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Original Research Article

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Modeling the Potential Geographical Distribution and Ecological Niche of Selected Fruit Fly (Diptera: Tephritidae) Species in Uganda

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ABSTRACT

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Key words

Bioclim, Ecological Niche, Fruit Flies, Maxent, Uganda,

Despite their overwhelming economic importance, efforts to assess the distribution of fruit flies (Diptera: Tephritidae) in Uganda have been minimal. Consequently, in this study, potential geographical distributions and climatic envelopes of 10 selected fruit fly species were modeled. Two presence-only predictive models namely, Maxent and Bioclim, were run using 19 bioclimatic parameters at a resolution of 30 arc seconds. New detections and existing records of fruit flies were used in the model. The climatic profiles of the selected fruit flies were described and the relative importance of the bioclimatic variables was explored. There was a close agreement between the two models about the distribution and suitability patterns matching the main fruit agro ecological zones. Precipitation (PC-1 = 61.4190%) and temperature (PC-2 = 29.214%) significantly shaped fruit fly niches across the country. Central and mid north zones provided the most suitable niches, while the western, northeastern and areas around Albert Nile were characterized as marginally suitable. The models were mostly robust in performance (AUC: 0.815 - 0.974), with model test performance ranging from random (*C. capitata*: 0.486) to excellent (*C. cosyra*: 0.965). Predicted marginal sites, such as higher altitude zones matched negative areas of the models, which reflected higher model prediction abilities. These results provide an initial insight into the bioclimatic tolerance ranges of fruit flies in Uganda and should assist in identification of sites for future sampling efforts and fruit fly management planning.

Introduction

Several fruit fly species constitute a potential threat to the fruit industry in Uganda. For instance, Mayamba *et al.*, (2014) reported up to 80% fruit losses due to fruit flies in Central Uganda. However, exhaustive studies on their distribution in the country are lacking. This knowledge on geographical suitability of the pest in the country is needed to design spatially explicit management strategies for the pest in order to minimize losses in the fruit industry.

Uganda is ecologically diverse with each agro ecological zone varying in endowment in natural resources and with a multitude of land use patterns across the country. This ecological diversity could lead to differences in spatial suitability of fruit flies in the country with consequent implications on management.

The distribution of a given species in a region is determined among other things by the species' ecological requirements that constitute a species' fundamental niche or the intersection of necessary multiple environmental conditions (Hutchinson, 1957).

A region may have suitable environmental conditions, but if other biological and historical realities are not in place, the species may not occupy its full potential geographical distribution (Brown *et al.*, 1996). For instance, a fruit fly's utilization of its ecological potential may be modified by interactions with other species (e.g. competitors, parasitoids, or parasites), reducing its fundamental niche into a fraction or subset that can be exploited — the realized niche (Hutchinson, 1957). Additionally, historical factors have often acted to restrict a species' distribution (Patterson, 1999).

Innovative methods such as niche-based modelling provide an option for potential species distribution. These techniques allow obtaining the range of environmental conditions/ tolerance (climatic envelope-CE) and areas in which a given species would be able to survive (Pearson, 2007; Rubio and Acosta, 2010). The methods assume that the resulting predictive distribution model is a function of the way in which species respond to the environmental variables, thus reflecting a subset of their fundamental niche (Patterson, 1999). This study therefore was set out to determine the geographical regions that are ecologically suitable for their establishment through modeling the potential distribution of selected fruit fly species in the country. Specifically, the study explored the climatic profiles underpinning the selected species distribution, to understand their niche requirements – a fact almost completely ignored for the selected species in the country.

Materials and Methods

Selected Species and Occurrence data

The specimens belong to 10 species in four genera: *Bactrocera invandens*, *Ceratitis anonae*, *Ceratitis cosyra*, *Ceratitis capitata*, *Ceratitis fasciventris*, *Ceratitis rosa*, *Trirhithrum coffeae*, *Bactrocera curcubitae*, *Dacus bivittatus* and *Dacus ciliatus*. The species were identified as the most economically important fruit fly species in the

Lake Victoria Crescent, Northern moist Farmlands and the Western Moist High Farmlands, the three most important mango growing agro-ecological zones in Uganda (Wortmann and Eledu, 1999). Additional countrywide records were obtained through deliberate detections and from existing scientific literature. The main sources of documented data were the Royal Museum for Central Africa (<http://projects.bebif.be/enbi/fruitly>) and the Global Biodiversity Information Facility (<http://www.gbif.org/>). Records were georeferenced either in situ, using a Map-60 Garmin-GPS, or with the use of different digital gazetteers available in the Internet (mainly Google Earth ©). They were plotted on maps and inspected visually to detect obvious errors. Multiple records with the same coordinates remained as one record in the analysis.

Environmental Variables

Nineteen (19) environmental variables were used to characterize the climatic conditions across Uganda (Table 1). These had a 30 arc-seconds (~1 km²) partial resolution and were derived from the WorldClim project (<http://biogeo.berkeley.edu>), following guidelines by Hijmans *et al.* (2005). These variables were chosen because such a combination thoroughly and effectively represents environmental dimensions with maximum relevance to the ecological distributions of the fruit flies. These parameters (bioclimatic variables) fall into two broad categories – temperature or precipitation variables (Table 1). Elevation data were available for reference purposes but not used as a predictor by themselves (Rubio and Acosta, 2010).

Model Building

The geographical range of the 10 species was modeled with two widely used, presence-only methods, Maxent and Bioclim. The Maxent algorithm (Phillips *et al.*, 2006) yields results ranging from 0 to 1, indicating relative suitability of a given grid cell (high values indicate a higher presence probability) (Graham and Hijmans, 2006; Phillips *et al.*, 2006).

