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Modelling the distribution of four *Dioscorea* species on the Mahafaly Plateau of south-western Madagascar using biotic and abiotic variables

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ABSTRACT

Wild yam species (*Dioscorea* spp.) provide important supplementary food and thus contribute directly to the livelihood and well-being of local people in SW Madagascar. Given the ongoing exploitation of this resource, there is a necessity to identify and predict yam species distribution along environmental gradients to improve our understanding of sustainable management of this resource. Therefore, the aims of the current study were to identify predictors for the distribution of important wild yam species and to spatially predict their availability. To this end species abundance and environmental variables were collected in the field using a systematic sampling approach within a yams collection area of four villages (58 plots). A redundancy analysis (RDA) was conducted to investigate the relationship between wild yam species and 12 environmental variables. Species distribution models and species response curves were established for the most abundant wild yam species using nonparametric multiplicative regression (NPMR). These models were subsequently used in conjunction with geospatial data for predictive mapping. RDA depicted a clear pattern of species habitats with *D. alatipes* occurring in dry spiny forests on calcareous soils at remote places, while *D. bemandry* and *D. fandra* were found in forest habitats on sandy soils with high harvest intensities. The NPMR models explained 88% (*D. alatipes*), 82% (*D. bemandry*) and 37% (*D. fandra*) of the variation in species abundance. Sensitivity analysis indicated the importance of vegetation structure, human interventions, and soil characteristics in determining wild yam distribution. Predicted distribution maps showed that the population of wild yam is scarce and mostly located in restricted areas of open spiny forests and dry spiny forest thickets, where harvest intensity is high. This study highlights the need for long-term assessment and public awareness actions on yam harvest practices as well as the importance of anthropogenic factors for the distribution of yam as a key forest resource in SW Madagascar.

1. Introduction

Plant genetic resource managers need to know how species are distributed, how abundantly they occur, what site preferences they have and how resilient they are to human use or other environmental disturbance to effectively protect habitats or to forecast changes in species distribution in response to biotic or abiotic stresses (Bustamante and Seoane, 2004). Distribution, abundance, and diversity of plant species are controlled by a number of factors, which are a major preoccupation of community ecologists. Climatic conditions have always played a major role in affecting species distribution and vegetation patterns (Gaston, 2003), but gradients of nutrients, water, and light may be similarly important (Guisan and Zimmermann, 2000; Austin, 2002). Several conceptual models showed that climate, topography, and geology are the primary environmental factors determining plant species distribution (Franklin, 1995) causing species-specific habitat niches. The species niche concept has been a central issue in ecology since decades and emphasized the existence of multiple causal factors for plant species distribution (Austin and Smith, 1990; Austin, 2002). In contrast to the fundamental niche, which is simply the response of species to environmental resources, the realized niche additionally includes the effect of biotic interactions such as predation, competition and dispersal limitation (Austin, 2002; Chase and Leibold, 2003).

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The Mahafaly Plateau in SW Madagascar is an example of an ecosystem that experienced a complex human-induced landscape transformation over the last centuries (Casse et al., 2004), resulting in major land cover changes (deforestation) and degradation of natural resources (Brinkmann et al., 2014). Simultaneously, this unique ecosystem provides a range of services to local inhabitants such as fuel wood and construction material, food, fodder and medicinal plants (SuLaMa, 2011). As one of the poorest regions in Madagascar, the local population depends to a high degree on the exploitation of natural forest resources, which include wild yam (*Dioscorea* spp., Dioscoreaceae) as an important supplementary food. The tubers of wild yam, in many parts of Madagascar called 'food for the poor', are mainly consumed during periods of seasonal food shortages and therefore represent a high traditional value in rural areas as they contribute directly to the livelihood and well-being of local communities (Perrier de la Bathie, 1925). Madagascar harbours at least 42 yam species, from which two new *Dioscorea* species have recently been described and 36 were reported to be endemic (Wilkin et al., 2008, 2009). *Dioscorea* spp. are distributed in various areas of Madagascar, ranging from the humid lowlands and the mountain regions to the dry and semi-arid zones (Jeannoda et al., 2003). However, most of the species are found in the dry regions (west and south) and many of these species survive under harsh environmental conditions (Abraham et al., 1996). Despite the growing interest on the diversity and use of Malagasy yams, relatively little effort has been made to study in detail their ecological response to environmental gradients. One study on the distribution of wild yams in SW Madagascar has not adequately identified the main factors affecting species distribution and availability (Tostain et al., 2010). While land cover, climatic gradients, regional variability on the actual use and knowledge of wild yams seem to determine their availability in West Africa (Devineau et al., 2008; Yasuoka, 2013), human impacts, such as over-exploitation and land clearing are important determinants in Madagascar (Ackermann, 2004; Ramelison and Rakotondratsimba, 2010).

To improve our ecological understanding on species distribution and to predict it across landscapes, species distribution models (SDMs) are often used (Franklin, 2010). Predictive maps are a possible outcome of SDMs to test hypotheses on habitat characteristics but also for resource management and conservation planning including biodiversity assessment (Gioia and Pigott, 2000; Kremen et al., 2008). In SDMs, climate, elevation, temperature, land surface and geology are important factors influencing species distributions at broader scales, while soil properties (Fu et al., 2004; Gerhardt and Foster, 2002) become increasingly important at smaller scales. The existing methods for SDM vary in terms of complexity, assumptions, data requirements and usability (Syphard and Franklin, 2009).

Generalized Additive Models (GAMs; Yee and Mitchell, 1991) have been used in SDMs as an alternative to Generalized Linear Models (GLMs; Guisan et al., 1999). Other statistical methods, such as classification tree analysis, have been used to better capture the complex, non-linear relationships between response variables and multiple predictors (Brinkmann et al., 2011; Hastie et al., 2005). McCune (2006) recently demonstrated the power of Nonparametric Multiplicative Regression Analysis (NMPR) in analyzing species response surfaces in a multi-dimensional niche space, which has subsequently been successfully used in other studies (Jovan and McCune, 2006; Lintz et al., 2011).

