

Projections of Climate-induced Future Range Shifts among Fruit Fly (Diptera: Tephritidae) Species in Uganda

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Abstract

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The potential impact of future climate change on fruit fly species distribution was assessed in Uganda using two general circulation models (HADCM and CCCMA) and two future predicted CO₂ emission scenarios (A2 and B2), under both full and no species dispersal modes. Future ranges were overall projected to decline by 25.4% by year 2050. Under full-dispersal, *D. ciliatus* > *C. cosyra* > *B. invadens* ranges were predicted to increase, while the rest are likely to decrease. In the no-dispersal scenario, a significant average decrease in size of niches is predicted. Range losses are predicted higher under B2 than A2. Future niches will likely shift to northern Uganda. The results should assist in the development of climate change adaptive pest management strategies.

Keywords: climate change; dispersal; *Bacrocera*; niche

Global climate continues to change (IPCC 2007). For agriculture, climate change will be significant, as such changes are associated with shifts in pest and disease ranges, posing new risks to food and farming (COOPER *et al.* 2013). To better understand the potential impacts of the current warming trends, considerable effort has gone into predicting the effect of future climate scenarios (MCKENNEY *et al.* 2007). MCKENNEY *et al.* (2007) examined the potential redistribution of North American plants as a result of climate change and dispersal, and found major redistribution pressures under the different scenarios.

Mean temperature increases of about 5°C in Peru during the 1997 El Niño resulted into decreased infestation by the leaf miner fly (*Liriomyza huidobrensis*), and an increased infestations by the bud midge (*Prodiplosis longifila*) (CISNEROS & MUJICA 1999). Range shifts among tephritid fruit flies also have been predicted to alter considerably with climate change. For instance, *Bactrocera cucurbitae*, *B. dor-*

salis, and *B. latifrons* have been projected to shift ranges throughout the Japanese Archipelago due to climate change (FAO 2008). Climate change has also been demonstrated to affect tephritid fruit flies at the regional scale (STEPHENS *et al.* 2007; DE MEYER *et al.* 2010) or in other countries (LIU *et al.* 2011).

In East Africa climate change has been reported: temperatures are rising, rainfall is increasing in some areas and declining in others, seasonal patterns and pest and disease distribution are changing, and extreme weather events are becoming more frequent and severe (COOPER *et al.* 2013). In Uganda, changing climate, characterised by increasing temperatures and infrequent rainfall peaks, especially in the drier periods has been reported (Climate Change Unit 2014). If species range shifts are the likely dominant species response to future climate change, then spatially explicit planning will be fundamental to estimating the rate and direction of pest species movements to ensure real time response.

This study therefore was set out to predict the potential impacts of climate change on the climatic ranges of 10 fruit fly species in Uganda under two dispersal and CO₂ emission scenarios interpolated through two general circulation models (GCMs). Specifically, this study aimed at understanding how local-level distribution patterns may be expected to change under future climate change and the comparative potential range shifts among the 10 species. The study would hopefully gauge the proportion of species under severe threat of exacerbation under the projected climate change scenarios and dispersal options, and the implications of these patterns for pest management in the country.

MATERIAL AND METHODS

The species assessed were: *Bactrocera invadens* (Drew, Tsuruta and White), *Bactrocera cucurbitae* (Cockfield), *Ceratatis capitata* (Wiedemann), *Ceratatis anonae* (Graham), *Ceratatis cosyra* (Walker), *Ceratatis fasciventris* (Bezzi), *Dacus punctatifrons* (Karsch), *Dacus bivittatus* (Bigot), *Dacus ciliatus* (Loew), and *Trirhithrum coffeae* (Bezzi). 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 fruit growing agro-ecological zones in Uganda (WORTMAN & ELEDU 1999) (Figure 1). Additional countrywide records were obtained through deliberate detections and from existing scientific literature and museum records. For all the 10 species modelled, a total of 259 unique coordinate points/sites taken from the whole Uganda were used in the model. 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 from 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.

