bio18; Figs 7–8), contributing 16.4% to the full model, and the annual precipitation (Bio12; Figs 9–10), contributing 10.6% to the full model.

Both models (Figs 1–4) predict the occurrence of *H. tamarisci* on several of the Leeward Islands and, rather locally, on a few of the eastern Windward Islands in the Caribbean. This prediction matches the known, but omitted records for Martinique. With exception of the Leeward Antilles (off the coast of Venezuela), the species might be more widely distributed in the Lesser Antilles than known.

Both models (Figs 1–4) clearly show that the absence of the 'New World' variant of *H. tamarisci* from the Leeward Antilles, the lowlands of the Guianas, the Llanos in Venezuela and Colombia, the lowlands of the Amazon basin, and the Gran Chaco can be ascribed to unfavourable ecological conditions, among which the high

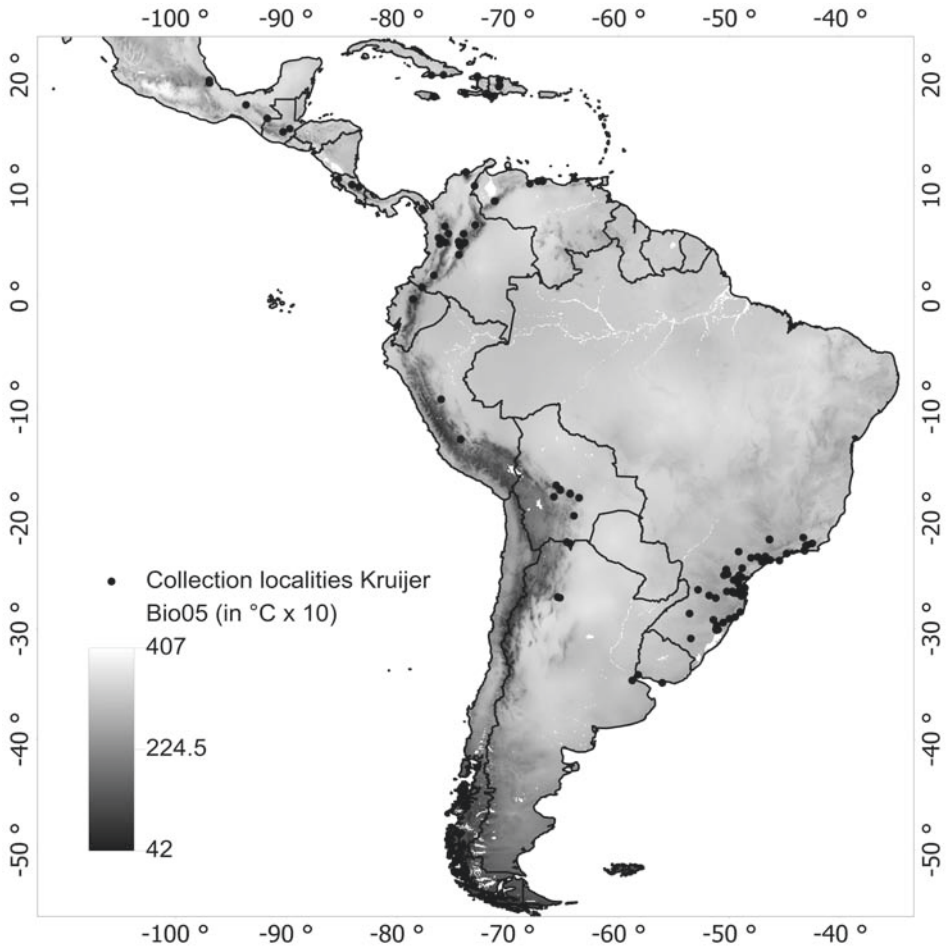


Fig. 5. The collection localities of the 125 unique records of Kruijer's data plotted on the bioclimatic variable Bio05 - Maximum temperature of warmest month (in °C × 10). Lighter grey tones indicate higher temperatures.

temperatures in the warmest month are clearly the delimiting factor (Bio5; Figs 5–6). Like for the overall distribution, other less important factors are the precipitation of the warmest quarter (Bio18; Figs 7–8) and the annual precipitation (Bio12; Figs 9–10).

