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Temporal and spatial patterns of *Bactrocera dorsalis* (Diptera: Tephritidae) populations in its southern limits of distribution: effects of climate and landscape on its range expansion

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Abstract

Bactrocera dorsalis (Hendel) (Diptera: Tephritidae) is an invasive tropical pest that is currently expanding in its geographical range into temperate regions. This study examined the temporal and spatial dynamics of *B. dorsalis* along an altitudinal gradient in Mpumalanga Province, South Africa, in its southernmost adventive limit, which experiences a temperate climate with dry winters. Populations were monitored from October 2020 to October 2022 at three sites with altitudes ranging from 452 to 1 741 m above sea level. At each site, clusters of attractant-based traps (methyl eugenol and three-component Biolure) were set up and serviced at least monthly. We analysed the effects of climate, time of the year, altitude, and landscape on *B. dorsalis* abundance. Single population peaks of *B. dorsalis* were recorded from mid-summer to autumn in all sites, with higher prevalence at the low-altitude site. In the low- and mid-altitude sites, catches were recorded year-round, while at the high-altitude site, there were no catches for four to six months after onset of winter. Higher *B. dorsalis* catches were recorded as temperatures increased and precipitation decreased. Catches were higher in commercial orchards and home gardens compared to abandoned orchards. These findings provide valuable information for improving simulation models of *B. dorsalis* distribution and population growth that can be used to inform the management of this pest.

Introduction

Worldwide, agriculture is being impacted by invasive alien insect pests due to increasing global trade, travel, and changes in the environment (Early *et al.*, 2016). While the establishment and population growth of invasive insect pests of tropical origin in temperate areas may be limited by winter temperatures (means and extremes), global warming and the associated milder winters could reduce these limitations (Osland *et al.*, 2021; Szyniszewska *et al.*, 2024). High resource consumption ability and low mortality at optimal temperatures were deemed as key factors contributing to the successful establishment of a species of tropical origin in a temperate climate (Amarasekare and Simon, 2020).

A number of true fruit fly (Diptera: Tephritidae) species are important agricultural pests in many parts of the world and they cause serious damage to the production and trade of commercial fruit. There have been a few cases of establishment of fruit fly pests of tropical origin in temperate fruit production areas. The Mediterranean fruit fly (medfly), *Ceratitis capitata* (Wiedemann), a polyphagous fruit fly pest of tropical sub-Saharan African origin, became well established in the Mediterranean basin as well as in temperate areas in South America and Western Australia (Bonizzoni *et al.*, 2004; Malacrida *et al.*, 2007). The olive fly, *Bactrocera oleae* (Rossi), stenophagous in nature, and also originating from the tropics in Africa (De Meyer and Ekesi, 2016), is now well established in temperate olive production areas in the Mediterranean basin and California, USA. The invasion of *B. oleae* from Africa to the Mediterranean basin seems to coincide with the post-glacial recolonisation of wild olives in the Mediterranean (Nardi *et al.*, 2010). The Queensland fruit fly, *Bactrocera tryoni* Froggatt, expanded its distribution from native tropical northeast Australia to temperate regions in South-East Australia (Gilchrist and Meats, 2010). The Oriental fruit fly, *Bactrocera dorsalis* (Hendel), expanded its distribution within its native range as for example in China where the pest expanded from tropical southern regions to the temperate northern regions (Ye and Liu, 2005; Zhao *et al.*, 2024a).

Bactrocera dorsalis originates from southern Asia (Zhang *et al.*, 2023). It is polyphagous in nature (Bess and Haramoto, 1961; Clarke *et al.*, 2005) infesting numerous fruit species that are produced commercially. Its invasion from Asia into Africa was first recorded in 2003 (Lux *et al.*, 2003) and the species is now well established in many parts of the continent (Mutamiswa *et al.*, 2021). *Bactrocera dorsalis* was declared established in the northern regions of South Africa in 2013 (Manrakhan *et al.*, 2015). More recently, outbreaks of *B. dorsalis* have been reported in southern Europe (Nugnes *et al.*, 2018). There have also been regular detections of *B. dorsalis* in North America (Zhao *et al.*, 2024b). While host fruit availability can fuel high population growth of *B. dorsalis* (Geurts *et al.*, 2014; Tan and Serit, 1994; Vayssières *et al.*, 2015), its growth rates can be limited by prevailing abiotic factors, such as temperature (Michel *et al.*, 2021) and rainfall (Mze Hassani *et al.*, 2016; Theron *et al.*, 2017).