The geographical range of the 10 species was modelled with Bioclim, a presence-only method. Bioclim model was built using its implementation in DIVA-GIS 5.4 (ECHARRI *et al.* 2009). Bioclim is a frequency distribution based algorithm, which extracts values of each bioclimatic variable that define the bioclimatic profile

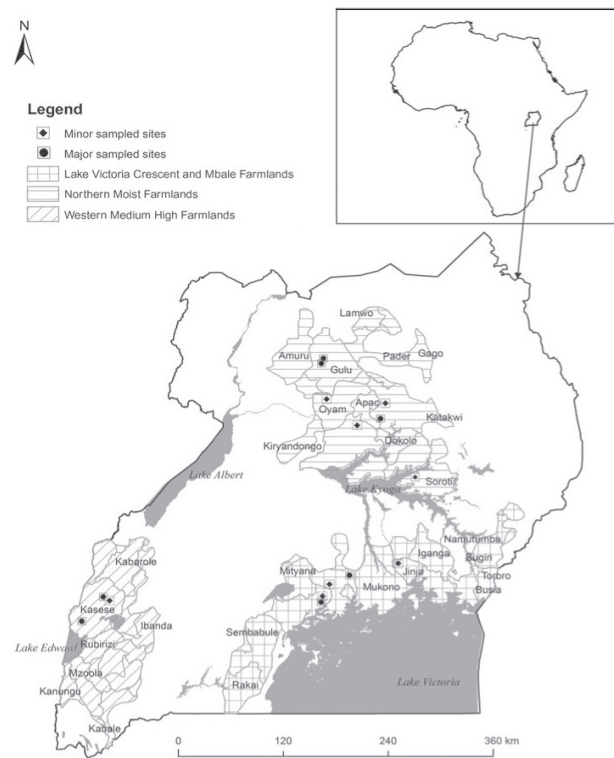


Figure 1. Location of the three agro ecological zones in Uganda and the major and minor sampling sites. Details of the agro ecological zones are provided by WORTMANN and ELEDU (1999)

of each species, delimiting the so called “envelope”, i.e. the climatic conditions that bound all occurrence localities (GUISAN & 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).

Climatic controls on current fruit fly distributions were summarised using the climatic niche of the 10 species using the climate envelope (CE) approach (NIX 1986). The study analysed CEs for full and no dispersal extreme scenarios. A CE was generated for each fruit fly species by first generating an estimate of minimum and maximum values of each climate variable of interest at each location where a species was observed. The climate variables used represented the mean values of humidity/moisture and temperature at a given location. For heat, annual mean temperature and mean temperature of the wettest quarter were chosen, while moisture gradients were represented by mean annual precipitation and precipitation of the coldest quarter. These had a 30 arc-seconds (~1 km²) partial resolution and were derived from

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the WorldClim project (<http://biogeo.berkeley.edu>). Elevation data were available for reference purposes but not used as a predictor by themselves.

From the extent of the current CE for each fruit fly species, areas of suitable climate habitat were delineated on maps for the 2000–2050 periods. Future climate variables were generated by two GCMs: HADCM and CCCMA under emission scenarios A2 and B2. Among GCMs, the Canadian GCM/CCCMA (BOER *et al.* 2000) and the UK-based Hadley GCM/HADCM (GORDON *et al.* 2000) are some of the most robust and commonly used models. In the A2 scenario, the human population is projected to be larger and greenhouse gas emissions are higher than in the B2 scenario (NAKICENOVIĆ 2000). To generate the future climate grids, average change surfaces were generated for the 2000–2050-time period by interpolating the changes predicted by each GCM and emission scenario (MCKENNEY *et al.* 2007). In the full-dispersal scenario (populations are able to migrate entirely into their future climate habitat), changes in CE were calculated by expressing the future CE area as a percentage of the current CE area. For the no-dispersal scenario (unable to migrate quickly enough), future maps were laid over the current maps and only the area of overlap was taken as the future distribution. Once the future CE was defined in this way, change metrics were calculated in the same way as for the full-dispersal scenario.

Model accuracy was evaluated using AUC (area under curve) in a receiver operating characteristic plot (ISABIRYE *et al.* 2015). AUC values vary from 0.5 (model not better than random) to 1.0 (perfect accuracy indicating that the model can discriminate perfectly between presences and absences of records (GRAHAM and HIJMANS 2006)). Two measures were used to assess the potential impact of climate change on fruit fly species composition in the three main mango-growing regions: Northern Moist Farmlands (NMF), Western Mid-altitude High Farmlands (WMHF), and the Lake Victoria Crescent (Figure 1). Predicted current and future local species richness at each of the regions were calculated and compared as recommended by BUISSON *et al.* (2010). To assess the potential reorganisation of fruit fly species, CE richness maps were generated for the current time period and the 2050 time period under the A2 and B2 scenarios. The CEs for all species were overlaid, the number of CEs that fell in any given grid cell was counted, and then the results cross of the two GCMs (MCKENNEY *et al.* 2007) was averaged.