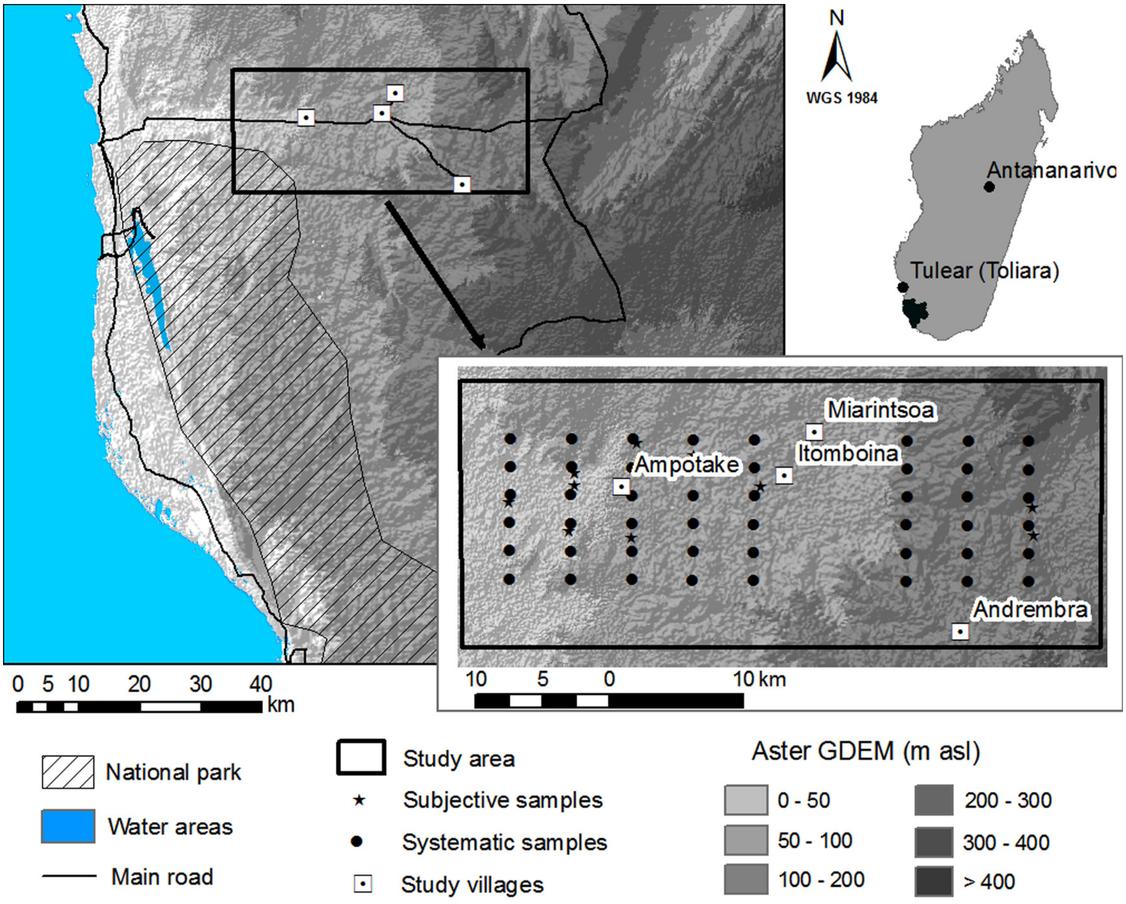

Fig. 1. Location of the study area and distribution of sample plots on the Mahafaly Plateau in SW Madagascar.

In view of the above, the aim of this study was to analyse the effects of environmental factors and their interactions on wild yam distribution on the Mahafaly Plateau and to predict yam species abundance using SDMs to define pressure zones for effective resource management. We hypothesized that the occurrence and abundance of wild yam species is largely determined by soil properties, vegetation structure and human interventions rather than topography.

2. Materials and methods

2.1. Study area

The study area is located in the northern part of the Mahafaly Plateau in SW Madagascar (23°46′–24°1′S, 43°54′–44°15′E) and comprises different forest habitats where people collect wild yam tubers (Fig. 1). This region is characterized by a semi-arid climate with a dry season from April to November and an annual mean temperature of 24 °C, classified as a hot arid steppe climate. The rainfall is very irregular, and varies strongly from the coastal zone to the 10 km distant plateau area, but the most reliable records indicate long term averages of <500 mm throughout the region (Hanisch et al., 2015). The natural vegetation consists of deciduous savannah forests with xerophytic species of the Didieraceae and Euphorbiaceae families. From the coastal plain to the inland, the area is characterized by different ecological zones: dry forest on sandy or ferruginous soils and dry spiny forest on tertiary limestone (Du Puy and Moat, 1998). This ecosystem harbours the highest level of plant endemism at the generic (48%) and species (95%) level in Madagascar (Mamokatra, 1999). The study region includes the recently extended Tsimanampetsotsa National Park, numerous "sacred forests", and community forests where the collection of forests products is not legally restricted. The zone is inhabited by three main ethnic groups (Mahafaly, Vezo, and Tanalana), which comprise mainly small holder farmers and herders with little formal education. Agricultural production, based on the cultivation of cassava (*Manihot esculenta* Crantz), maize (*Zea mays* L.) and different varieties of beans, is hampered by unpredictable rainfall. Consequently people are often affected by food insecurity (WFP, 2013) and rely on the collection of forest products that provide food, medicinal plants fuel wood and construction material, to sustain their livelihoods. This has increased the pressure on forests resources outside the park area and led to forest degradation with high forest losses (45%) during the past 40 years (Brinkmann et al., 2014).

So far, a total of 24 yam species are known from SW Madagascar (Tostain et al., 2010). Their local name '*oviala*' means 'tuber from the forest' and in rural areas they are used as supplementary food during lean periods (Jeannoda et al., 2003, 2007). The collection of wild yam tubers is a common practice for 90% of the households in the Mahafaly region to supplement their diet (Andriamparany et al., 2014).

2.2. Field inventory and indigenous soil classification

Five important species of wild yams have been identified during recent field studies (*D. alatipes*, *D. bemandry, D. nako*, *D. fandra*, and *D. soso*) of which the first two are particularly important (Andriamparany et al., 2014). Since the aboveground lianas of *Dioscorea* spp. are only visible for a few months after the onset of rainfall, proper species identification was limited to a short time period, and a field inventory was therefore conducted from January to March 2013. Study site selection was based on existing data of an ethnobotanical survey (Andriamparany et al., 2014). Altogether, four villages (Ampotake, Miarintsoa, Itomboina and Andremba) were selected and the corresponding wild yam collection area of these villages delineated the study area (Fig. 1; 350 km^2) for field inventory and SDMs.

Using a systematic sampling approach, 48 plots of 400 m^2 each placed every 2 km along eight transects were used for a yam species inventory. Because of environmental heterogeneity, ten additional plots were placed between the systematic ones. The geographical locations and altitude of each plot were recorded with a handheld GPS unit (GARMIN, eTrex, HCx, Ireland; accuracy ± 2 m). For each plot, yam species were identified and their abundance was recorded by counting the number of individuals per species. The harvest intensity of wild yams was estimated based on the number of harvest holes at each plot, which were typically left open after local people have collected tubers (Andriamparany et al., 2014). Five soil samples were taken at 0–20 cm depth from the centre and corners of each plot. Subsequently, these were mixed to obtain a homogenous sample for analysis of soil chemical and physical properties.

Due to a lack of detailed soil maps for the study region and insufficient data on soil classification, we used an indigenous soil classification approach to characterize the different soil types for subsequent yam species distribution modelling. Since our main objective was to differentiate the existing soil types in the study region, we used a simplified participatory method. During interviews with ten wild yam collectors per village ($N = 40$),

Table 1
Description of environmental variables used for the analysis of wild yams (*Dioscorea* spp.) distribution on the Mahafaly Plateau in SW Madagascar.