The isolated single location (Figs 1–4) at Morro Gonzales in mainland Chiloé Province, Chile, matches perfectly the prediction by the models. It is, however, not known whether this occurrence represents a successful dispersal and colonisation event after termination of the last glacial period (most likely) or a remnant of a historic distribution of the species during the last glacial period (or predating distributions). Only two specimens of *H. tamarisci* are known to come from Chile.

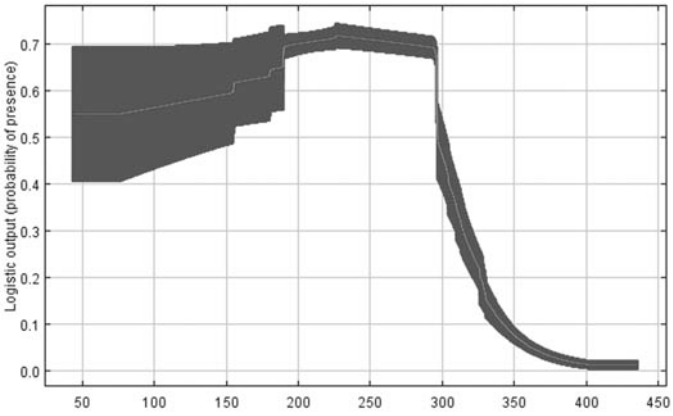


Fig. 6. The response curve for the bioclimatic variable Bio05 based on 10 times cross-validated Maxent models. This plot reflects the dependence of predicted probability of presence on Bio05. Bio05 contributes 43.9% to the full model.

They come presumably from the same collection (Lechler, LPC 595; BR, PC; Kruijer 2002) and were probably growing intermingled with *H. didictyon* Müll.Hal. The specimen in PC was picked out another specimen of Lechler, LPC 595, an exsiccate series of which most specimens under number LPC 595 belong to *H. didictyon* (Kruijer 2002). The specimen in BR is an original specimen of Lechler's exsiccata series and contains well developed, fruiting material of *H. tamarisci*. Hence, more populations may be expected to occur in the predicted areas in Chile, at least in the surroundings of Morro Gonzales, perhaps with plants of *H. tamarisci* growing in small numbers in mixed colonies with *H. didictyon* or other mosses.

For eastern Brazil, the models predict larger areas of potential occurrence than the known distribution of *H. tamarisci*, especially extending more westwards and northwards (Figs 1–4). Since this area of Brazil is most densely populated and most affected by man, the occurrence of the species may have been reduced due to agriculture and urbanisation. However, *H. tamarisci* may have simply been overlooked and may actually be more widely distributed in eastern Brazil than known, hiding itself in town parks, etc.

DISPERSAL AND MAINTENANCE OF THE DISTRIBUTION AREA: The mixed reproductive strategy of *H. tamarisci* consists of sexual reproduction in combination with asexual propagation by means of filiform multicellular gemmae as well as by means of normal but detachable frond leaves and foliate distal parts of frond axes (Kruijer 2002; Pfeiffer et al. 2000). This strategy obviously plays an important role in the maintenance of the large distribution area of *H. tamarisci* in the New World.

The near-perfect match between the distribution of the species in the New World and its potential distribution (AUC = 0.921), i.e., the ecological conditions that determine suitable habitats for the species, indicates that the species has been able to keep up rather well with the climatic change after the termination of the last glacial