Given the invasive nature of *B. dorsalis* and the limiting abiotic factors identified, its potential establishment in parts of the world beyond its native range has been investigated in a number of studies using climate-based models (De Meyer *et al.*, 2010; De Villiers *et al.*, 2016; Dong *et al.*, 2022; Hill and Terblanche, 2014; Hong *et al.*, 2015; Stephens *et al.*, 2007). Some of these models relied solely on the known geographical distribution of the pest (De Meyer *et al.*, 2010; Dong *et al.*, 2022; Hill and Terblanche, 2014), while others incorporated distribution, ecophysiological studies, and phenology (De Villiers *et al.*, 2016; Hong *et al.*, 2015; Stephens *et al.*, 2007), leading to greater confidence in the accuracy of the potential geographic range estimates. In all models, cold stress was identified as the main limiting factor for the establishment and overwintering capability of *B. dorsalis* (De Meyer *et al.*, 2010; De Villiers *et al.*, 2016; Dong *et al.*, 2022; Hill and Terblanche, 2014; Hong *et al.*, 2015; Stephens *et al.*, 2007). In the most recently published CLIMEX model on the potential distribution of *B. dorsalis*, indices used in the model were calibrated using the observed phenology of the pest mostly in tropical Africa (De Villiers *et al.*, 2016). Following the publication of the model, however, *B. dorsalis* expanded its distribution range into temperate regions in the northern parts of South Africa (Manrakhan *et al.*, 2015). A characterisation of *B. dorsalis* in its most southern limit of its current distribution in southern Africa, compounded with altitude, is expected to provide better parameter values for an improved model on the potential expansion and growth of *B. dorsalis* in temperate regions, which are currently at threat of invasion.

The objectives of the study were to (1) characterise the temporal and spatial distribution of *B. dorsalis* in temperate climatic conditions in South Africa and (2) determine the effects of climatic data (temperature, relative humidity, and precipitation), time of the year, altitude, and landscape characteristics, which include site type and fruit presence, on the abundance of *B. dorsalis*.

Materials and methods

Study sites

Three trapping sites were selected across an altitudinal gradsect in Mpumalanga Province, South Africa (fig. 1): (1) a commercial citrus farm, Mbombela (previously Nelspruit) (25°27′49.21′′S, 31°1′34.56′′E; altitude: 452–686 masl) (Supplementary Fig. S1), (2) a commercial citrus farm, Schoemanskloof (25°24′26.31′′S, 30°37′9.86′′E; altitude: 871–980 masl) (Supplementary Fig. S2), and (3) an area (altitude: 1664–1741 masl) encompassing the town of Ermelo (26°32′8.60′′S, 29°59′15.61′′E) and surrounding apple farms extending towards Davel (26°30′49.95′′S, 29°42′00.66′′E) (Supplementary Fig. S3). Study sites were selected in Mpumalanga Province because *B. dorsalis* was found to be present in the province since 2013 (Manrakhan *et al.*, 2015). Like other provinces in the northern and northeastern areas of South Africa, Mpumalanga represents the southernmost extent of the adventive distribution of *B. dorsalis.* According to the Koppen-Geiger system (Kriticos *et al.*, 2012; Peel *et al.*, 2007), all three sites are classified into the temperate climate category with dry winter (Cw). While Mbombela falls into the Cw with hot summer (Cwa), Schoemanskloof and Ermelo fall into the Cw with warm summer (Cwb) (Kriticos *et al.*, 2012; Peel *et al.*, 2007). These two climate categories however differ from the Mediterranean climate characterised by dry summer (Kriticos *et al.*, 2012; Peel *et al.*, 2007). Sampling across these three sites enabled us to examine the dispersion patterns of *B. dorsalis* along an altitudinal/climatic gradient, as well as investigate the environmental factors associated with its range dynamics.