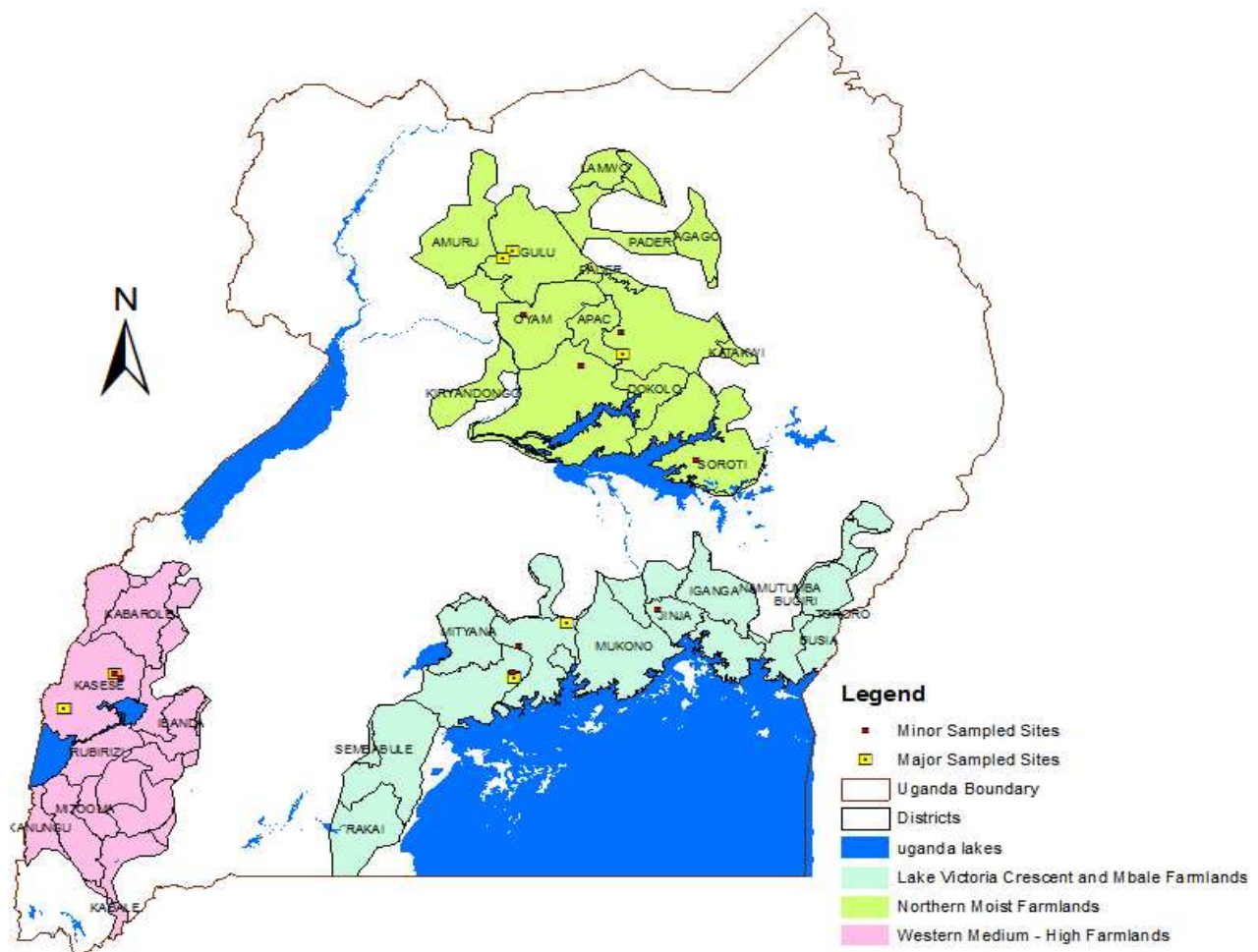


Fig.1: The location of the three Agro ecological zones in Uganda and the major and minor sampling sites. Details of the agro ecological zones are provided by Wortman and Eledu (1999).

To estimate the relative contribution of each variable in the final model, a jackknife analysis was applied (Phillips *et al.*, 2006). The Bioclim model was built using its implementation in DIVA-GIS 5.4 (Hijmans and Graham, 2006; Echarri *et al.*, 2009). Bioclim is a frequency distribution based algorithm which extracts values of each bioclimatic variable that define the bioclimatic profile of each species delimiting the so called “envelope”, i.e. the climatic conditions that bound all occurrence localities (Guisan and Zimmermann, 2000). In the potential distribution maps, grid cells are scored as suitable (if within the envelope; i.e. the presence of the species can be expected) or unsuitable (if outside the envelope).

Model Evaluation and Bioclim Envelope Assessment

The original data set was split and a subset of 25% presence points was set apart as a test sample. The model was then run using the remaining 75% of the original presence data (training sample), randomly resampled in 20 repetitions (Pearson, 2007; Echarri *et al.*, 2009). Models obtained in these repetitions were superimposed to get a first visual evaluation of their mutual consistence and with the model built using the full dataset. Subsequently, the accuracy of the model was evaluated by calculating the AUC (area under curve) in a receiver operating characteristic plot. AUC values vary from 0.5 (model not better than random) to 1.0 (perfect

accuracy as indicative that the model can discriminate perfectly between presences and absences of records (Graham and Hijmans, 2006). To assess the influence of bioclim variables on fruit fly species niches, Principal Component Analysis (PCA) of the bioclim envelopes was done. PCA in this case was used for reduction of the data set to only two variables (the two first components) using Pearson (n-1) correlation type and varimax rotation (Kaiser normalization) rotation.

RESULTS

Records of Fruit Flies and Potential Distribution in Uganda

Existing and new records of fruit fly distribution in Uganda were made across the country in most of the major agro-ecological zones with the exception of the North eastern short grass plains, Northern grass-farm bush transition, North central farm bush, in northern Uganda, while in the west, Bushenyi, South western-medium-high farmlands, Kabale-Rukungiri highlands and the Kisoro-Kibale highlands zones. In all the zones, detection for *Bactrocera invadens* was very predominant, while *Dacus cilliatu*s was the most specialized species, recording a few detections in selected zones (Wortman and Eledu, 1999).

Bioclimatic profiles of fruit fly species

The bioclimatic profiles of the niches of the ten species are summarized in Tables 2. All the 19-bioclimatic variables were classified into two principal components: precipitation (PC-1 = 61.419%) and temperature (PC-2 = 29.214%) and overall cumulative variability of the first three components accounting for 96.814% (Table 1). PC-3 was related to elevation and temperature seasonality; hence temperature variability was increasingly significant along the altitude gradient. Some temperature variables were correlated with

precipitation components (Bio2, Bio4, and Bio7), while precipitation seasonality (Bio15) was correlated significantly on the temperature component.