RESULTS

The Area under Curve values (AUC) were of high accuracy ranging between 0.815–0.974 in *C. capitata* and *C. cosyra*, respectively. However, for some species test data AUC were random: *B. cucurbitae* (0.500) and *C. capitata* (0.486). Apart from the statistical meaning, the modelling proved to be in agreement with the expected fruit fly range (ISABIRYE *et al.* 2015). In the full-dispersal scenario, three species CEs increased in size, while the rest decreased (Table 1). There were significant differences ($\chi^2 = 30.830$, $df = 9$, $P = 0.000$) among the 10 species in their potential response to climate change. Particularly, *B. invadens* is projected to increase its current range in the face of climate change, while *C. cosyra* showed better resilience to climate change (Figure 2). The most concerning species with the highest rate of dispersal potential under changing country climate is *D. ciliatus* (Table 1). The species is predicted to increase its current range from 1.61 to 10.4 million ha across the country by 2050 (Table 1 and Figure 2). Among those with projected declining CEs, *Dacus bivittatus* > *Bactrocera cucurbitae* > *Ceratatis anonae* were the most climate change vulnerable; their future CEs are projected to decrease by more than 75% in size (Table 1 and Figure 3).

The average centres of future CEs are predicted to generally shift northwards for most species, with

Table 1. Fruit fly species projected changes in climate–envelope area (%)/ranges under the two dispersal scenarios

Species	Dispersal	No dispersal	Average
<i>Bactrocera invadens</i> (Drew, Tsuruta and White)	3.1	–6.9	–1.9
<i>Bactrocera cucurbitae</i> (Coquillett)	–85.8	–99.9	–92.8
<i>Ceratatis capitata</i> (Wiedemann)	–24.6	–74.5	–49.5
<i>Ceratatis anonae</i> (Graham)	–77.8	–97.6	–87.7
<i>Ceratatis cosyra</i> (Walker)	26.4	–30.9	–2.2
<i>Ceratatis fasciventris</i> (Bezzi)	–48.8	–72.3	–60.5
<i>Dacus punctatifrons</i> (Karsch)	–59.1	–96.0	–77.6
<i>Dacus bivittatus</i> (Bigot)	–93.0	–99.9	–96.5
<i>Dacus ciliatus</i> (Loew)	545.5	–47.0	249.3
<i>Trirhithrum coffeae</i> (Bezzi)	–14.1	–54.3	–34.2
Average change in envelope area	17.2	–67.9	–25.4

some species registering drastic shifts (Figure 3). The highest future species richness and suitability was projected in the North-Western Wooded Savannah (NWS), Northern Moist Farmlands (NMF), Arua Farmlands (AF), and Western Mid-Altitude Farmlands (WMHF), and in the some parts of Central Buruli Farmlands (CBF). These zones are predicted to offer the future ecological niches of *C. anonae*, *D. bivittatus*, *B. cucurbitae*, and *D. punctatifrons*. The Karamoja region in northeastern Uganda will generally be unsuitable for the future distribution of most species, as it is currently (Figures 2 and 3).

In the no-dispersal scenario, species' future CEs will drastically decrease in size by the year 2050 (Table 1). In this mode, too, the differences among species vulnerability to future climate change were significant ($\chi^2 = 31.038$, $df = 9$, $P = 0.000$). The most climate change vulnerable species are *B. cucurbitae* = *D. bivittatus* > *C. anonae* > *D. punctatifrons*, while the least affected were *B. invadens* > *D. ciliatus* and *T. coffeae* (Table 1). *D. bivittatus*, *B. cucurbitae*, and *C. anonae* under the no-dispersal scenario were only likely to retain marginal niches in WMAE, but the latter two are also predicted to retain isolated patches in the NMFs and Usuk Sandy Loams (USL) zones. In contrast, *D. punctatifrons*' distribution will be marginally possible in the NMF and NWS zones.