The sites varied in size. Mbombela covered an area of 782.62 ha, Schoemanskloof covered an area of 459.09 ha, while Ermelo town covered an area of 1 709.69 ha and the stretch from Ermelo to Davel covered an area of 3 803.88 ha.

In commercial citrus farms, fruit fly control practices in the form of baiting and/or placement of methyl eugenol (ME)-based attract and kill products targeting *B. dorsalis* males were implemented between January and September each year as per recommendations in the citrus industry of southern Africa (Manrakhan, 2024).

Each site was divided into 1 km × 1 km grid cells. In each site, the land use in each grid cell was categorised as follows: commercial orchard, abandoned orchard, or home-garden. In each grid cell, the presence and absence of fruit trees were recorded. The fruit trees recorded in the three sites and their fruit ripening periods are described in table 1. The fruit ripening periods given in table 1 were based on general fruit phenology pattern of typical ripening times for each of the fruit species in South Africa, and were confirmed through observations made during site visits.

Daily minimum, maximum and mean temperature, relative humidity, and precipitation data were obtained from nearby weather stations (Hortec Ileaf Weather Services, Somerset West, South Africa). The selected weather stations were located 7.5, 8.0, 32.8, and 15.2 km away from the study sites for Mbombela (Station ID: Stellenrus, 25°28′34′′S 31°05′59′′E), Schoemanskloof (Station ID: Rietvly, 25°22′58′′S 30°32′42′′E), Ermelo town (Station ID: Igni, 26°29′58′′S 30°18′51′′E), and Davel (Station ID: Voorsog, 26°22′36′′S 29°41′40′′E), respectively.

Trapping

Bactrocera dorsalis populations were characterised in the three study sites using an ME-based trapping system (targeting males) and a food attractant-based trapping system (targeting females). These trapping systems are recommended for *B. dorsalis* and have been shown to be effective for monitoring of this pest in South Africa (FAO/IAEA, 2018; Manrakhan *et al.*, 2017). The ME-based trapping system consisted of the commercially available and registered Invader lure (River Bioscience (Pty) Ltd,