Groups of variables	Variable		Unit	Values/Frequency ($n = 58$)[*]
	Code	Scientific names and descriptions		
Wild yam species	DIAL	*Dioscorea alatipes*	Number of individuals plot^{-1}	13.2 ± 27.5
	DIBE	*Dioscorea bemandry*	Number of individuals plot^{-1}	3.5 ± 162
	DIFA	*Dioscorea fandra*	Number of individuals plot^{-1}	3.9 ± 11.2
	DINA	*Dioscorea nako*	Number of individuals plot^{-1}	0.1 ± 0.8
Soil (indigenous classes)	CAL_1	*harambato*	Presence/absence	25
	CAL_2	*harantomboaka*	Presence/absence	7
	CAL_3	*havoa*	Presence/absence	3
	FER_1	*tany lahy*	Presence/absence	12
	FER_2	*tany lembe*	Presence/absence	3
	SAN_0	*tany fasika*	Presence/absence	8
Topographic conditions	Elev	Elevation	Meters	178.1 ± 68.8
	Slope	Slope	Degrees	2.6 ± 2.6
Vegetation structure	Open_Veg	Open vegetation	Presence/absence	47
	NoFrag_F	Non-fragmented forests	Presence/absence	13
Human interventions	Harv_Int	Harvest intensity of wild yam tubers	Number of holes plot^{-1}	4.9 ± 11.5
	Road_Dis	Road distance	Kilometer	2.9 ± 1.9

[*] Mean ± Standard deviation.

general information on indigenous soil types (name, characteristics, site suitability for agriculture and wild yam species) were compiled. The most important local criteria for soil classification were the physical aspects such as soil colour and texture. After classifying the indigenous soil types, local people assisted during field survey to identify the local soil names for each plot.

2.3. Analysis of soil parameters

The composite soil samples of the plots were air dried, sieved and analysed in the laboratory. Standard analyses were conducted to determine plant-available phosphorus (P; P-Bray II method for soil with $\mathrm{pH} < 7$ and P-Olsen for $\mathrm{pH} > 7$), total nitrogen (N_{total}), pH (pH-water), calcium (Ca), organic carbon (C_{org}), potassium (K), and soil texture (percentage of clay, silt and sand). To determine how indigenous soil classes differed in terms of soil properties (P, N_{total}, pH, Ca, K, C_{org}, texture), a discriminant analysis was conducted using SPSS 20.0 (IBM Corp., Armonk, NY, USA). The results were evaluated using structure coefficient matrices, canonical correlation coefficients, eigenvalues and Wilk's Lambdas. For predictive mapping of yam species distribution, we created maps of each measured soil parameter (P, N, pH, Ca, K, C_{org}, texture) with Ordinary Kriging, using the spatial analysis tool in ArcGIS 10.0 (ESRI, Redlands, CA, USA).

2.4. Analysis of yam species distribution

Among the five sampled yam species in the study region, *D. soso* was excluded from the data analysis, because of its rare occurrence. To investigate the relationship between the abundance of the four remaining yam species and 12 environmental variables (Table 1), a constrained ordination method was conducted.

The model included the identified indigenous soil classes as environmental factors. Further environmental variables were extracted from existing geographical data. The topographic conditions (slope and elevation) were derived from a Digital Elevation Model (ASTER GDEM Version 2, date of acquisition 17.10.2011, a product of NASA/METI). To describe the vegetation structure, existing data on land cover and forest fragmentation for the Mahafaly Plateau (classified for the year of 2013 by Brinkmann et al., 2014) was used to identify areas with open vegetation (barren land, cropland, savannah, shrubland) and non-fragmented forest areas. Human interventions were estimated based on the harvest intensity measured during the field inventory (number of harvest holes) and the distance to the main road. The latter was calculated using the Euclidian distances between each plot and the main road within ArcGIS.

Prior to analysis, the nominal variables (soil classes, open vegetation, non-fragmented forests) were recoded using a set of dummy variables; data of species abundance were logarithmically transformed. Additionally, the species data set were tested for spatial autocorrelation, which is known to violate the assumption required to use statistical models and often results in biased parameter estimates (Dormann et al., 2007). Therefore, absence of spatial autocorrelation was checked using Moran Indices by applying GeoDa software (499 randomized permutations; https://geodacenter.asu.edu/software; Anselin et al., 2006). Results revealed no spatial autocorrelation ($P > 0.05$; Appendix 1).

To choose the appropriate ordination method for statistical analysis of yam species distribution in CANOCO (version 4.5, Microcomputer Power, Ithaca, NY, USA), the length of environmental gradient was determined using a Detrended Correspondence Analysis (DCA). Because of linear species response (gradient length: 3.043; Lepš and Šmilauer, 2003), a Redundancy Analysis (RDA) was used. A forward selection for explanatory variables was conducted manually using partial Monte Carlo permutation tests to check the significance of each variable and remove non-significant variables from the model. The significance of the constrained axes were statistically tested by the Monte Carlo Permutation test (499 permutations) and the sum of all canonical eigenvalues was used to estimate the proportion of explained variation.

2.5. Modelling of yam species distribution

To predict the distribution of wild yams species and to study their response along soil gradients, we used Nonparametric Multiplicative Regression Analysis (NPMR), which is a niche based habitat modelling approach developed by McCune (2006). The modelling was restricted to the three most abundant species, *D. alatipes*, *D. bemandry* and *D. fandra,* to avoid unreliable predictions of rare species.

Altogether, 15 environmental variables related to topographic conditions, vegetation structure, human interventions and soil parameters, were included in the NPMR models. NPMR models and Species Response Curves (SRC) were generated using Hyperniche V.2 software (McCune, 2011). NMPR started with a calibration, in which species abundance was used to build the model in order to estimate abundance more effectively based on the predictors. In a second step, the most powerful subset of predictors was identified and smoothing parameters of the Gaussian weighting function for each predictor were determined. Our NPMR models were based on local mean with Gaussian weighting. With a stepwise free search function a range of models with different combination of

Table 2
Properties of the indigenous soil classes in the study area according to the perception of the local people on the Mahafaly Plateau in SW Madagascar.