Generally, the results predicted fruit fly species range decline due to the anticipated climate changes during the 2050 future period (Table 1). However,

there were significant differences in response ($\chi^2 = 30.97$, $df = 9$, $P = 0.000$) among the 10 species, with only one species (*D. ciliatus*) showing higher potential for resilience to the projected climate change (Table 1). *B. invadens* and *C. cosyra* also showed negligible decline in their proportional areas in the intermediate dispersal option (average of both dispersal scenarios) (Table 2). Under this option, results showed that the species most at risk were *D. bivittatus* > *B. cucurbitae* > *C. anonae* > *D. punctatifrons*, all with approximate loss of over 75% over the 2050 future period (Table 1). Southern and western Uganda will not likely be attractive to most fruit flies.

The 10 species were predicted to show considerable changes in area of occupancy, with habitat losses higher under the B2 (30.56 ± 22.6%) but not significantly different ($P > 0.653$) with A2 (16.38 ± 21.8%) emission scenarios (Figure 4A). *D. ciliatus* registered increased habitat size fairly even in both scenarios, while *C. cosyra* showed reduced and increased habitats under A2 and B2 scenarios, respectively (Figure 4). Species most at risk under the A2 scenario were *B. cucurbitae* > *D. bivittatus* > *C. anonae* > *D. punctatifrons*, while in B2, followed the order *C. anonae* > *B. cucurbitae* > *D. bivittatus* > *C. fasciventris* over the 2050 future period (Figure 4A). Emission scenarios and dispersal options jointly explained significant variability in habitat changes ($F = 3.102$, $df = 3, 76$, $R^2 = 10.9\%$, $P = 0.032$).

The two climate-change models were qualitatively consistent in predicting distribution effects and future

Table 2. Predicted species richness and turnover under the four models and two dispersal scenarios in the three main mango-growing regions under

Model	WMHF		LVC		NMF	
	richness	turnover (%)	richness	turnover (%)	richness	turnover (%)
Dispersal						
CCMA-A	4	60	3	70	8	20
CCMA-B	4	60	3	70	8	20
HAD-A	6	40	6	40	10	0
HAD-B	4	60	3	70	9	10
Mean	4.5	55	3.8	62.5	8.8	12.5
No dispersal						
CCMA-A	4	60	3	70	5	50
CCMA-B	4	60	3	70	5	50
HAD-A	6	40	6	40	7	30
HAD-B	3	70	2	80	5	50
Mean	4.3	57.5	3.5	65.0	5.5	45.0

WMHF – Western Moist High Farmlands; LVC – Lake Victoria Crescent; NMF – Northern Moist Farmland; scenario A depicts increased while B reduced future carbon levels