Generally, all species were responsive to both precipitation and temperature variables though at varying degrees and orders. However, *D. cilliatu*s was significantly negatively correlated with the precipitation component (PC1) and the temperature component (PC2). The 10 species classified into three broad groups *viz.* group one (*C. cosyra*), group two (*D. cilliatu*s, *C. anonae*, *B. invadens*, and *D. punctatitrons*), group three (*C. capitata*, *C. fasciventris*, *T. coffeae*, *D. bivittatus* and *B. cucurbitae*). Among the three groups, highest similarities in requirements were recorded among *D. bivittatus* and *B. cucurbitae* > *C. capitata* and *C. fasciventris*, and > *C. anonae* and *B. invadens*. The bioclimatic envelopes or the climatic component of the fundamental ecological niche, or the 'climatic niche' of the 10 species are provided in Tables 2.

Potential Range

Generally, there was close agreement by the two models (Maxent and Bioclim) on the distribution probability and suitability patterns (Fig.2, I-XI). The outputs of both models generally match the main fruit agro ecological zones (Lake Victoria Crescent, Northern Moist Farmlands and Western Mid Altitude High Farmlands (Wortman and Eledu, 1999). The central and mid northern areas were consistently recorded the highest probability and suitability as was the case for most incidence records (Fig.1). Northern moist farmlands, Central farm and bush lands and Usuk sandy farm-grasslands (here after all referred to as Northern moist farmlands, NMF), Central buruli farmlands, Western clay loam farmlands and Central wooded savanna (here after referred to as Central wooded savanna, CWS), Southern and Eastern lake Kyoga basin (SELKB), and

Table 1: Result of the Principle Component Analysis (PCA) of the Bioclimatic variables (Environmental variables) in relation to the ten (10) species assessed in the study. PC-1, 2, and 3 denote the first three Principle Components in that order.

Variable	Variable type	Factor Loadings		
		PC-1	PC-2	PC-3
Bio1	Annual mean temperature	0.087	0.900	0.005
Bio2	Mean diurnal range: mean of monthly	0.633	0.093	0.216
Bio3	Isothermality: (P2/P7) × 100	0.021	0.928	0.043
Bio4	Temperature seasonality (SD × 100)	0.309	0.157	0.521
Bio5	Maximum temperature of warmest month	0.086	0.902	0.005
Bio6	Minimum temperature of coldest month	0.014	0.982	0.003
Bio7	Temperature annual range (P5 – P6)	0.572	0.211	0.167
Bio8	Mean temperature of wettest quarter	0.013	0.982	0.004
Bio9	Mean temperature of driest quarter	0.067	0.931	0.001
Bio10	Mean temperature of warmest quarter	0.062	0.935	0.001
Bio11	Mean temperature of coldest quarter	0.013	0.983	0.003
Bio12	Annual precipitation	0.980	0.014	0.005
Bio13	Precipitation of wettest month	0.980	0.014	0.005
Bio14	Precipitation of driest month	0.980	0.014	0.005
Bio15	Precipitation seasonality	0.118	0.263	0.171
Bio16	Precipitation of wettest quarter	0.980	0.014	0.005
Bio17	Precipitation of driest quarter	0.980	0.014	0.005
Bio18	Precipitation of warmest quarter	0.980	0.014	0.005
Bio19	Precipitation of coldest quarter	0.980	0.014	0.005
<i>C. anonae</i>		0.781	0.364	0.201
<i>D. bivittatus</i>		1.184	0.400	0.002
<i>C. capitata</i>		0.519	0.404	0.016
<i>D. ciliatus</i>		0.218	2.831	0.000
<i>T. coffeae</i>		0.680	0.282	0.023
<i>C. cosyra</i>		1.570	0.113	0.166
<i>B. cucurbitae</i>		1.184	0.400	0.002
<i>C. fasciventris</i>		0.463	0.329	0.003
<i>B. invadens</i>		0.545	0.384	0.183
<i>D. punctatifrons</i>		1.353	0.156	0.195
Eigen-value		11.670	5.551	1.174
Variability (%)		61.419	29.214	6.180
Cumulative %		61.419	90.633	96.814

Jinja and Mbale farmlands and Lake Victoria Crescent (Lake Victoria Crescent and Mbale farmlands, LVCMF) recorded the highest suitability ranges for all the species.

B. invadens, *T. coffeae*, *C. fasciventris*, *C. cosyra*, and *D. bivittatus* suitable areas/ niches were higher under Bioclim, while *C. anonae*, *C. capitata*, *C. cosyra*, *B. cucurbitae* and *D. punctatifrons* showed higher suitability under Maxent (Fig.3, I - XI and 4, All). The highest range was recorded for *T. coffeae*, *C. fasciventris*, *C. capitata*, and *B. invadens*, while the least range species were *B. cucurbitae*, *D. ciliatus*, *D. bivittatus* and *C. anonae*. Among all the zones, SELKB recorded to be the most suitable for all species but the *D. ciliatus*, *C. anonae* and *B. cucurbitae* (Fig.2, I - XI). Similar findings were made for the NMF, except that in this case *B. cucurbitae* bioclimatic requirements were fairly suitable. Bioclim also indicated potential distribution of fruit flies in the poorly sampled greater Karamoja region which was initially thought to be too warm for establishment (Figures 2, XI). Likewise, both models project species ranges north- and north western, although with differing intensities (Fig.2, I - XI and 4, All). The projections into the north and south western are more continuous though with low probability in Maxent, but with fairly good representation in Bioclim (Figure 2, II, IV, V, VII, and VIII).

In western Uganda, south western-medium-high farmlands, Kabale-Rukungiri highlands and the Kisoro-Kibale highlands zones are generally unfavorable sites for fruit fly distribution but these are potential zones for *T. coffeae*, *D. bivittatus* and *B. invadens* (Fig.3, II, VIII and X). Generally, drier and high altitude zones were found unsuitable for all the species in the study. Indeed, with the exception of *C. capitata*, *C. fasciventris*, *C. cosyra* and *T. coffeae*, Maxent model gives low probability for high

altitudes and the extreme northern and southern zones while Bioclim remarkably ranks the same sites as a marginal sites (Fig.3, I-XI). Both models over predict suitability for some species including over water bodies.

Limiting Factors and Relative Importance of Variables

The relative important of bioclimatic variables is illustrated in Fig.3. Precipitation variables played the highest role in clearly restricting distribution of *B. invadens*: the five most limiting factors (Bio12 > Bio13 > Bio 18 > Bio16 > Bio 19) were all precipitation variables, while some temperature variables also affected site suitability (Bio4 > Bio3 > Bio9 > Bio 6). Extreme lows and highs of the limiting variables associated with the far north eastern (Northern short grass plains), areas surrounding the Albert Nile and the South western grasslands are unfavorable, while SELKB, NMF, CWS and some parts of LVC attain the optimum precipitation, temperature seasonality and Isothermality conducive for *B. invadens* (Fig. 3).