Indigenous soil classes			Nomenclature
Name	Soil properties	Perceptual aspects	Soil map classification^1
Harambato (CAL_1)	Dark soil, large and bare rocks, loamy, high litterfall, dry spiny forest thicket, hilly landscape	Suitable for *D. alatipes*$^{+++}$, fertile, maize cultivation	Tertiary limestone
Harantombake (CAL_2)	Dark soil, loamy, rocks are not large and not bare, upper soil visible on the surface of rocks, high litterfall, dry spiny forest thicket, hilly landscape	Suitable for *D. alatipes*$^{++}$,less fertile, suitable for maize cultivation	Tertiary limestone
Havoa (CAL_3)	Light yellow soil, sandy loam, light, hard, and dry soil with small stones, dry spiny forests thicket, hilly landscape	Bad soils, suitable for *D. alatipes*$^{++}$	Tertiary limestone
Tany lahy (FER_1)	Light red soil, dry, loamy, very hard soil, wooded savannahand open spiny forests, lowland	Unfertile soil "dead soil", not suitable for cultivation, suitable for *D. fandra*$^{+}$	Unconsolidated sands
Tany lembe (FER_2)	Dark red soil, soft and wet, loamy sand, dense spiny forests, lowland	Fertile soil, suitable for *D. nako*$^{++}$, *D. fandra*$^{++}$ $^{+}$, cultivation of beans	Unconsolidated sands
Tany fasika (SAN_0)	Red soil, sandy, open spiny forests, lowland	Suitable for *D. bemandry*$^{+++}$, *D. nako*$^{+}$	Unconsolidated sands

[1] Soil type based on Du Puy & Moat (Moat & DuPuy 1997); plus signs represent the indigenous perception of wild yam species availability (+++ very abundant, ++ abundant, + occasional).

predictors were calculated to choose the best model for each species (McCune, 2006). To choose the best predictors, the relative importance of particular predictors within the model was evaluated using the sensitivity analysis in Hyperniche. Sensitivity values range from 0 to 1 and greater sensitivity indicates higher influence of that variable in the model (McCune, 2006). For model validation, the cross R-Squared ($\times R^2$) was calculated based on the residual sum of squares (RSS) divided by the total sum of squares (TSS), which differs from the traditional R^2 (Antoine and McCune, 2004). Consequently, negative $\times R^2$ are common for weak models if RSS > TSS. The resulting SDMs were further evaluated with a Monte Carlo permutation test (1000 randomized runs). Based on the NPMR results, SRC were computed for each species using the correspondent identified best predictors (pH, C_{org}, K, N_{total}, silt, and clay content) and produced as series of two dimensional response graphs. Finally, in the application phase, predictive maps were generated for the selected models using the GIS function in Hyperniche. Prior to prediction, ESRI grids (in ASCII format) were prepared for all predictors selected to build the best models (road distance, open vegetation structure, non-fragmented forests, harvest intensity, pH, C_{org}, K, N_{total}, silt, and clay content). Predicted relative abundances of wild yams were plotted against the observed ones, and Pearson's correlation coefficients were calculated to evaluate the accuracy of the modelled abundance maps.

3. Results

3.1. Indigenous soil classification

Altogether, six indigenous soil classes (Table 2), which were used to describe the soil types in the natural environment, were identified by the local population. Classifications were mostly based on soil physical parameters (texture, stoniness, hardness, colour, water content, topographic position, land cover and site suitability aspects). For example '*harambato*' refers to 'rocky soils on a hillside' and '*tany lahy*' to 'male soil' similar to 'hard soil'. Although the Mahafaly Plateau is mainly known for its calcareous soils derived from tertiary limestone, soil texture and stone content was highly variable and an important criterion for soil differentiation by the local people. For the perception of colour tones, especially for red soils, respondents used very detailed descriptions (light red, dark red, bright red) to differentiate the unconsolidated sands and ferruginous soils. Other soil properties such as hardness, moisture content and thickness of litter were also used for soil description, but to a much lesser extent, whereas land cover or vegetation type and the topographic position were used very frequently. Similarly frequent was the use of site suitability aspects for crop cultivation ('good for maize cultivation' or 'dead soil').

Discriminant analysis revealed that soil physical and chemical properties differed significantly between soil classes except for plant-available phosphorus (Table 3). The first canonical discriminant function explained already 80.5% of the variance (Wilks's Lambda = 0.82; $P < 0.001$). Using the structure matrix, we identified that the first discriminant function was associated with six variables (C_{org}, Ca, N_{total}, pH, sand and silt); the most important discriminating factors being C_{org}, N_{total} and Ca.

3.2. Yam species distribution along environmental gradients

Using multivariate analyses, clear relationships among the four wild yam species and the selected environmental variables were detected. Altogether, eight significant explanatory variables (Appendix 2) were included in the RDA analysis (four indigenous soil types, harvest intensity, road distance, open vegetation and non-fragmented forests). The combined effect of explanatory factors explained 50.9% of the total variability of the four wild yam species distributions, from which 96.1% are explained by the first two axes (Fig. 2, Table 4). A Monte Carlo permutation test revealed a significance level of $P = 0.002$.

Axis 1 explained 34.3% of the total variability in the species data and was positively correlated with the distance to road and calcareous soil types (CAL_1, CAL_2), which were characterized by a high content of Ca, N_{total}, C_{org}, and silt. This axis represents a soil gradient from the closed forests on calcareous rocks, which are mostly situated far away from the road, to the ferralitic soils at lower altitudes. Occurrence of *D. alatipes* was positively correlated with the first axis and situated in the first quadrant, whereas *D. nako* occurred in the third quadrant of axis 1, where the environmental factors 'ferralitic soils' (FER_1 and FER_2, characterized by a high P and clay content) and 'open vegetation' prevailed.

The second axis explained 14.6% of the variance in the species data. This axis represented a gradient from the ferralitic soils with higher silt and clay content to the red sandy soils, where *D. fandra* and *D. bemandry* occurred. The yam harvest intensity and non-fragmented forests were positively correlated with the second axis. *Dioscorea bemandry* and *D. fandra* were abundant on sandy soils, in non-fragmented forests, affected by highest harvest intensity.

3.3. Species distribution models (SDMs) and species response curves (SRCs)

Species distribution models had the highest fit for *D. alatipes* ($\times R^2 = 0.88$), followed by *D. bemandry* ($\times R^2 = 0.82$) and *D. fandra* ($\times R^2 = 0.37$). Every added predictor improved the fitness of each

Table 3
Physical and chemical soil properties of the indigenous soil classes on the Mahafaly Plateau in SW Madagascar and results of the discriminant analysis.

Measured soil properties	Indigenous soil classes						Discriminant analysis[1]		
	CAL_1	CAL_2	CAL_3	FER_1	FER_2	SAN_0	Wilks' Lambda[2]	Sig.	Structure matrix
pH	7.5 ± 0.1	7.6 ± 0.1	7.5 ± 0.4	6.9 ± 0.7	7.6 ± 0.3	6.8 ± 0.7	0.608	***	0.351
$C_{org(\%)}$	4.6 ± 1.4	3.5 ± 1.1	1.8 ± 1.2	1.4 ± 0.9	1.2 ± 0.4	0.9 ± 0.7	0.306	***	0.720a
$N_{total(\%)}$	0.4 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.1 ± 0.05	0.1 ± 0.04	0.1 ± 0.03	0.324	***	0.695a
P (ppm)	5.9 ± 3.6	5.2 ± 4.7	1.8 ± 0.2	9.8 ± 8.6	1.8 ± 1.8	7.1 ± 3.6	0.832	ns	−0.095
Ca (meq/100 g)	13.6 ± 5.1	11.5 ± 3.8	6.4 ± 5.9	4.0 ± 3.8	7.5 ± 3.3	2.2 ± 3.3	0.448	***	0.537a
K (meq/100 g)	0.9 ± 0.3	1.1 ± 0.3	0.8 ± 0.8	0.6 ± 0.4	1.6 ± 1.04	0.4 ± 0.4	0.677	***	0.203
Clay (%)	4.7 ± 1.7	7.7 ± 3.1	8.6 ± 5.1	8.8 ± 3.9	8.0 ± 3.0	5.8 ± 4.8	0.746	***	−0.199
Silt (%)	20.7 ± 4.3	21.7 ± 1.4	14.3 ± 9.1	9.2 ± 6.1	21.0 ± 7.8	5.8 ± 6.0	0.383	***	0.569
Sand (%)	74.6 ± 4.8	70.6 ± 2.4	77.0 ± 14.2	82.0 ± 7.7	71.0 ± 10.4	88.5 ± 10.6	0.585	***	−0.325
Eigenvalue = 4.232									
Percentage variance = 80.5									

[1] All values depict the first canonical discriminant function; ([a]) Largest absolute correlation with discriminant functions; ([2]) the smaller the Wilks's lambda, the more important is the independent variable for discriminant function; (ns) non-significant; (**) significant at 5% and (***) at 1%.