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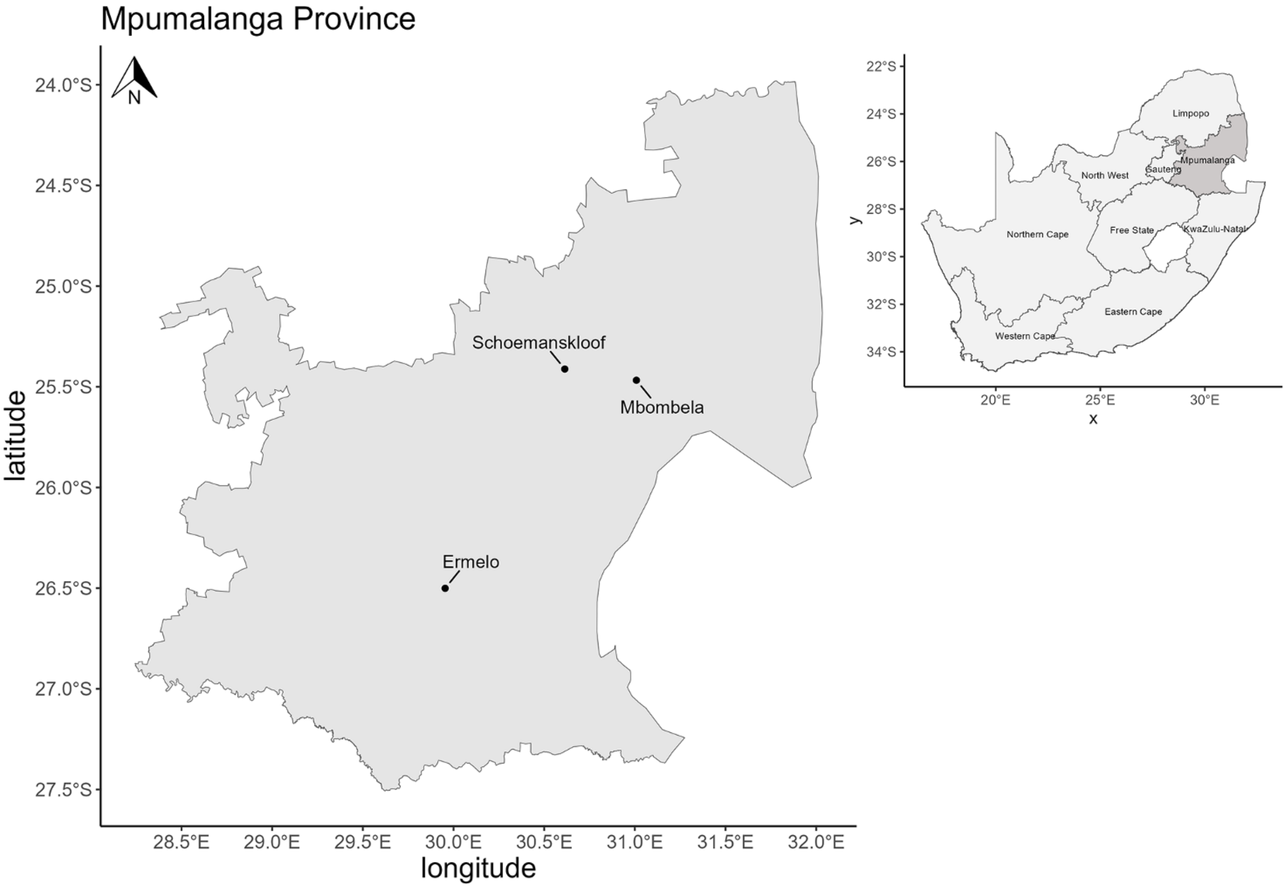

Figure 1. Locations of the study sites in Mpumalanga province, South Africa, where *B. dorsalis* populations were captured and characterised.

Gqeberha, South Africa), which was contained within a Lynfield trap (River Bioscience). Invader Lure contains 15 g of ME per dispenser. The food attractant-based trapping system consisted of the commercially available and registered three-component Biolure fruit fly (Chempac, Suider Paarl, South Africa), which was contained in a Chempac Bucket trap (also Chempac). The three-component Biolure fruit fly contains ammonium acetate (211 g/kg), trimethylamine hydrochloride (91 g/kg), and 1,4-diaminobutane (Putrescine) (3 g/kg). In each trap, there was a 3-g dichlorvos (195 g/kg active ingredient) strip to kill attracted flies.

The two trapping systems were placed in pairs in selected locations within a selected grid cell. Trap locations were strategically selected to ensure ease of access and to maximise efficiency during trap retrieval. A minimum distance of 30 m was maintained between trapping systems within each selected location. In the commercial citrus farm in Mbombela, a total of 20 traps (10 ME-baited traps and 10 Biolure-baited traps) (Supplementary Fig. S1) were placed in 10 grids. In the commercial citrus farm in Schoemanskloof, 24 traps (12 ME-baited traps and 12 Biolure-baited traps) (Supplementary Fig. S2) were placed in 12 grid cells. In the Ermelo town and nearby apple farm site, a total of 24 traps (12 ME-baited traps and 12 Biolure-baited traps) (Supplementary Fig. S3) were placed in 12 grid cells.

Trapping was initiated in all areas in October 2020 and was checked at least once a month until October 2022. Trapped flies were collected in vials and brought back to Citrus Research International, Nelspruit, for identification of *B. dorsalis*. Male and female *B. dorsalis* identified in each trap were recorded. Attractants and dichlorvos strips were changed every two months.