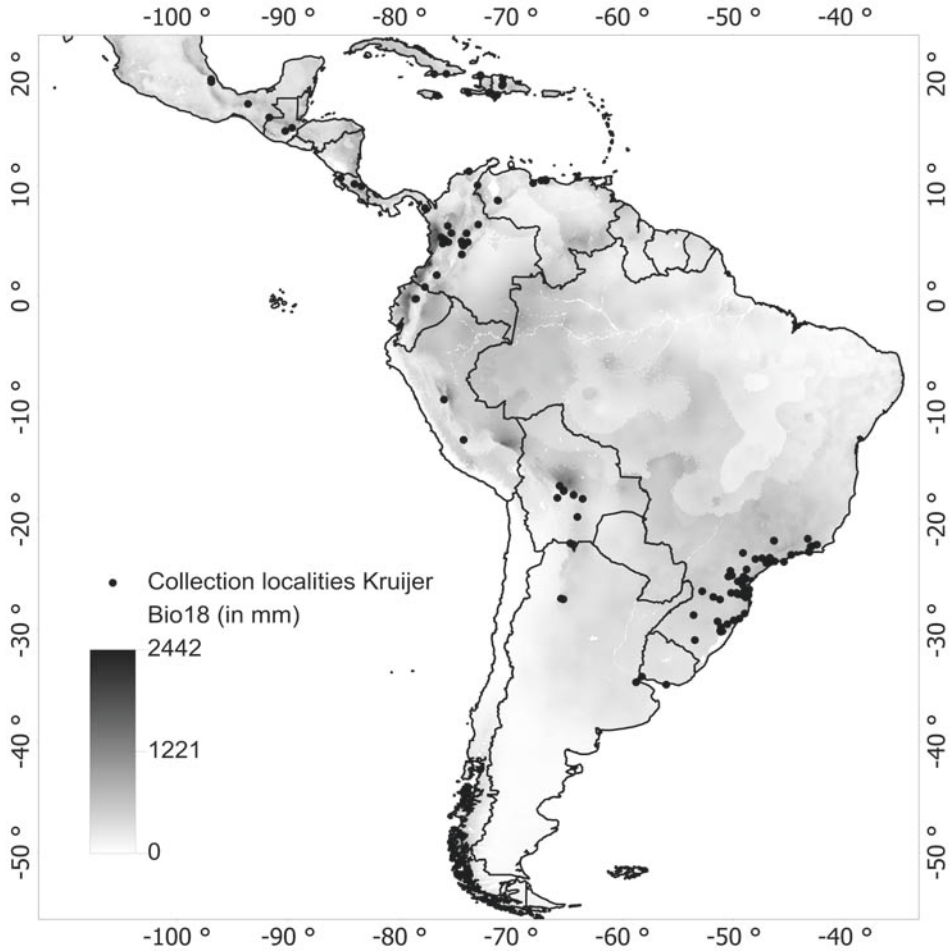


Fig. 7. The collection localities of the 125 unique records of Kruijer's data plotted on the bioclimatic variable Bio18 - Precipitation of warmest quarter (in mm). Darker grey tones indicate higher precipitation.

period. The mixed reproductive strategy has probably been a factor of utmost importance for this process, because it gives the species the ability to colonise new habitats in short periods of time and over rather long distances. We assume that, due to its mixed reproductive strategy in combination with its, for a moss, broad ecological amplitude (Kruijer 2002), the species is well adapted to respond to Quarternary climatic changes. The mixed reproductive strategy and its potential for dispersal are discussed in detail below.

In *H. tamarisci*, like in other bryophytes, asexual propagation may play, in addition to clonal growth (Kruijer, pers. observations; Longton & Schuster 1983; Pfeiffer et al., 2006; Schuster 1983), an important role in building up local populations after

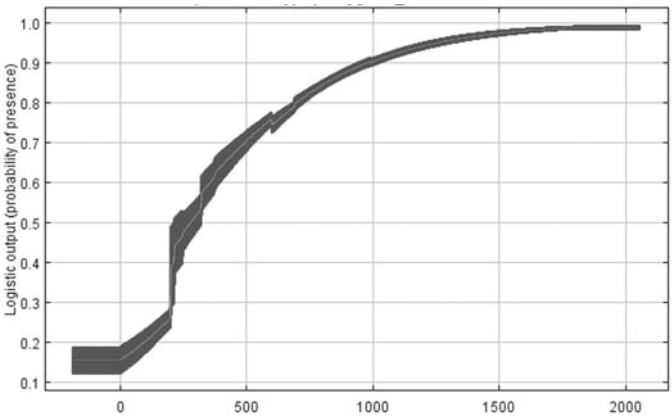


Fig. 8. The response curve for the bioclimatic variable Bio18 based on 10 times cross-validated Maxent models. This plot reflects the dependence of predicted probability of presence on Bio18. Bio18 contributes 16.4% to the full model.