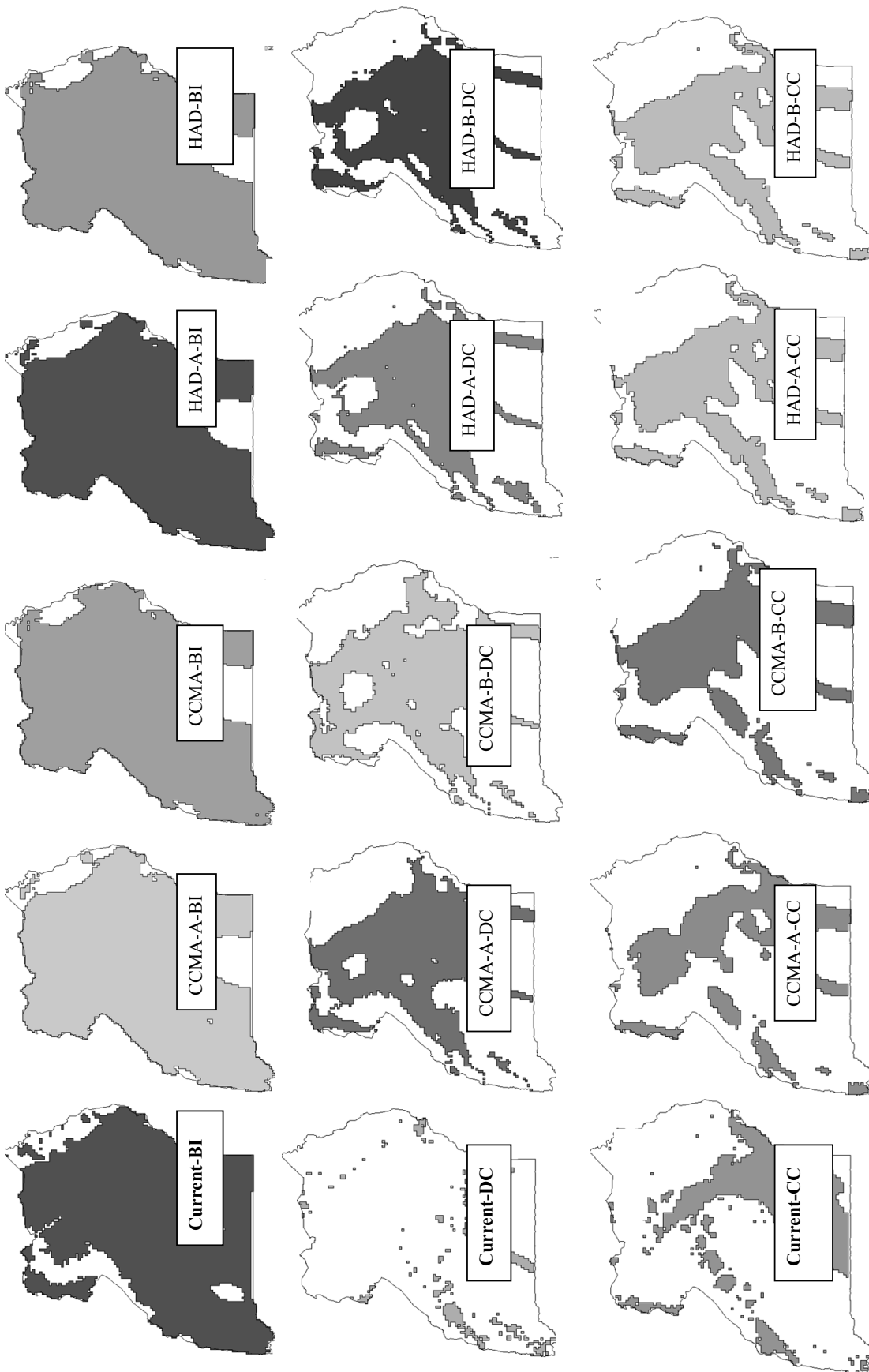


Figure 2. Change in the size of climate envelopes predicted by four climate-change models for the three fruit species with gains from a 1950–2000 baseline to the 2050 future period for the dispersal scenario in which species move entirely into future climatic niches

BI – *B. invadens*; DC – *D. ciliatus*; CC – *C. cosyra*



Figure 3: Change in the size of climate envelopes predicted by four climate-change models for the three fruit species with losses from a 1950–2000 baseline to the 2050 future period for the dispersal scenario in which species move entirely into future climatic niches

DB – *D. bivittatus*; BC – *B. cucurbitae*; CA – *C. anonae*

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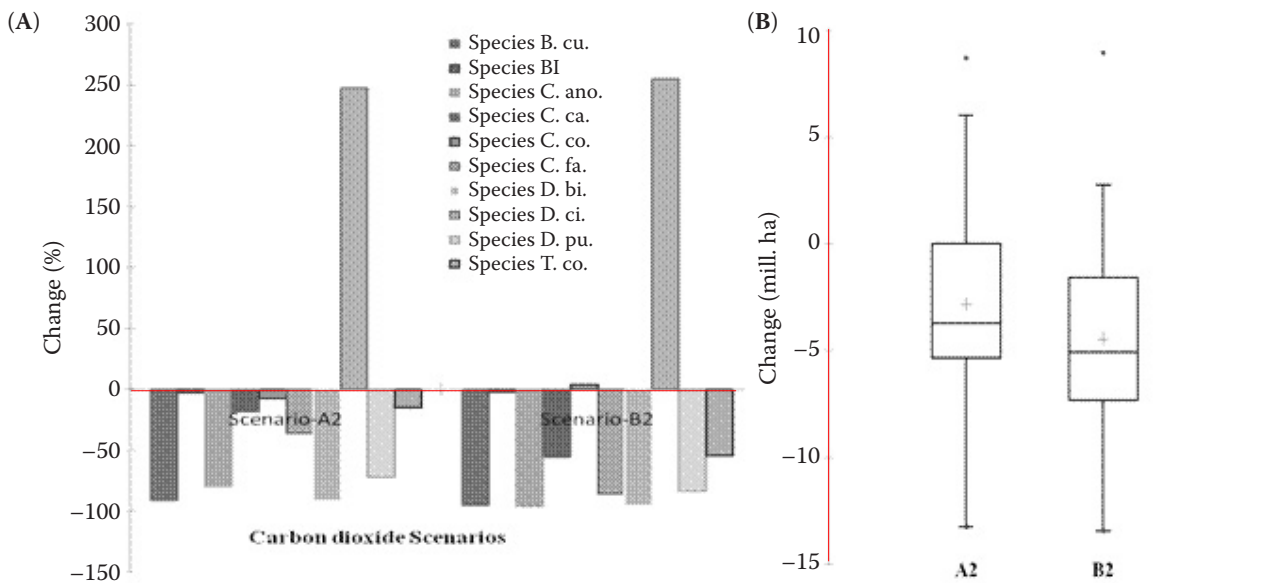