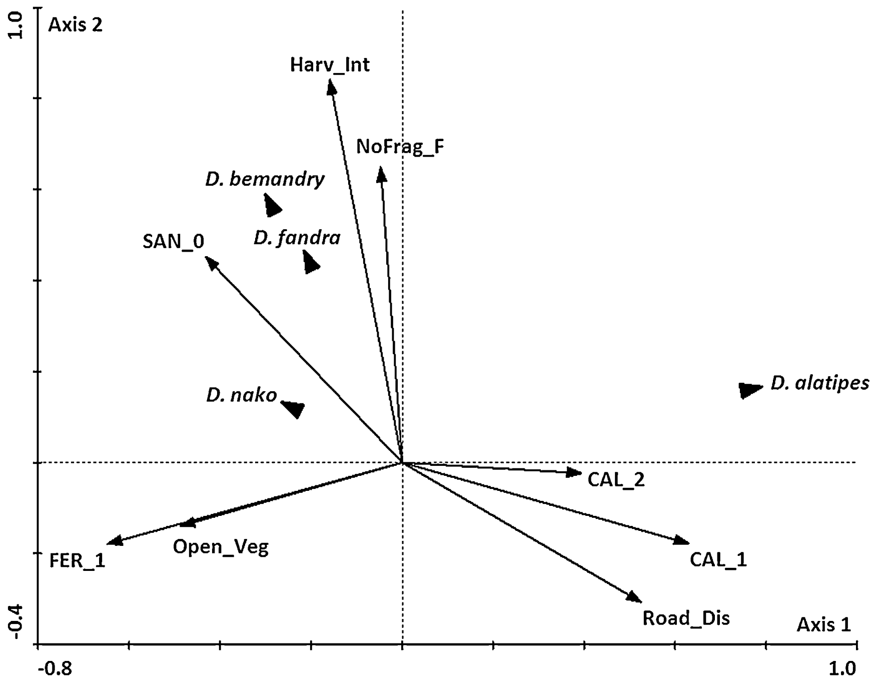

Fig. 2. Ordination diagram of RDA showing the first and second ordination axes to display the relation of wild yam (*Dioscorea* spp.) species (arrows with empty lines) and explanatory, environmental factors (arrow with solid lines) on the Mahafaly Plateau in SW Madagascar.

Table 4
Correlation matrix of the two first ordination axis of an RDA of wild yams (*Dioscorea* spp.) occurrence on the Mahafaly Plateau in SW Madagascar.

Explanatory factors		Axis 1	Axis 2
Main associated species on the axis		*D. alatipes*, *D. nako*	*D. bemandry*, *D. fandra*
Vegetation structure	Open vegetation	−0.386	−0.106
	Non-fragmented forests	−0.037	0.49
Human interventions	Distance to the road	0.417	−0.232
	Harvest intensity	−0.126	0.635
Soil	FER_1	−0.513	−0.135
	CAL_1	0.499	−0.135
	CAL_2	0.312	−0.018
	SAN_0	−0.343	0.342
Species-environment correlations		0.79	0.76
Eigenvalues		0.34	0.15
Cumulative variance (%)		67.4	96.1

model by 5%, which might explain the high $\times R^2$ for the *D. alatipes* model with six predictors (Table 5). In contrast, NPMR models of *D. bemandry* and *D. fandra* were only based on five predictors. Monte Carlo permutation tests revealed that two models were statistically significant. Out of the nine soil parameters included in the analysis, pH, C, K, N, silt and clay were identified as the best soil predictors for wild yam distribution.

Table 5
Summary of NPMR models for the three selected wild yam species (*Dioscorea* spp.) on the Mahafaly Plateau in SW Madagascar.

SDM	*D. alatipes*		*D. bemandry*		*D. fandra*	
	Predictor	Sensitivity	Predictor	Sensitivity	Predictor	Sensitivity
1st	Road_dis	0.136	Road_dis	0.230	Harv_Int	0.099
2nd	Open_Veg	0.000	Harv_Int	0.028	NoFrag_F	0.027
3rd	NoFrag_F	0.154	NoFrag_F	0.016	N_{total}	0.231
4th	pH	0.167	C_{org}	0.017	K	0.005
5th	C_{org}	0.008	Silt	0.004	Clay	0.032
6th	K	0.004	–	–	–	–
xR^2	0.88		0.82		0.37	
P-	value	0.04		0.04		0.09

–Not included in the model.

Analysis of SRC revealed three step-function and two sigmoid curves, as well as one skewed hump-shaped curve. The remaining two SRCs, for *D. fandra* along a potassium gradient and *D. fandra* along a gradient of clay content showed no specific curve shape. Although skewed, only *D. alatipes* showed the classical shape of a unimodal response curve along an environmental gradient with an optimum at pH 7.2–7.5 and a rapid decline above or below this range.

For C_{org} and K, *D. alatipes* showed a sigmoid relationship, indicating that this species is widely abundant under high K and C_{org} contents in the soil (Fig. 3B and C). *Dioscorea bemandry* and *D. fandra* presented similar SRC step-function shapes along with N, silt and C, where species abundance declines after a certain threshold (around 1% for C_{org}, 5% for silt, and 0.1% for N_{total}). Highest species abundances were reached with low C_{org}, N_{total} and silt content in the soil.