colonisation, maintenance of local populations in space or time, and may contribute to local abundancy (compare, e.g.: Longton & Schuster 1983; Schuster 1983; Kimmerer 1991, 1994; Pohjamo et al. 2006). The usually colourless to brown filiform gemmae are produced in distal half of ultimate frond axes. They are up to 16 cells long and measure 15–95 µm long and 12–40 µm wide (Kruijer 2002). The occurrence of caducous branches as such is already quite uncommon in pleurocarpous mosses (e.g., Correns 1989; Imura & Iwatsuki 1990; Imura 1994; Frey & Kürschner 2011), but caducous distal parts of frond axes are, to our knowledge, thus far only known to occur in seven other species of the Hypopterygiaceae (Kruijer 2002), albeit that this phenomenon might be overlooked in other groups of pleurocarpous mosses. The detached distal parts of frond axes have been observed to act as true propagules (Kruijer, pers. observation).

The gemmae and the caducous leaves and distal parts of frond axes of *H. tamarisci* are almost certainly too big for aerial transport over intermediate and long distances and are even unlikely to be transported over distances of ten kilometres or more (cf. Longton & Schuster 1983). Dispersal of vegetative propagules will, therefore, generally result in local dispersal only. Local dispersal, however, may significantly contribute to local abundancy, which has been observed for *H. tamarisci* in, e.g., the Central Cordillera of the northern Andes of Colombia, where Wolf (1993) found almost pure stands of the species on tree bases in an altitudinal zone between 1725 and 1980 m altitude.

Local abundancy, in turn, may significantly contribute to the number of sporophytes that are produced in the local patches hence increasing the chances of short- to long-distance dispersal and subsequent colonisation of new patches and suitable habitats at various distances. In *H. tamarisci*, fruiting is common, in particular in Central and South America, where in total 65% of the specimens examined have sporophytes,