Precipitation variables were critically more important in the distribution of *D. punctatifrons*, but the effect was more to annual precipitation distribution than annual means (Fig.3). Quarter (Bio19 and Bio17), monthly means (Bio14) and precipitation variability/ seasonality (Bio15) were the most limiting variables. Low monthly (Bio14) and quarterly (Bio17) precipitation of the driest period significantly negatively affected *D. punctatifrons*, while increasing precipitation seasonality beyond 33 (coefficient of variation) leads to low suitability, just like extremes of precipitation of coldest quarter. Two more variables linked to temperature (Bio3: Isothermality) and precipitation (Bio16: Precipitation of wettest quarter) are relevant when the range is considered in totality, i.e. they show the higher decrease in the gain when omitted (Fig. 3). Consequently, the importance of temperature and precipitation variables in constraining the climatic niche of *D. punctatifrons* into central and marginally western Uganda is emphasized (Fig. 2 I).

Table 2: Mean (average), Minimum (lower boundary) and Maximum (upper boundary) bioclimatic variables/ conditions (temperature (°C) and rainfall (mm)) of the niches of 10 fruit fly species. BIOI-BIO19 are defined in Table 1.

Variable	<i>C. anonae</i>			<i>D. bivittatus</i>			<i>C. capitata</i>			<i>D. ciliatus</i>			<i>T. coffeae</i>			<i>C. cosyra</i>			<i>B. cucurbitae</i>			<i>C. fasciventris</i>			<i>B. invadens</i>			<i>D. punctatifrons</i>		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
Bio1	28.1	31.1	26.2	30.5	31.6	27.3	29.7	31.6	26.2	21.5	27.5	21.5	29.3	31	24.6	27.9	31.7	16.4	30.5	31.6	27.3	29.4	31.6	25.8	29.1	34.1	16.4	27.6	30.8	25.8
Bio2	13.5	14.2	13.2	15.3	15.3	13.1	14.9	16.3	12	14	13.3	14	14.8	15.3	14.4	14.3	15.9	13	15.3	15.3	13.1	14.7	15.6	14.9	14.6	17.5	13	13.4	15	14.9
Bio3	94.3	93.8	94.9	94.9	94.5	94.3	94.8	95.1	93.8	97.5	94.4	97.5	94.9	94.7	96.4	95.1	94.8	99.1	94.9	94.5	94.3	94.8	94.7	96.3	94.9	95.1	99.1	94.5	94.5	96.3
Bio4	106.1	106.1	106.1	72	72	72	133.9	133.9	133.9	303.6	303.6	303.6	146	146	146	484	484	484	72	72	72	132.9	132.9	132.9	238.2	238.2	238.2	105.3	105.3	105.3
Bio5	29	32	27	31.4	32.5	28.1	30.6	32.6	27	22.1	28.3	22.1	30.2	31.9	25.4	28.7	32.7	16.8	31.4	32.5	28.1	30.2	32.6	26.6	30	35.1	16.8	28.4	31.7	26.6
Bio6	14.7	16.9	13	15.3	16.3	14.3	14.9	15.5	14.2	7.7	14.3	7.7	14.7	15.8	10.4	13.7	15.9	3.7	15.3	16.3	14.3	14.8	16.1	11.1	14.5	16.7	3.7	14.2	15.8	11.1
Bio7	14.3	15.1	13.9	16.1	16.2	13.9	15.7	17.1	12.8	14.4	14.1	14.4	15.6	16.2	14.9	15	16.8	13.1	16.1	16.2	13.9	15.5	16.5	15.5	15.4	18.4	13.1	14.2	15.9	15.5
Bio8	15.2	17.2	13.9	15.7	16.6	14.9	15.5	15.9	14.9	8.3	14.9	8.3	15.2	16.3	10.9	14.1	16.3	4.1	15.7	16.6	14.9	15.3	16.5	11.9	15	17.4	4.1	14.8	16.2	11.9
Bio9	27.1	29.1	25.4	28.7	29.4	26.5	28.1	29.5	25.4	20.6	26.9	20.6	28	29.4	23.8	26.4	29.6	15.3	28.7	29.4	26.5	27.9	29.5	25.2	27.6	31.5	15.3	26.5	28.9	25.2
Bio10	26.7	28.7	25	28.3	29	26.1	27.7	29.1	25	20.3	26.6	20.3	27.6	28.9	23.5	26.1	29.2	15.1	28.3	29	26.1	27.5	29.1	24.9	27.2	31.1	15.1	26.2	28.5	24.9
Bio11	14.1	16	12.9	14.6	15.5	13.8	14.4	14.8	13.8	7.7	13.8	7.7	14.1	15.1	10.2	13.1	15.2	3.9	14.6	15.5	13.8	14.2	15.3	11	14	16.2	3.9	13.7	15.1	11
Bio12	1191.9	1383	842	1015.1	1240	904	1081.4	1383	904	114.5	1361	114.5	1063.6	1391	707	1296.1	1622	1226	1015.1	1240	904	108.4	1383	842	1192.4	1622	768	1253.9	1383	114.2
Bio13	889.1	1031.7	628.1	757.3	925	674.4	806.7	1031.7	674.4	854.2	1015.3	854.2	793.4	1037.7	527.4	966.9	1210	914.6	757.3	925.4	674.7	808.7	1031.7	628.1	889.5	1210.9	572.9	935.4	1031.7	851.9
Bio14	997.6	1157.6	704.8	849.6	1037.9	756.6	905.1	1157.6	756.6	958.4	1139.2	958.4	890.2	1164.3	591.8	1084.9	1357.6	1026.2	849.6	1037.9	756.6	907.3	1157.6	704.8	998.1	1357.6	642.8	1049.5	1157.6	955.9
Bio15	305.7	327.1	248.6	258.5	276.5	210.2	322.7	345.3	262.4	183.8	196.7	149.5	362.4	387.7	294.7	267.8	286.6	217.8	258.5	276.5	210.2	333.7	357.1	271.4	285.5	305.5	232.2	150.3	160.8	122.2
Bio16	793.8	921.1	560.8	676.1	825.8	602.1	720.2	921.1	602.1	762.6	906.4	762.6	708.4	926.4	470.9	863.2	1080.3	816.5	676.1	825.8	602.1	721.9	921.1	560.8	794.1	1080.3	511.5	835.1	921.1	760.6
Bio17	932.1	1081.5	658.4	793.8	969.7	706.9	845.6	1081.5	706.9	895.4	1064.3	895.4	831.7	1087.8	552.9	1013.6	1268.4	958.7	793.8	969.7	706.9	847.7	1081.5	658.4	932.5	1268.4	600.6	980.6	1081.5	893
Bio18	817.6	948.7	577.6	696.4	850.6	620.1	741.8	948.7	620.1	785.5	933.6	785.5	729.6	954.2	485	889.1	1112.7	841	696.4	850.6	620.1	743.6	948.7	577.6	818	1112.7	526.8	860.2	948.7	783.4
Bio19	612.6	710.9	432.8	521.8	637.4	464.7	555.8	710.9	464.7	588.5	699.6	588.5	546.7	715	363.4	666.2	833.7	630.2	521.8	637.4	464.7	557.2	710.9	432.8	612.9	833.7	394.8	644.5	710.9	587