Figure 4. Proportional changes in habitat size of predictions under the two carbon dioxide emission scenarios for the 10 fruit fly species (A) and box plots for carbon dioxide scenarios (B) from a 1950–2000 baseline to the 2050 future period. Box plots show median, mean, 25th and 75th percentiles, and 10th and 90th percentiles

B. cu. – *B. cucurbitae*; BI – *B. invadens*; C. ano. – *C. anonae*; D. bi. – *D. bivittatus*; C. fa. – *C. fasciventris*; D. ci. – *D. ciliatus*; T. co. – *T. coffeae*; D. pu. – *D. punctatifrons*; C. co. – *C. cosyra*; C. ca. – *C. capitata*

range shifts on fruit fly species. However, CCCMA consistently predicted more extreme changes in size than the HADCM. However, among the species, there were significant differences in the two model predictions for future changes ($F = 3.174$, $df = 19, 60$, $R^2 = 50.1\%$, $P = 0.000$). The highest differences in change magnitude were noted among *C. capitata*, *C. fasciventris*, and *T. coffeae*, with all being consistently more with CCCMA. The only model contradiction in occupancy prediction direction was in *C. cosyra*—CCMA predicted declines, while HADCM the inverse.

Species richness was predicted to generally decrease from the current 10 species by 2050, but the decrease significantly differed across the three zones ($\chi^2 = 11.7$, $df = 2$, $P = 0.003$). The highest decrease was predicted in WMHF, while the least was in the NMF under dispersal mode, while a similar trend was predicted for the non-dispersal mode: WMHF > LVC > NMF (Table 2). Indeed, dispersal modes differed significantly ($V = 21.000$, $df = 1$, $P = 0.034$), with the full-dispersal predicting higher mean richness (5.7 ± 2) compared to no dispersal mode (4.4 ± 1). Among the models the order of predicted species decline was: HAD-B > CCMA-A = CCMA-B > HAD-A (Table 2).

Similarly, species turnover across the three zones showed declines in species composition, and the difference among zones was significant ($\chi^2 = 11.34$, $df = 2$, $P = 0.003$) (Table 2). Post-hoc analysis showed that

the LVC ($63.75 \pm 5.3\%$) had higher potential turnover than WMHF ($56.25 \pm 3.8\%$) and LVC ($28.75 \pm 6.9\%$), the former two were not significantly different. Turnover under the two dispersal modes differed significantly ($\chi^2 = 0.000$, $df = 1$, $P = 0.031$), but conversely to the species richness. The full-dispersal predicted less mean turnover ($43.33 \pm 7.3\%$) than the no dispersal mode ($55.83 \pm 4.3\%$). Among the models the predicted order of species turnover followed exactly the same order as that under species richness: HAD-B > CCMA-A = CCMA-B > HAD-A (Table 2). Occupancy in the LVC, WMHF, and the greater southern Uganda is predicted as unlikely, as the sites showed poor potential future colonisation by most species, contrary to NMF assemblages.

DISCUSSION

Generally, the results predicted declining CE sizes in the future climates, which is in agreement with other studies that have predicted range shifts among tephritid fruit flies with climate change (FAO 2008). The three species most at risk (*Dacus bivittatus* > *Bactrocera cucurbitae* > *Ceratatis anonae*) have relatively narrow CE parameter ranges, and very specific climatic requirements that could limit their future adaptation (McKENNEY *et al.* 2007). This specificity

in CE sizes of the three species suggests that their future distribution will be hampered critically by climate variability, particularly their temperature ranges that are rarely found under the 2050 future climate scenarios. This is the converse for *B. invadens* and *C. cosyra*.