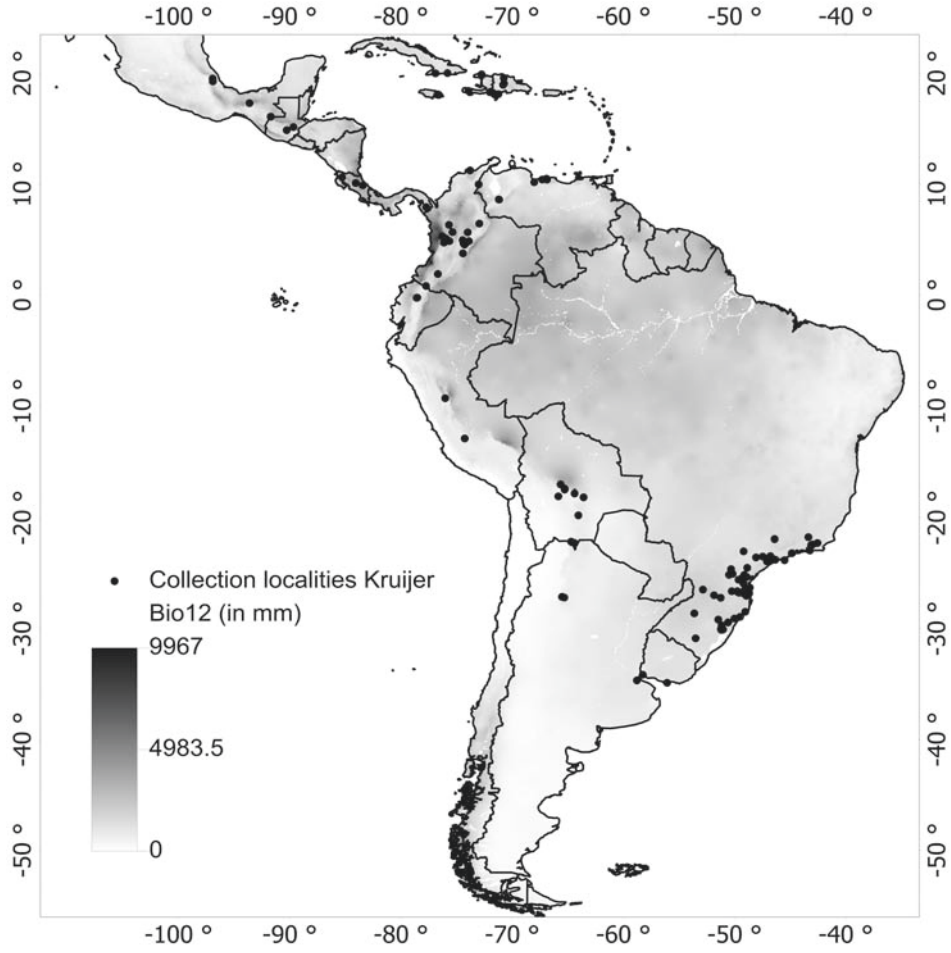


Fig. 9. The collection localities of the 125 unique records of Kruijer's data plotted on the bioclimatic variable Bio12 - Annual precipitation (in mm). Darker grey tones indicate higher precipitation.

varying regionally from from 43% in the Caribbean to 76% SE Brazil and adjacent areas (Kruijer 2002). The spores of *H. tamarisci* measure between 11–17 µm in diameter (Kruijer 2002). In bryophytes, a significant number of released spores fall in close proximity of the parent colony (e.g., Miles & Longton, 1982; Kimmerer 1991; Stoneburner et al., 1992). Pohjamo et al. (2006) estimated that less than half of the spores of the liverwort *Anastrophyllum hellerianum* (Nees ex Lindenb.) R.M.Schust., measuring 9–12 µm in diameter, were dispersed over 10 m distance. Local spore deposition may have a similar function in facilitating the persistence of local populations (Pohjamo et al. 2006) as local dispersal of vegetative propagules is thought to have. A small proportion of air-borne spores is likely to be transported

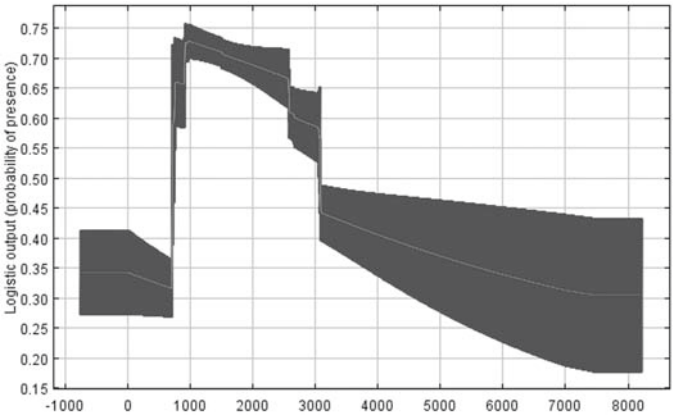


Fig. 10. The response curve for the bioclimatic variable Bio12 based on 10 times cross-validated Maxent models. This plot reflects the dependence of predicted probability of presence on Bio12. Bio12 contributes 10.6% to the full model.

over longer distances (e.g., van Zanten 1978, 1983; van Zanten & Pócs 1981; Longton & Schuster 1983). Such a small proportion, however may represent a high number of spores, for populations may produce spores in massive numbers (e.g., Longton & Schuster 1983; Stoneburner et al., 1992). For two colonies of *Atrichum angustatum* (Brid.) Bruch & Schimp. (spore size 9–14 µm), Stoneburner et al. (1992) estimated that, respectively, 2.4 and 4.5 million of spores were still airborne at 15 m. How far which proportion of air-borne spores are able to travel is not known, but the spores of *H. tamarisci* are, in principle, small enough for direct dispersal over distances of up to several thousands of kilometres by air streams (cf. Longton & Schuster, 1983; van Zanten & Pócs, 1981; van Zanten & Gradstein, 1988). The possibilities for bryophytes for long-range dispersal by spores and the problems for retaining spore viability under conditions of long-range dispersal by air streams have been thoroughly investigated and discussed by van Zanten (1976, 1978, 1983, 1992), van Zanten & Pócs (1981), and van Zanten & Gradstein (1988). Resistance to UV irradiation is the limiting factor of long-range dispersal and resistance to desiccation is correlated with resistance to UV irradiation (van Zanten, pers. comm.). Strong UV irradiation at high altitudes (e.g., jet streams, c. 10–12 km alt.) is almost certainly lethal for spores of most tropical bryophyte species (van Zanten, pers. comm.; cf. van Zanten & Gradstein 1988). UV irradiation and other stress conditions decrease with altitude, however, and van Zanten (pers. comm.) and van Zanten & Gradstein (1988) claimed that wet or intermittently dry air streams at (or below) c. 3000 m altitude offer good possibilities for sufficient survival of spores in time and number for long-range dispersal of such species.