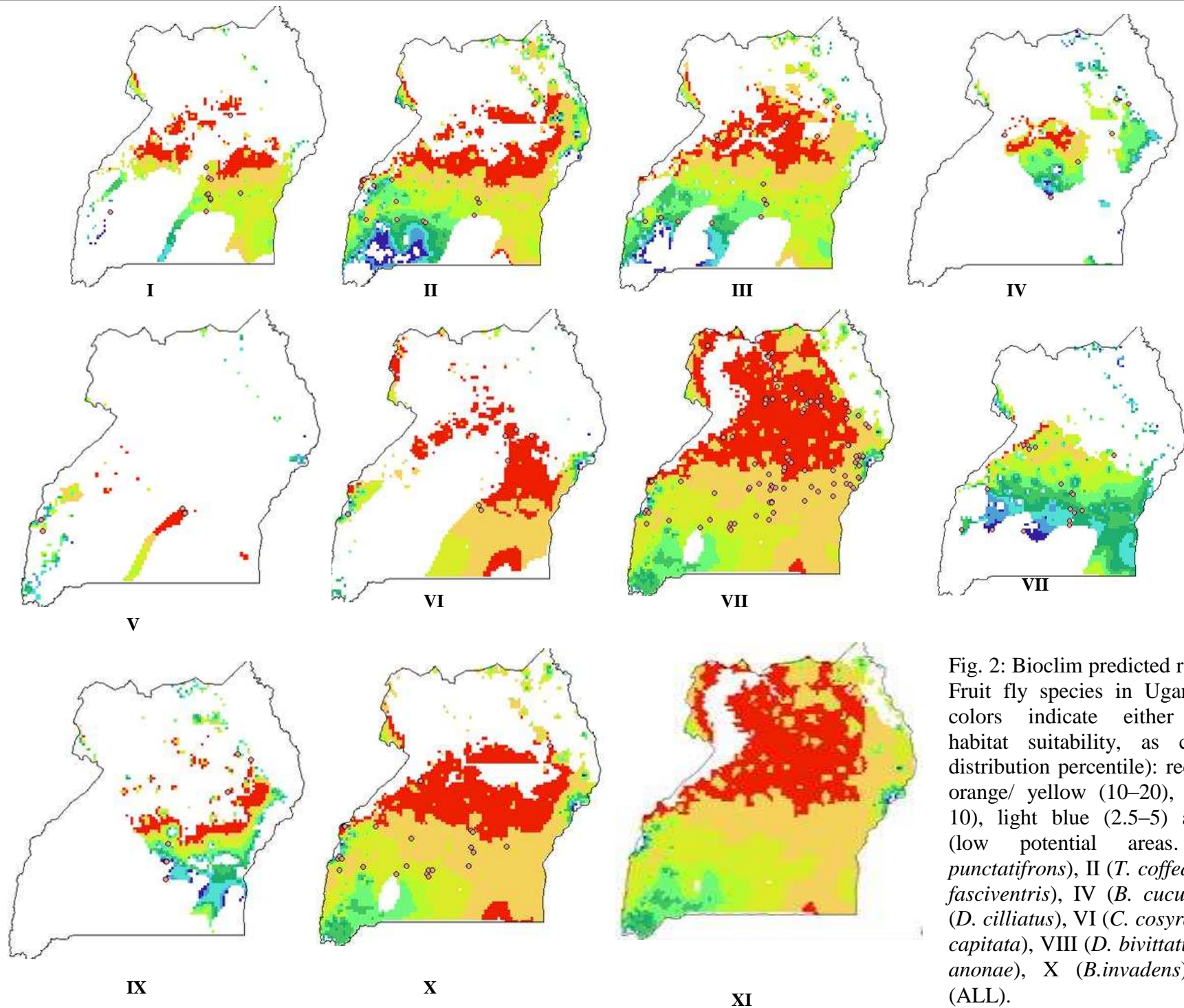


Fig. 2: Bioclim predicted range of 10 Fruit fly species in Uganda. Code colors indicate either climatic/habitat suitability, as cumulative distribution percentile): red (20–34), orange/ yellow (10–20), green (5–10), light blue (2.5–5) and white (low potential areas. I (*D. punctatifrons*), II (*T. coffeae*), III (*C. fasciventris*), IV (*B. cucurbitae*), V (*D. cilliatius*), VI (*C. cosyra*), VII (*C. capitata*), VIII (*D. bivittatus*), IX (*C. anonae*), X (*B. invadens*) and XI (ALL).

Precipitation variables played a significant role in restricting the distribution of *C. anonae* too. The six most limiting factors (Bio15 > Bio17 > Bio 14 > Bio18 > Bio 19 > 12) were all precipitation variables with a few temperature (Bio7 > Bio4 > Bio2) variables also affecting site suitability variability. The optimum conditions for *C. anonae* are in sites with low precipitation seasonality (Bio15), annual temperature consistence (low range: Bio7), small temperature seasonality (Bio4) and diurnal temperature (Bio2). Low monthly (Bio14), precipitation of warmest quarter (Bio18) and quarterly (Bio17) precipitation of the driest period significantly negatively affected *C. anonae*. Unit increase up to optimum (sigmoid) increases the probability of incidence, while extremes annual precipitation (Bio12) and precipitation of coldest quarter (Bio19) lead to low site suitability (Fig. 3).