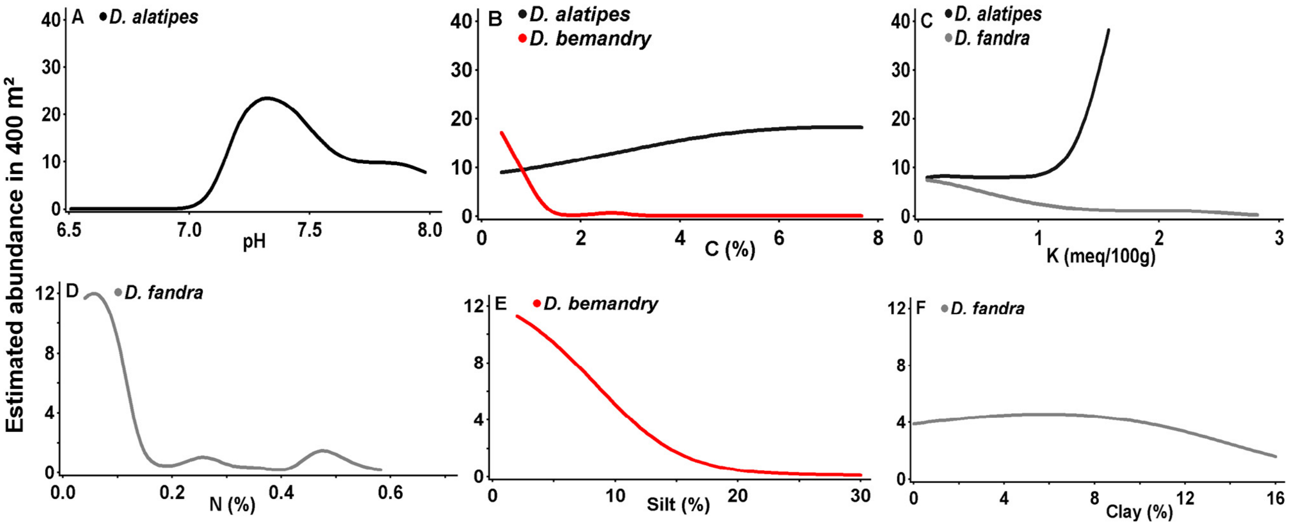

Fig. 3. Nonparametric multiplicative regression (NPMR) response curve for selected wild yam (*Dioscorea* spp.) species along edaphic gradients on the Mahafaly Plateau in SW Madagascar.

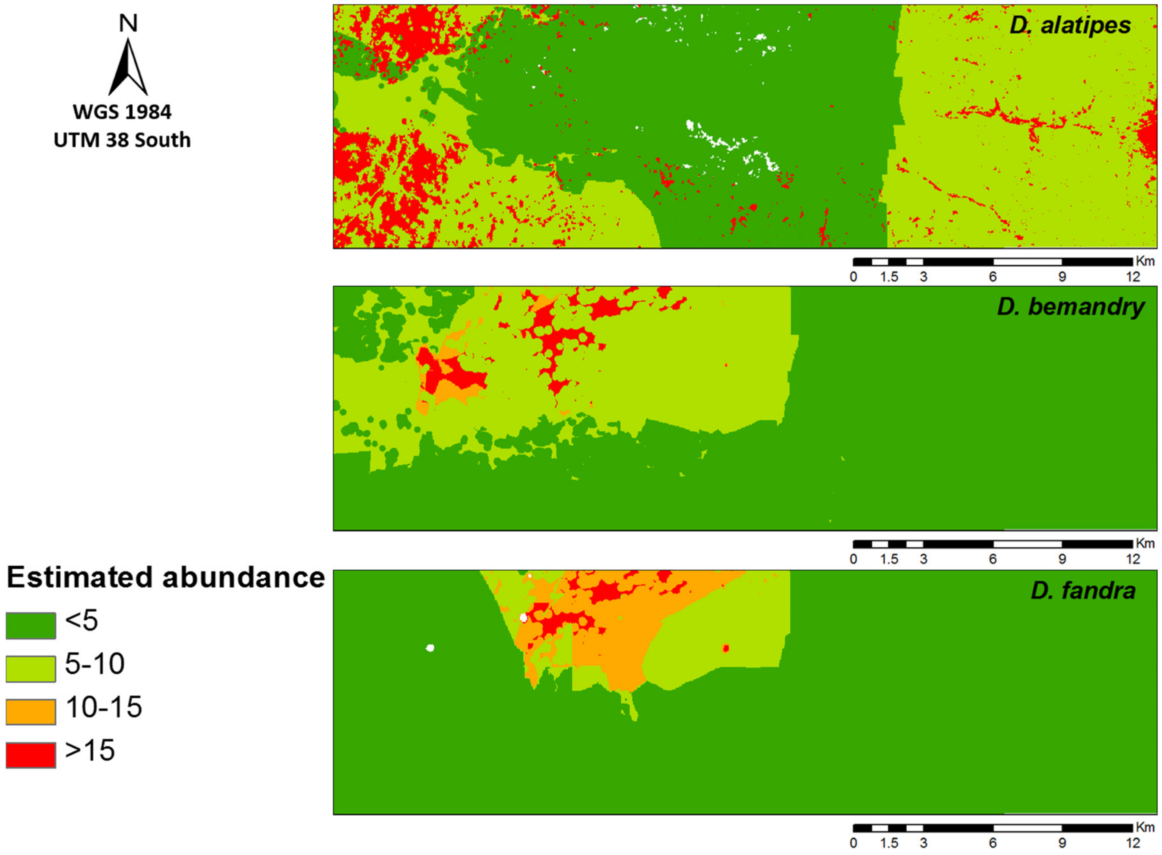

Fig. 4. Predictive maps for three wild yam (*Dioscorea* spp.) species on the Mahafaly Plateau in SW Madagascar using corresponding Nonparametric Multiplicative Regression (NPMR) models. Abundance classes represent the predicted number of individuals of yams within 400 m^2. Areas where prediction was impossible are highlighted in white colour. For details on the study region see Fig. 1.

3.4. Predictive mapping of yam species

Predictive maps of three wild yam species were generated using the NPMR models for one of the most important collection area of wild yams near the villages (Fig. 4). Highest species abundance (>15 individuals in 400 m^2) was predicted for only 8.7% of the total area for *D. alatipes*, 2.1% for *D. bemandry* and 1.1% for *D. fandra*. *D. bemandry* and *D. fandra* showed a patchy distribution with low abundances (<5 individuals in 400 m^2) for a large part of the area, and high abundances were restricted to the northern part of the zone between the villages Miarintsoa and Ampotake. *Dioscorea alatipes* showed a different and more evenly distribution with highest abundance far away from the villages.

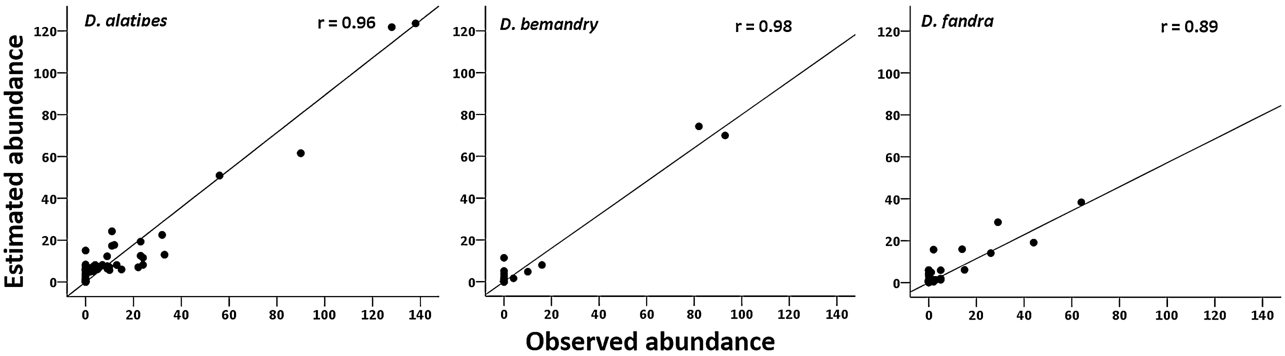

Fig. 5. Accuracy assessment for the predicted wild yam (*Dioscorea* spp.) species distribution on the Mahafaly Plateau in SW Madagascar estimated form NPMR models. Each data point represents a single sample and goodness of fit indicated with a trendline and Pearson's correlation coefficient r.