Van Zanten (in Kruijer 2002) showed, however, that it is unlikely that spores of *H. tamarisci* will survive intercontinental aerial long-range transport, although the occurrence of rare transoceanic dispersal events cannot be ruled out. On the other

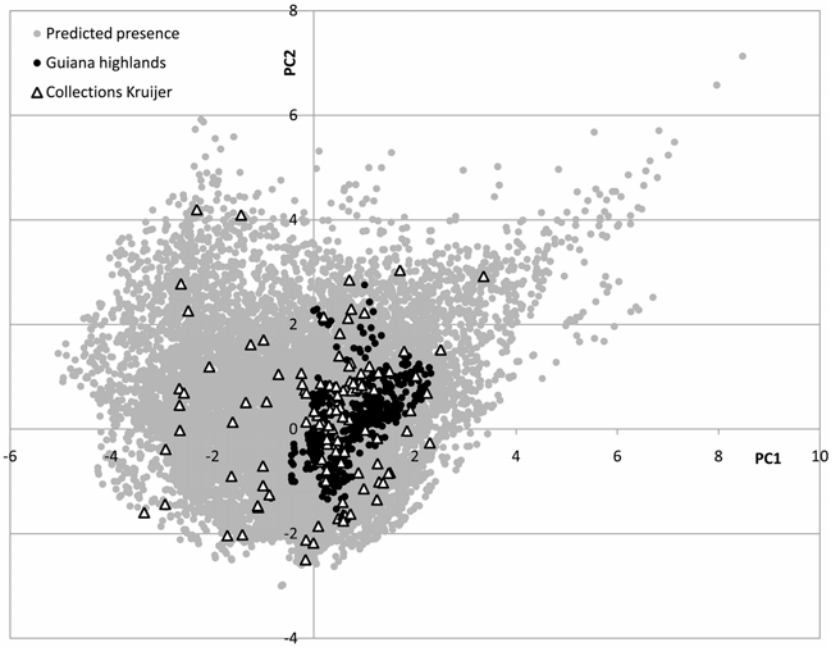


Fig. 11. Result of the PCA for the seven variables that explained more than 2.5% of the Maxent model based on Kruijer's data for those grid cells where *H. tamarisci* was predicted to be present (10 percentile threshold). Black dots indicate the Guiana Highlands. Triangles indicate collection localities.

hand, the results of van Zanten's experiments also showed that successful direct spore dispersal is feasible at shorter ranges, i.e., up to c. 2000 km (cf. Shaw et al. 2006) and within continents, e.g., South and Central America, especially under conditions with low UV irradiation, e.g., at low altitude, and in streams with moist air. However, stepwise dispersal may be the dominant factor in intracontinental migration processes of bryophytes (e.g., Schuster, 1983).

Unexplained absence: Both models predict potential occurrence of *H. tamarisci* in the Guiana Highlands, where it is not known to occur (Figs 1–4). It is clear from the model predictions (Fig. 1–4) and the PCA (Fig. 11) that the absence of *H. tamarisci* in the Guiana Highlands cannot be ascribed to unfavourable ecological conditions of the 21 uncorrelated bioclimatic (including elevation) and edaphic variables used for this study. Albeit that for the central parts of the Guiana Highlands annual precipitation (Bio12; Figs 9–10) and precipitation of the warmest quarter (Bio18; Figs 7–8) might act as negative factors for occurrence. It may be, of course, that the delimiting ecological factor for the Guiana Highlands was not included in the bioclimatic and edaphic variables that were used for the models, but it is unknown which and what kind of factor this might be. Assuming that time has not been the delimiting factor for *H. tamarisci* reaching these areas after termination of the last glacial period, the possible explanations for these discrepancies between the prediction of the models and actual distribution of *H. tamarisci* are discussed below.