Higher temperature means of the driest quarter (Bio9), temperature annual range (Bio7) and temperature seasonality (Bio4), coupled with low Isothermality (Bio3) and precipitation of warmest quarter and moderate precipitation of coldest quarter increase suitability for *B. cucurbitae*. This combination of bioclimatic variables restricts *B. cucurbitae* to central and sporadic distribution to the east and northeastern Uganda (Fig.2). The three most important precipitation variables for *C. capitata* were Bio14, Bio15 and Bio17, while the temperature variables included Bio2 and Bio3. Low values of Bio15 and the temperature variables increased *C. capitata* suitability, while the reverse was the case for Bio14 and Bio15. The observed wider range distribution predicted for *C. capitata* under the Maxent model (Fig.3) is commensurate with this requirement, while eastern Uganda distribution is also predicted under the Bioclim model (Fig.2 VII).

Areas with higher volumes of precipitation of driest month and quarter were associated with higher

probabilities of *D. bivittatus*, *C. cosyra* and *C. fasciventris* incidence and increased precipitation seasonality negatively affected suitability for these species. Precipitation of warmest quarter increased but higher levels of Isothermality decreased *C. cosyra* suitability. Likewise, precipitation of coldest quarter (Bio19) decreased, while increased Isothermality increased *C. fasciventris* suitability. Suitability of *D. bivittatus* was increased by the moderate precipitation of coldest quarter and temperature seasonality and decreased by increased temperature annual range and maximum temperature of warmest month. Areas suitable for *T. coffeae* were characterized with comparatively low Bio12, Bio13, Bio15, Bio16, Bio19, and Bio4 (Fig. 3).

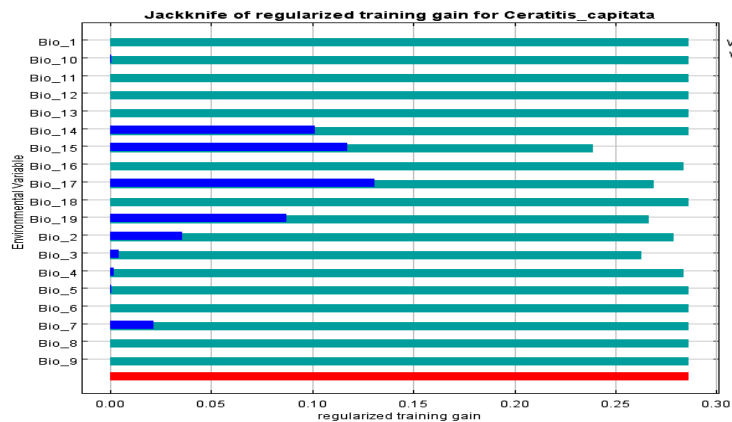
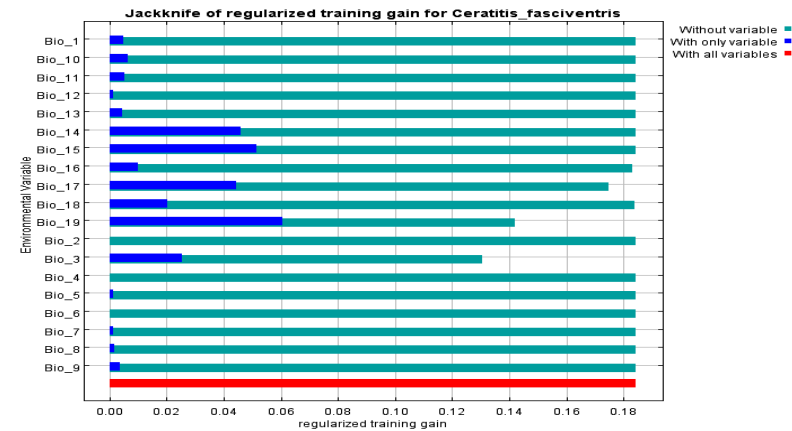
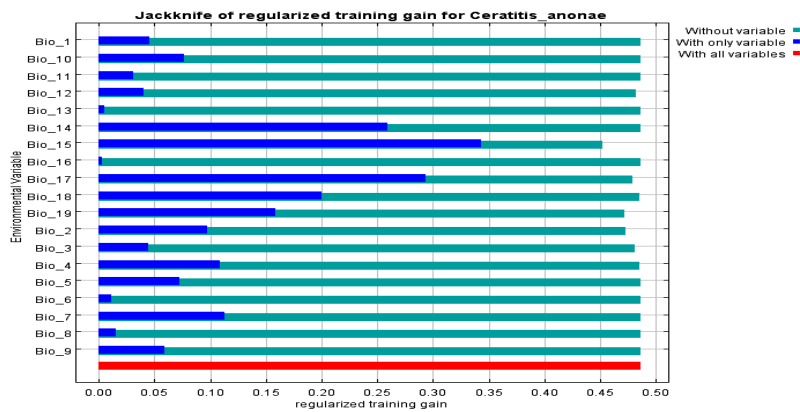
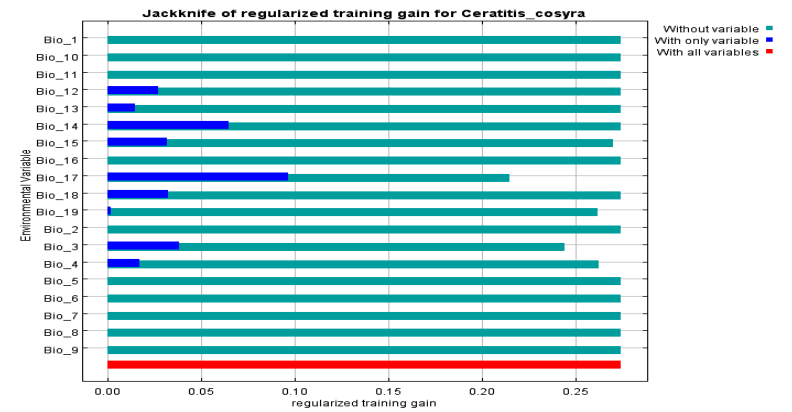
Model Performance

The Maxent generated models proved mostly excellent in performance both for the training and test data (Fig. 3). The Area under Curve values (AUC) were of high accuracy ranging between 0.815 – 0.974 in *C. capitata* and *C. cosyra*, respectively for training data. However, for some species test data AUC were random: *B. cucurbitae* (0.500) and *C. capitata* (0.486), while excellent AUC for test data were recorded with *C. cosyra* (0.965), *D. punctatifrons* (0.904) and *B. invadens* (0.902). Apart from the statistical meaning, the modeling proved to be in agreement with the expected fruit fly range. Higher altitude zones in Kasese, Kisoro, Mbale and Karamoja farmlands (Fig. 2 and 3) matched negative areas of the models, which reflected a correct prediction in this sector.