Data analysis

Counts of adults captured in each grid and trapping point were transformed to flies per trap per day (number of flies in a trap divided by the number of trapping days). Data analysis was performed using R version 4.4.1 (R Foundation for Statistical Computing, Vienna, Austria) and SPSS Statistics v29.0 (Armonk, NY: IBM Corp). R analyses were conducted in the RStudio Team (2020).

A generalised estimating equation (GEE) model with a negative binomial distribution was used to estimate the effects of altitude (per trap), mean daily temperature (average of mean, maximum, and minimum values between monitoring dates), mean daily precipitation, mean daily relative humidity, land use, and presence of fruit on the number of captures. A GEE model was selected because it accounts for within-trap correlation over time while accommodating irregular monitoring intervals (Hardin and Hilbe, 2012), which makes the use of a mixed-effects model unsuitable for this dataset. Month was included as a fixed factor to account for seasonal variation in captures, as GEE models do not accommodate random effects. Only the male captures were used in all analyses, since the female captures throughout this study were very low. Incidence rate ratios (IRRs) with 95% confidence intervals (CIs) were used for the parameter estimates of negative binomial GEEs. IRR indicates the relative change in the rate of the outcome

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Table 1. Records of fleshy fruit bearing species and their general fruit ripening periods indicated as grey-shaded horizontal bars within the three trapping sites for *Bactrocera dorsalis* in Mpumalanga province, South Africa in (1) Ermelo and neighbouring apple farms, (2) commercial citrus farms in Schoemanskloof, and (3) Mbombela

Site	Fruit trees within site	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Ermelo	*Acca sellowiana* (O. Berg) Burret		▨	▨	▨	▨							
	Citrus spp. (unknown species)		▨	▨	▨	▨							
	Eriobotrya japonica (Thunb.) Lindl									▨	▨	▨	
	[a]*Malus communis* (Suckow) Borkh	▨	▨	▨	▨	▨							
	Opuntia ficus-indica (L.) Mill	▨	▨	▨									
	Prunus domestica L.	▨	▨										▨
	Prunus persica (L.) Batsch	▨	▨	▨							▨	▨	▨
	Pyrus communis L.	▨	▨	▨									
	Vitis vinifera L.	▨	▨										▨
Schoemanskloof and Mbombela	[a]*Citrus sinensis* (L.) Osbeck				▨	▨	▨	▨	▨	▨			
	[a]*Citrus reticulata* Blanco				▨	▨	▨	▨					

[a]Fruit species that are grown commercially in these trapping sites.

(capture rate) for each unit increase in the independent variable. IRRs greater than 1 indicate an increase in capture rate, while IRRs less than 1 indicate a decrease in capture rate.

Moran's I statistic was used to assess spatial autocorrelation in the three sites across different distance thresholds. These thresholds were chosen to represent the minimum, median, and maximum distances between traps. For each threshold, Moran's I statistic and associated p-values are provided, indicating the degree of spatial clustering and its statistical significance. Moran's I statistic was previously used in a study to determine the spatial autocorrelation of *C. capitata* in a study in Northern Greece (Papadopoulos *et al.*, 2003). The moran.mc function from the spdep package in R was used (Pebesma and Bivand, 2023), which performs a Monte Carlo test for Moran's I, allowing for the assessment of spatial autocorrelation by comparing observed spatial patterns against random permutations. Contour plots were generated in R using the ggplot2 package to visualise the spatial distribution of the data allowing for easy identification of areas with significant clustering or spatial autocorrelation.