The observed species abundances were significantly correlated with the predicted abundance for all species, with high Pearson correlation coefficients ranging from 0.89 to 0.98 (Fig. 5). Correlation coefficients were highest for more abundant species (*D. bemandry* and *D. alatipes).* The visual assessment of plots suggested that there were only a few plots, with very high predicted abundance, especially for *D. alatipes* and *D. bemandry*.

4. Discussion

4.1. Indigenous soil classification

Many studies have shown the value of local knowledge on soils, which can provide important insights for more effective soil surveys and land management planning (Barrera-Bassols et al., 2006a,b; Lo Nethononda et al., 2011). Similar to another ethnopedological study (Barrera-Bassols et al., 2003), the local population on the Mahafaly Plateau used typical soil characteristics for soil classification. The high discriminating power of discriminant analyses for most chemical and physical soils properties confirms that indigenous people are aware of soil differences, which often enables them to easily recognize soil productivity and site suitability for agriculture (Shah, 1995). There is a need to develop a more integrated methodological approach for ethnopedology, and one of the main issues mentioned in several ethnopedological reports is the inconsistency of indigenous soil classes at larger scale (Niemeijer, 1995; Sillitoe, 1998). The main objective of our ethnopedological survey was to differentiate the soil types and provide practical results in studying local resource availability and land use practices of the current livelihood system. Thus, the identified local soil names in our study region cannot be extrapolated to other regions with different ethnicities, livelihood types and habitats.

4.2. Yam species distribution along environmental gradients

The results confirmed our hypothesis and indicated that edaphic factors, vegetation structure, and human interventions have a stronger influence on the occurrence of wild yam on the Mahafaly Plateau than topographic conditions. This might be due to the small topographic gradient in our study region, ranging from 55 m to only 200 m above sea level. The relative importance of topographic factors at the local scale may be variable (Moeslund et al., 2013), but climatic and geological features are affecting species distribution at larger scales (Gerhardt and Foster, 2002). Other studies found that human interventions strongly affect wild yam availability at local scales (Sato, 2001; Devineau et al., 2008; Yasuoka, 2013).

A clear gradient has been delimitated for two major species (*D. alatipes* and *D. bemandry*) which is in line with studies conducted on wild yam species distribution in the same region (Tostain et al., 2010). The most prevailing gradient in the RDA ordination represented the differences in the soil substrate from calcareous rocks to unconsolidated, ferallitic sands. Only *D. alatipes* occurred on calcareous soils in dry spiny forest thickets with a closed canopy, which constitutes a restricted distribution zone for locally endemic species (Olson and Dinerstein, 2002) and a remarkable botanical richness (Du Puy and Moat, 1998). *Dioscorea alatipes* might be one of the 'specialists' species, adapted to extreme environmental conditions on poor and shallow limestone soils (Alcantara, 2007). Availability of phosphorus is often the most limiting factor for plant growth in calcareous soils due to the high amount of carbonates (Carreira et al., 2006; Leytem and Mikkelsen, 2005).

In contrast to the report of Tostain et al. (2010), who observed the occurrence of *D. nako* on calcareous soils in the southwestern region of Madagascar, we found *D. nako* on ferralitic soils. *Dioscorea fandra* and *D. bemandry* were related to sandy soils with low nutrient contents, high harvest intensity and non-fragmented forests at lower altitudes. This was also confirmed by Tostain et al. (2010) for *D. bemandry*. According to Andriamparany et al. (2014), *D. bemandry* is highly appreciated by local people in this region and thus harvested intensively, mostly in an unsustainable way (damage of the lianas and harvest of the entire tubers, while harvest holes are left open). The negative effects of unsustainable wild yam harvest techniques on yam regeneration and soil structure (Ackermann, 2004; Andriamparany et al., 2014) and the alarming degradation processes reported by Brinkmann et al. (2014) raise concern about the future viability of wild yam populations.

4.3. Yam species distribution models and species response curves

The average neighborhood size of all SRC models was higher than their respective minimum average neighborhood size needed for estimation, indicating that the model has enough data points for successful prediction of the species response for the given environmental variables (Beyene et al., 2014). Furthermore, the total number of samples in this study was higher than the recommended minimum value of 50 samples for an acceptable ecological response curve (Coudun and Gégout, 2006). More intensive sampling does not always significantly increase the accuracy in determining the curve characteristics (Virtanen et al., 1998; Stockwell and Peterson, 2002) because the shape of SRC is particularly determined by species and gradient properties.

Compared to linear (Carl and Kühn, 2008) or logistic (Pearce et al., 2000) regressions, GLMs (Guisan et al., 1999) and GAMs (Yee and Mitchell, 1991; Guisan et al., 2002), NPMR models show non-linear species abundance relationships and account for interactions among predictors (McCune, 2006). Although the combination of predictors was slightly different for each model, ten variables were identified as important predictors for the three SDMs: road distance, open vegetation, non-fragmented forests, harvest intensity, pH, C_{org}, N_{total} K, silt and clay content. This was also confirmed by other studies, where land use, vegetation types, anthropogenic pressure and soil characteristics were the most important factors influencing the density and spatial availability of wild yams (Devineau et al., 2008; Rakotondratsimba, 2008; Dansi et al., 2013).

In our modelling approach, the choice of predictors during the calibration phase of the analysis strongly determined model quality as it was based on the concept of multiple causal factors (Hutchinson and Bunting, 1987) rather than selecting only significant predictor as we did in using ordination methods. In SDM the inclusion of environmental predictors from more than one hierarchical scale tended to yield more accurate predictions (Meyer and Thuiller, 2006). The use of factor gradients with a possible direct physiological effect (pH, temperature) or resource gradients (water, light, nutrient) that are growth relevant are also suggested (Austin and Smith, 1990; Iverson and Prasad, 1998). We used soil chemical and physical parameters instead of indigenous soil classes for SDM. Since wild yam is traditionally used as supplementary food by the local people in SW Madagascar (Perrier de la Bathie, 1934), we included not only environmental predictors but also variables that describe human interventions. The performance of NPMR varied among species and explained 88% (*D. alatipes*), 82% (*D. bemandry*) and 37% (*D. fandra*) of the variation in the relative abundance. Except for *D. fandra*, the fitness of the models proved the power of NPMR in modelling plant species distribution similar to other studies (Yost, 2008; Fenton and Bergeron, 2008; Rood et al., 2011). One reason for the weak model of *D. fandra* could be the lack of suitable environmental predictors such as water availability for SDM.