The distance between the Guiana Highlands and the nearest populations of *H. tamarisci* as such can almost be excluded as the limiting factor for dispersal of this species. The shortest distance between the summit of the table mountains in the NW of the Guiana Highlands and the nearest locality of *H. tamarisci*, located in NW Venezuela, is c. 500 km, that between the NE of the Guiana Highlands and the nearest locality is c. 900 km. Although our models predict that at present-day the Guiana Highlands cannot be reached by stepwise migration, these distances are well within the range of possible successful direct spore dispersal of *H. tamarisci*.

Moreover, the distances between the Guiana Highlands and the nearest populations of *H. tamarisci* might have been much shorter during glacial periods due the downward vertical shift of the vegetation during glaciations, of which the maximum shift for the last glaciation for this region has been estimated as being 1100 m (Rull 2004, 2005), resulting in better possibilities for successful direct spore dispersal. The downward vertical shift might also have increased the possibilities for stepwise dispersal. However, further investigation towards the palaeoclimatic conditions of the region in the Quaternary in relation to the ecology of *H. tamarisci* needs further study.

Vegetation structure and rainfall might hamper the dispersal of spores to higher air streams and hence intermediate- and long-distance dispersal. In the case of the Guiana Highlands, however, it seems unlikely that vegetation structure nowadays hamper the dispersal of spores from colonies of *H. tamarisci* in, e.g., Caracas and surroundings (e.g., Mägdefrau 75, 76, U) to higher air streams. Buck (1989) hypothesised that prevailing winds, which are from the south and east and come from over the lowlands of the Amazon basin, which act as source of spores of lowland species only, are the major cause of the depauperate moss flora (excluding *Sphagnum* L.) of the Guiana Highlands. Although Buck's (1989) hypothesis is interesting and needs further study, it seems to contradict the diverse liverwort flora present in the Guiana Highlands (Buck 1989). In the case of *H. tamarisci*, which does not occur in the Amazon basin, the easterly trade winds may indeed significantly hamper spore dispersal towards the Guiana Highlands by wind streams from the nearest populations located north and west, but in June and July spore transport by air streams might be possible in local weather systems in the Intertropical Convergence Zone, e.g., under unstable atmospheric conditions prior to storms in the morning and early afternoon with thermal turbulence and convective updrafts.

Taking into account the possibility of competitive exclusion as the underlying process causing the absence of *H. tamarisci* from the Guiana Highlands, we have no idea which competative moss species may be involved there. If such competitors exist, they do not belong to the Hypopterygiaceae. Apart from this, it is not certain whether competitive exclusion principle is relevant here, since under ecological conditions where evaporation is one of the delimiting factors, plants of separate moss species may actually benefit from growing intermingled in mixed colonies to reduce their evaporation rates and to retain their water content as long as possible. Numerous herbarium collections examined by Kruijer for his revision (Kruijer 2002) were mixed collections, in which two or three, sometimes even four, species of Hypopterygiaceae grew intermingled, often accompanied with other moss species as well.

Probably most mysterious is the absence of *H. tamarisci* from the Guiana Highlands (Figs 1–4; Kruijer 2002), where, certainly from a bryological point of view, human disturbance and landuse change is insignificant. The Guiana Highlands are known to have a complex topography, with table mountains with flat and extensive summits ranging from 1500–3000 m elevation, which are separated from the surrounding lowlands by up to 1000 m high vertical escarpments and basal slopes (Rull 2005). The species might have simply been overlooked in this rather inaccessible area, but botanists have been collecting there (e.g., Buck 1989) and the plants can easily be recognized by non-bryologists, and even non-botanists. According to Buck (1989), the entire moss flora (excluding *Sphagnum*) of the Guiana Highlands is truly poor. It seems, therefore, more likely that the missing of localities of *H. tamarisci* from this area reflects true absence. If so, the absence of *H. tamarisci* from the Guiana Highlands is wanting a better explanation, which needs further study.

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