Results

Temporal dynamics of B. dorsalis populations

In all sites and in each study year, *B. dorsalis* populations were found to have unimodal peaks (fig. 2). Catches of *B. dorsalis* males were generally higher in ME-baited traps compared to catches of *B. dorsalis* females in Biolure-baited traps (fig. 2). A total of only 154 females were captured in 34 traps compared to 36 698 males in the same number of traps. Each year, peaks of catches were recorded between January and May, corresponding to the period from mid-summer to early autumn in the northern parts of South Africa. The timing of the peak catches differed between sites/altitudes, with the earliest peak in Mbombela and the latest peak in Ermelo (fig. 2). Catches of *B. dorsalis* males were significantly affected by the period of the year and altitude (table 2). In the low- and mid-altitude sites, catches of *B. dorsalis* males dropped to very low levels after May. In the high-altitude site, after the peaks of catches, there were periods of four to six months with zero catches of *B. dorsalis* males. Generally, the daily trap catch rate of *B. dorsalis* was higher in the low-altitude Mbombela compared to the high-altitude Ermelo (fig. 2 and table 2).

Effects of climatic factors on abundance of B. dorsalis

Trap catch rates of *B. dorsalis* were strongly influenced by temperature, relative humidity, and precipitation (table 2). At each site, during both study years, peaks in *B. dorsalis* catch rates were preceded by increases in maximum, mean, and minimum temperatures, while catch rates declined sharply following decreases in temperatures (fig. 3). A 1 °C increase in the mean temperature

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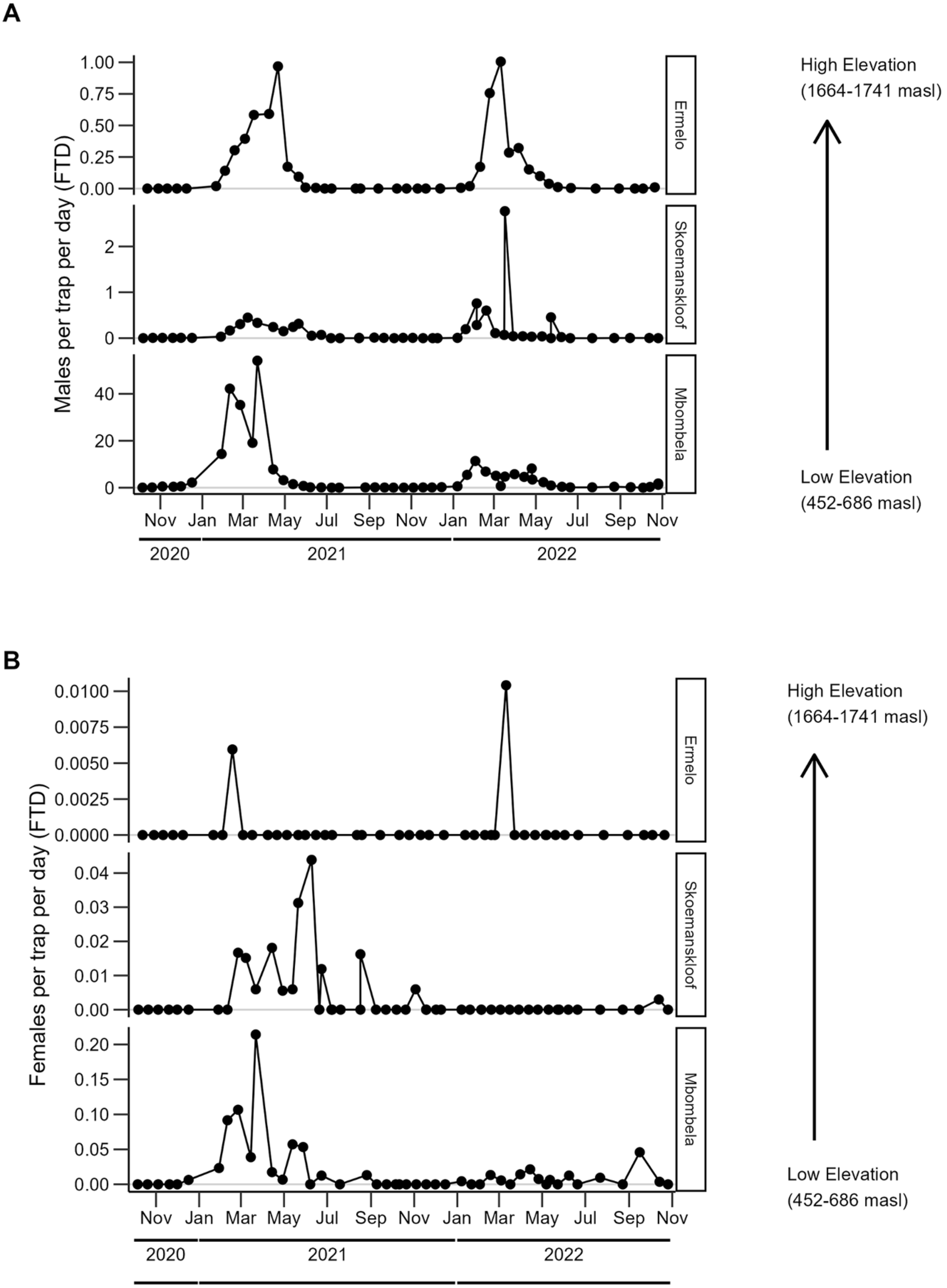