Discussions

Potential Distributions of the 10 species in Uganda

This study presents the first local attempt at understanding the spatial suitability of fruit fly distribution in Uganda. The results suggest higher suitability for most species considered (Figure 3). The 10 species modelled are predicted to be ubiquitous



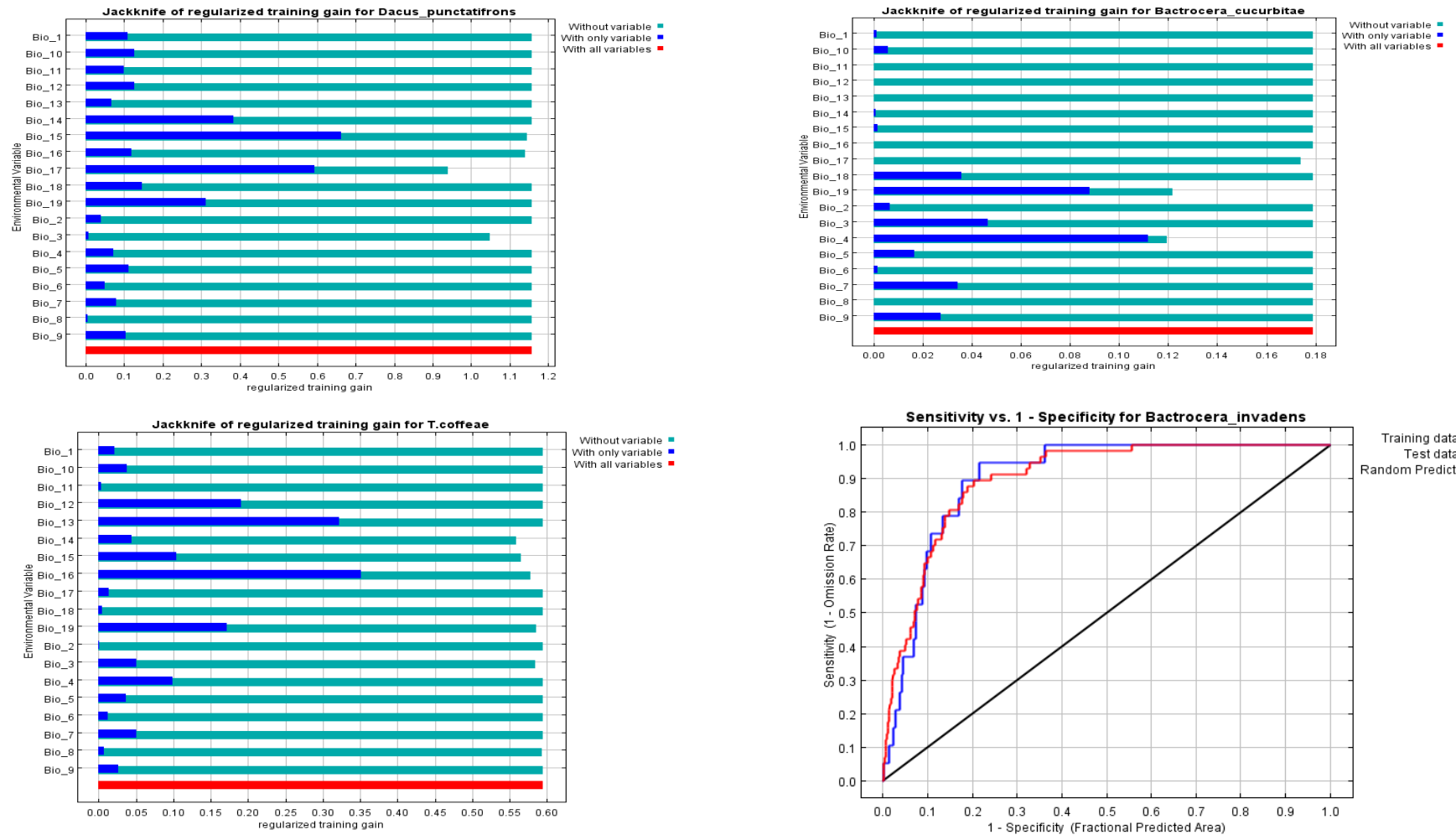


Figure 3: Maxent based Jackknife of the regularized training gain: without variable (light blue), with only variable (blue), with all variables (red) and the 10 Receivership Operating Curves (ROC). Code colors in the close-up maps indicate suitability shown as probability: red (0.90–1), orange (0.80–0.90), green (0.65–0.80), and light blue (0.50–0.65). ROC curves show the area under curves both for training and test data. The Receivership Operation Curve (ROC) for *B. invadens* is indicated in the lower bottom corner.

in the central (LVC and MF) and mid-northern regions, areas associated with favorable precipitation (1215 mm - 1328 mm) distribution and optimum temperatures for fruit flies. These suitable areas receive two rainy seasons with the main season from March to May with a peak in April and secondary season from August to November with a peak in October/November. The areas experience a main dry season December to February, and a secondary dry season between June and July. Temperature ranges from 15 – 32.5 °C, while altitude ranges from 914 – 1,800 m ASL (Wortman and Eledu, 1999), encompassing the majority of the fruit fly species envelopes.

Most species have the potential to extend north and southwestwards and inhabit considerable areas there. The suitability of the extreme south, northeastern, Rwenzori, Elgon and around Albert Nile is low for most species; hence these areas might remain restrictive to the spread of fruit flies. These distributions correspond very well to an intolerance of high altitudes, aridity potentials (north-eastern) and precipitation extremes (Stephens *et al.*, 2007; De Meyer *et al.*, 2010; Geurts *et al.*, 2012).