The SRCs improved our understanding on yam species–environment relationships. The most important soil parameters for the distribution of three selected wild yam species were selected based on the sensitivity analysis of the SDMs. The Hyperniche software allowed several ways to represent SRC, but we chose the two dimensional response graphs, because the interpretation of single gradients is relatively straightforward and easy to conduct (Jovan, 2003). The ecological niche of a species is optimally described by a bell-shaped symmetric unimodal curve (Austin, 2002), which has been widely used in ecological studies (Potapova et al., 2004; ter Braak et al., 2004). However, we found more frequently step and sigmoid SRC shapes and only *D. alatipes* showed a hump-shaped response for the pH-gradient. Intra- and inter-specific interactions, competition and environmental stress factors can cause linear, skewed and multimodal responses (Oksanen and Minchin, 2002; McCune, 2011) and real world datasets are rarely representative for all species responses (Lawesson and Oksanen, 2002), which was confirmed by our analyses. Skewness is common (Franklin, 2010) and its causes can be diverse (Austin and Smith, 1990), but it might be the direct effect of harvest intensity in our study. Environmental changes (Haire et al., 2000), human activities (Le Lay, 2002) and mortality-causing disturbances (Huston, 2002) can create complex response shapes to species environmental gradients. The species abundance of a sigmoid function increased slowly at the beginning with a rapid decrease after reaching an optimum and was determined for *D. alatipes* by a potassium gradient. Such sigmoid curves possibly depict a part of an unimodal distribution over a long environmental gradient (McCune, 2011) and this might be true for *D. alatipes*, which mainly occurs on calcareous soils under extreme habitat conditions such as hot, dry, rocky limestone. A step-function was determined for *D. bemandry* and *D. fandra* along gradients of C_{org}, N_{total}, silt and clay contents. This shape showed a sudden decrease of abundance at specific thresholds and may reflect the effects of the establishment of a new vegetative population after a disturbance (McCune, 2011).

Altogether, *D. alatipes* was abundant under slightly alkaline soils with high soil C_{org} and N_{total}. *Dioscorea bemandry* and *D. fandra* seems to perform better at low soil nutrient levels (C_{org}, N_{total} and K) and low silt content. However, we cannot make a clear statement on the 'specialist *versus* generalist' approach (Peers et al., 2012) because we did not build SRC models along the same gradient for all species. In contrast to *D. alatipes*, however, *D. fandra* might be a typical example of a generalist, since it occurs over a large range of soil gradients.

4.4. Predictive mapping of yam species

The predicted yam species maps confirmed our own field observations, except for *D. fandra* where the weakness of the NPMR model resulted in unreliable predictions. *Dioscorea bemandry*, which was the most frequent collected species in Ampotaka (Andriamparany et al., 2014), mainly occurred within a limited area near the village, whereas *D. alatipes* was more evenly distributed with a high abundance. However, the predicted clumped occurrence of *D. bemandry* does not reflect its reported frequent distribution in SW Madagascar (Tostain et al., 2010). It is likely, that the optimum microhabitat of *D. bemandry* on sandy soils (Tostain et al., 2010) was underrepresented within our studied area. In fact, sandy soils are not very frequent in our sampled zone (Du Puy and Moat, 1998). A reduced regeneration might be another reason for the low occurrence of *D. bemandry*, probably because of high harvest intensities and a resulting overexploitation, which threatens the natural regeneration of wild yam throughout Madagascar (Ramelison and Rakotondratsimba, 2010).

The estimated abundances of yam species were slightly lower than the observed values especially for high abundances. For *D. alatipes* abundance was highest in non-fragmented forests at remote places, whereas *D. bemandry* and *D. fandra* occurred mainly in open forest habitats near roads, where harvest intensity was very high. If we compare the total density for all wild yam species, our results were similar to that of Sato (2001), but different from those of Yasuoka (2013) in Cameroun, where dispersal of annual yams by hunter-gatherers inside their campsites increased the density.

To better detect habitat differences or dispersal barriers at smaller scales, the inclusion of further environmental factors such as water availability, which was not investigated in the current study, could increase model accuracy. The selection of explanatory variables as well as the prediction accuracy of the model generally depends on the sampling strategy of each dependent variable (Edwards et al., 2006) and prediction was limited to the spatial boundaries of the predictors (McCune, 2011). Nevertheless, the general underlying yam species-environment relationships and patterns may be extrapolated to similar regions in SW Madagascar once predictor variables are available.

The current harvest practice by small-holder farmers lead to overharvesting and forest degradation (Harvey et al., 2014). The predicted maps for yam species may help to define hot spot areas and pressure zones and serve as a basis for conservation and management planning of forest resources. Due to overharvesting of tubers combined with unsustainable harvest methods (Ackermann, 2004), there is obviously a decline of wild yam populations on the Mahafaly Plateau. However, an impact of harvest intensity can only be properly investigated over much longer observation periods (Hall and Bawa, 1993), and we were unable to detect a clear negative correlation between harvest intensity and species abundance. Nevertheless, our data indicated a decrease in the number of saplings. Similar to sustainable management approaches for other native species (e.g. for wild flowers in South Africa; Privett et al., 2014), certain harvest practices can maintain or increase yam population by replanting plant parts, a technique which was successfully used for wild yams in Cameroun (Yasuoka, 2013). Conservation projects such as Crop Wild Relatives (FAO) are already working on the valorisation and the *in situ* conservation of wild yams in Madagascar in the view of their vital importance for food security, especially in rural areas.

5. Conclusions

Wild yams are important for people's livelihood on the Mahafaly Plateau and harvesting wild yam tubers is an important strategy to alleviate the effects of food insecurity in that region. In the view of the current over-exploitation, detailed information on wild yam distribution along environmental gradients is urgently needed for more efficient resource management. Our results show that soil properties, vegetation structure and human interventions directly affect the distribution of wild yam species. Combining biotic and abiotic factors improved the fitness of our species distribution models and allowed to predict the abundance of three wild yam species on the Mahafaly Plateau. Human intervention and interactions among predictors lead to relatively complex species response curves along environmental gradients. The species distribution models provide information on the actual availability of wild yam resources to improve the monitoring on the Mahafaly Plateau, where the Tsimanampetsotsa National Park is one of the main zones for biodiversity conservation while dealing with forest exploitation by the local communities. The observed niche characteristics of yam species should be interpreted with caution and an extrapolation of the current results is limited to the Mahafaly Plateau. For larger scale prediction, long term observations would be needed for different habitats in SW Madagascar. This should include experiments on the cause-effects relationships between soil properties and occurence of wild yam that have been identified as apparently important in our study. For future research on the management of forest resources, we recommend to combine environmental factors with socio-economic variables, particulary human interventions, especially when dealing with intensively used resources that provide multiple services for local communities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2015.06.019.

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