Figure 2. Phenology of *Bactrocera dorsalis* males (A) and females (B) revealed by trapping data collected in three study sites in Mpumalanga province, South Africa: Mbombela, Schoemanskloof and Ermelo-Davel on an altitudinal gradsect between 2020 and 2022.

between monitoring dates raised the likelihood of *B. dorsalis* captures by 1.3 times, after adjusting for the effects of month and trap altitude as covariates in the GEE model (table 2). Seasonal declines in precipitation led to increased *B. dorsalis* captures across all three locations (fig. 3). There was a negative relationship between precipitation and capture rates. For each 1-mm increase in mean daily

Table 2. Results of the negative binomial generalised estimating equation model to determine the effects of environmental factors (time of year (month), altitude, land use, presence of fruit, temperature, relative humidity, and precipitation) on catches of *Bactrocera dorsalis* male. Model variables with values of $p < 0.05$ were statistically significant

Independent variable	Wald's test (df)	IRR (95% CI)	*p*-value
Month	127.541 (1)	0.734 (0.696, 0.775)	<0.001
Altitude	22.747 (1)	0.999 (0.999, 0.999)	<0.001
Mean temperature	234.687 (1)	1.389 (1.331, 1.448)	<0.001
Mean precipitation	37.387 (1)	0.810 (0.757, 0.867)	<0.001
Mean relative humidity	7.931 (1)	1.039 (1.012, 1.067)	0.005
Month	219.875	0.723 (0.693, 0.755)	<0.001
Altitude	29.553 (1)	0.999 (0.998, 0.999)	<0.001
Land use (reference group: abandoned orchard)	25.406 (2)		<0.001
Orchard		2.503 (1.708, 3.667)	<0.001
Home garden		2.601 (1.380, 4.900)	0.003
Presence of fruit	2.106 (1)	0.686 (0.412, 1.141)	0.147
Mean temperature	193.390 (1)	1.364 (1.305, 1.425)	<0.001
Mean precipitation	47.208 (1)	0.830 (0.787, 0.875)	<0.001
Mean relative humidity	6.927 (1)	1.079 (1.020, 1.142)	0.008

precipitation between monitoring dates, male captures decreased by 17% (table 2). Trap catch rates of *B. dorsalis* were however positively influenced by relative humidity (table 2).