Bactrocera invadens is the most serious fruit fly pest in the country (Nemeye, 2005; Okullokwany, 2006) and the region (Mwatawala *et al.*, 2006a; Rwomushana *et al.*, 2008; Geurts *et al.*, 2012), and has the widest host/distribution range because of its ability to tolerate diverse environmental conditions (De Meyer *et al.*, 2010). The predicted distribution of *B. invadens* in this study is consistent with other regional studies (Ekesi and Billah, 2006; De Meyer *et al.*, 2010). The observed ardent response of *B. invadens* to precipitation and some temperature variables confirmed the earlier findings that *B. invadens* prefer hot and humid environments (De Meyer *et al.*, 2010). Annual precipitation must be high, although it does not have to be continuous, as was the case of *B. invadens* quarterly and monthly means relevance in the findings.

Suitable *B. invadens* identified in central and mid north zones are characterized by moisture rich short dry season, a distinct dry period with driest-month precipitation (Wortman and Eledu, 1999), favorable for *B. invadens* (Ekesi and Billah, 2006; De Meyer *et al.*, 2010. Mwatawala *et al.* (2006a) too confirmed these findings.

With slight exceptions mainly with *C. capitata* and *D. ciliatus*, suitability breadth of the rest of the species in this study agree with the earlier potential distribution predictions by Ekesi and Billah (2006) (Fig. 2 and 3). This is probably because the latter in most cases used few incidence points and modeled at a larger African scale. For instance, their predictions for *D. ciliatus* and *D. punctatifrons* were all based on one incidence point, while most of the other species were based on less than five points in the Ekesi and Billah (2006) study. The latter also predicted a more northern extent for *C. capitata* (based on two points), while this study's results showed a more central and wider extent. The use of fewer sample points may be the reason, although according to Pearson (2007), Maxent can still retain high success rates and predictive qualities when the sample sizes are small. Central and mid-northern zones were found to be highly suitable for *C. capitata*, but differences between the two models were evident, as De Meyer *et al.* (2008) too reported.

Principal Component Analysis (PCA) and Jackknife tests indicated that precipitation and temperature variables have more influence on potential distributions and suitability of all species in this study. Temperature has a significant influence on fruit fly physiology, such as population density, gross fecundity, female and male longevities and generation time (Duyck and Quilici, 2002). The relationship between temperature variables and suitability observed for *C. capitata* has already been reported elsewhere (White and Elson-Harris, 1992; Duyck and Quilici, 2002). A humid atmosphere and soil, instead of precipitation directly has been reported to influence the survival of fruit fly pupae, which favors desiccation resistant species such *C. capitata* to survive in drier zones.

hence increasing their breadth (Duyck *et al.*, 2006).

Substantial overlap appears to exist in the potential distributions of most species. For example, *B. invadens*, *T. coffeae*, *D. bivittatus* and *C. faciventris* seem to have broadly similar potential ranges (Fig. 2, II, III, IV, V). An obvious difference in the predictions among these species is the extreme wetter southern zones slightly suitable for *B. invadens* and *D. bivittatus*, but poorly tolerant to the other two. Low temperatures and higher humidity in those sites, favour *B. invadens* over *T. coffeae* and *C. faciventris* that is more sensitive to low humidity (Rwomushana *et al.*, 2008); which would support the study's predictions. Rwomushana *et al.* (2008) also reported significant differences in performance of *C. cosyra* over *B. invadens* under fluctuating temperature. *B. invadens* was more competitive under low temperatures (characteristic on the southern parts of Uganda), which might explain the absence of *C. cosyra* suitable niches in this region. This might provide some insight into the unknown extent to which these species co-exist in the wild.

Precipitation distribution is an important determinant fruit fly species ranges, assuming optimum temperature. Much of Uganda has meaningful altitudinal differences in short distances, so that both temperature and precipitation gradients are common. This probably limits distribution on northeastern and mostly western zones. The close relationship *Bactrocera* and *Ceratitis* species ranges depicted in the models in this study most likely influences partitions and suitability between the two genera (Rubio and Acosta, 2010; Geurts *et al.*, 2012).

Bioclim and Maxent Predictive Capabilities

Superiority of the Maxent algorithm over Bioclim (Fig. 2 and 3) is consistent with related studies (Elith *et al.*, 2006; Phillips *et al.*; 2006; Rubio and Acosta, 2010). This is partly because the prediction maps made

by Maxent are generally suitable for processing at a high threshold, which gives a qualitative suitability judgment for each grid (Rubio and Acosta, 2010). However, the bioclimatic analysis proved to be a valuable means to get insight of the fundamental niche features of the ten fruit flies in Uganda, which will improve the ecological knowledge of Tephritids in the country.

One of the fundamental criticisms of Ecological Niche Modelling (ENM), particularly Bioclim method is that models are not built with vegetation variables, as was the case in this study. Vegetation is generally assumed to be a critical determinant in the presence or absence of most species (Rubio and Acosta, 2010). In that sense, the correct prediction of absence, as matched in most northeastern, Elgon and Rwenzori peaks was "absent", offers further support of the soundness of the models. This predictive value is appreciated as a remarkable strength of ENM (Rubio and Acosta, 2010).

It has been suggested that no single modeling method has the complete truth (Elith *et al.*, 2006), so that comparative analyses like this may help to gain a better understanding. Ranges obtained with Bioclim, despite its lower computational performances, probably look biogeographically more realistic for fruit fly species that have been previously predicted to be ubiquitous across the country. However, Bioclim appears to be more sensitive to the record set bias and to concentrate more in areas where point density is higher, such as central Uganda, which has been reported elsewhere (Rubio and Acosta, 2010). Both Bioclim and Maxent agreed in detecting a presumable high suitability zones, where detection has not been done yet: North eastern short grass plains, Northern grass-farm bush transition, North central farm bush, in northern Uganda, while in the west, Bushenyi, South western-medium-high farmlands, Kabale-Rukungiri highlands and the Kisoro-Kibale highlands zones.

Conclusions

Fruit flies pose a significant threat countrywide. Among the abiotic factors for suitability, precipitation and temperature were found the most significant that determined distribution of fruit flies. Both models used in this study were in close agreement spotting the distribution and suitability patterns matching the main fruit agro ecological zones. Central and mid north zones provided the most suitable habitats, while the western, north eastern and areas around Albert Nile were characterized as marginal. The continued study of the species is warranted, particularly their ecological impacts. These results provide an initial insight into the bioclimatic tolerance of fruit flies and also help in identifying sites for future sampling and management efforts. Several avenues exist to improve the accuracy and value of habitat suitability maps for these species, including, inclusion of edaphic and host plant data. There is also an urgent need for widespread monitoring surveys to ground-truth the suitability across the country. Such information will help evaluate modeling performance and also reduce apparent commission errors.

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