The Ethiopian fruit fly (*D. ciliatus*) projected range increase of up to 250% of the current areas is probably due to the fact that it is known to prefer drier conditions characteristic of Ethiopia, hence projected warming trends should be suitable. Under the A2 emissions scenario, predicted CEs were smaller and more northerly than CEs predicted under the B2 scenario, as also reported by MCKENNEY *et al.* (2007). In the A2 scenario, the human population is larger and greenhouse gas emissions are higher than in the B2 scenario (NAKICENOVIC 2000). The species, whose range showed potential increases and shifts, demonstrated capacity to shift their distributions in response to future climate change, while those whose range declined may be incapable of such shifts. Because climate change will likely beat the response capacity of many fruit flies, tephritid vulnerability to climate change may even be more extensive than anticipated.

The assumptions of the dispersal hypothesis (SCHLOSS *et al.* 2012) might have implications on the estimates of the percentages of species that will actually reach and colonise suitable habitats (SUTHERLAND *et al.* 2000). Dispersal paths in invertebrates are generally limited by their small size, and this might inhibit their ability to keep pace with future climate change, making them more vulnerable to warming trends. However, it is likely that occasional colonists will keep up with the gradual changes. Because the models did not consider topography, rivers, roads, and other dispersal barriers, which may impede movement, it is possible that the dispersal option overestimates the percentage of fruit flies that will keep pace with climate change (MCKENNEY *et al.* 2007). It therefore stands to reason that the study's dispersal mode predictions represent the upper limit of species' movement potential rather than a likely dispersal scenario. The relatively higher estimate of species vulnerability to climate change under the no dispersal, unlike the full dispersal scenario, is probably because the latter does not incorporate landscape permeability, which the former does (SCHLOSS *et al.* 2012). This is particularly true where permeability is set to zero, as generally insects see a landscape as more permeable because they can be windblown.

The availability of appropriate hosts between some species' ranges and regions of future suitable climate will increase the percentage of species that are able to keep pace with climate change by offering oviposition options along the dispersal trajectories. Where more permeable landscapes with larval hosts and appropriate soil condition for pupae development do not occur, dispersal may be less successful due to the potential for decreased survival and reproduction in less suitable habitats. This offers an opportunity for the design of future management strategies. Managing alternative hosts for the migratory fruit fly species and incorporating species-specific habitat barriers along the dispersal routes would realistically curtail species migration to suitable climates.

While the results have higher levels of prediction confidence, the uncertainties in bioclimatic modelling could have caused over- or under-estimates in these results (SCHLOSS *et al.* 2012). For example, false assumptions of climatic intolerance due to modelling only the realized niche, and therefore ignoring species interactions and other non climatic determinants of range boundaries, may increase the projected distance a species needs to travel to suitable climate and cause overestimates of the percentages of species unable to track climate change (SCHLOSS *et al.* 2012). In addition, correlative models have inherent uncertainties associated with their inability to project the suitability of novel climates and to account for evolution. Future fruit fly range expansions may occur from other species populations that are already closer to regions of future suitable climate or from other pest species that were not considered in this study. Incorporating fruit, vegetation, and soil (aridity index) as predictor variables might result in more interesting results. For instance, when future distribution of the three most vulnerable species in this study were assessed using temperature, rainfall, and aridity index (Precipitation over Potential Evaporation, P/PE), they all showed extinction.

The observed higher percentage (90%) of species unable to reach suitable climates may be the result of lower latitudinal gradients in climate in Uganda and/or higher sensitivity to climatic changes due to narrower climatic niches of the fruit fly species. Indeed, with the exception of *D. ciliatus*, the majorities of the species in this study are least likely to survive effects of climate change and will most probably experience climate-change-induced reductions in suitable habitats. Among those likely to be curtailed by climate change, Cucurbit feeders (*Dacus bivittatus*

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and *B. cucurbitae*) are projected to be the most likely causalities (habitat loss of about 95%), followed by *Ceratatis* genera, which constitutes most of the native species. In terms of pest management, this implies that despite the negative effects of climate change, in the case of fruit flies, the projected changes are likely to aid in the management of most cucurbit feeders and some *Ceratatis* species. Further assessment of the potential vulnerabilities of other native fruit flies species in this *Ceratatis* genus to climate change will help inform management efforts about the role of climate change in the management of pestiferous *Ceratatis* species.

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