Spatiotemporal patterns of B. dorsalis captures

The spatial patterns of male *B. dorsalis* trap captures in the three study sites throughout the sampling period are shown in figs. 4–6. The general monthly spatial patterns of *B. dorsalis* male captures across all sites are also presented in Supplementary Fig. S4. At the low-altitude site, captures were recorded year-round in both study years with no clear spatial distribution patterns observed (fig. 4). The spatial autocorrelation was significant and negative in three out of the 25 trapping months indicative of dispersion during those times (table 3). At the mid-altitude site, captures occurred year-round in both study years (fig. 5). The spatial autocorrelation was significant in six out of the 25 trapping months (table 4). Spatial autocorrelation was positive only in January 2022 at the shortest distance threshold tested (table 4), indicating clustering of catches during that month. This clustering was visible in the central area of the polygon (fig. 5). In some of the months of low *B. dorsalis* prevalence in the mid-altitude site, spatial autocorrelation was significant and negative indicative of dispersion (table 4). At the high-altitude site in Ermelo town, catches of *B. dorsalis* were consistently clustered on the eastern side from January to June (fig. 6). In the first study year, there was a clustered spatial pattern every month from February to May at either the minimum or median distance thresholds of 3 000 and 5 000 m (table 5). The significant spatial autocorrelation values coinciding with the peak of *B. dorsalis* abundance in Ermelo support the observed spatial clustered pattern. In the second year of the study, a clustered spatial pattern was found only in March at the median distance threshold supported by the significant and positive spatial autocorrelation (table 5). Across the entire Ermelo-Davel polygon at the high-altitude site, *B. dorsalis* catches were also concentrated in an apple orchard on the western side from January to June in the first study year, but not in the second study year (fig. S5).

The type of land use was found to influence *B. dorsalis* catch rates (table 2). Commercial orchards had 2.5 times more captures than abandoned orchards when adjusted for month and altitude. Home gardens had 2.6 times more captures than abandoned orchards, also after adjusting for month, altitude, and other covariates included in the GEE model. The presence of fruit trees, however, did not influence catches of *B. dorsalis* males (table 2).

Discussion

In this study, populations of *B. dorsalis* were characterised for the first time across an altitudinal gradsect in a temperate climate in the southernmost extent of its geographical range. In all sites monitored, peaks of *B. dorsalis* catches in traps occurred between mid-summer (January) and autumn (May) when climatic conditions were suitable for population growth. The observed patterns matched those found in the earlier years of the establishment of this species in two of the northern provinces of South Africa at locations with altitudes lower than 800 masl (Theron *et al.*, 2017). In this study, however, we observed a complete absence of catches for four to six months after the start of winter in June at the highest altitude site (>1 600 masl), which also experienced the lowest mean temperatures during winter (mean minimum temperatures being mostly below 10 °C). The phenology of *B. dorsalis* at the highest-altitude site closely resembled patterns previously documented in a temperate region in Wuhan, Hubei Province, central China, (Han *et al.*, 2011) and in a high-altitude site (>1 600 masl) in the subtropical region of Baoshanba, Yunnan Province, southwestern China (Chen and Ye, 2007), where *B. dorsalis* also completely disappeared from traps for four to six months starting at the onset of winter (December). In contrast, in the two other sites at mid and low altitudes in this study, *B. dorsalis* catches were recorded throughout winter, albeit at low numbers.

Low or zero catches of *B. dorsalis* in these trapping sites in the northern areas of South Africa from winter to early summer were likely due to low temperatures and low relative humidity prevailing during this period. Our analysis revealed strong effects of temperature, relative humidity, and precipitation on *B. dorsalis* abundance. Higher temperatures and relative humidity were associated with increased catches, while increased precipitation had the opposite effect. Winter at all sites was marked by decreases in maximum, and minimum temperatures, as well as relative humidity and precipitation.

Our findings on temperature effects align with previous studies showing that cooler temperatures significantly slow the development and reproduction of *B. dorsalis*. For instance, a reduction of mean constant temperature from around 30 °C to around 15 °C led to a three- to four-fold increase in developmental time of immature stages under laboratory conditions (Michel *et al.*, 2021; Rwomushana *et al.*, 2008; Vargas *et al.*, 1996). Michel *et al.* (2021) found no development of *B. dorsalis* from eggs to larvae at a constant temperature of 10 °C, while Choi *et al.* (2020) recorded no egg laying for the species at a constant temperature of 13.5 °C. In our study, the drop in maximum temperatures at the highest

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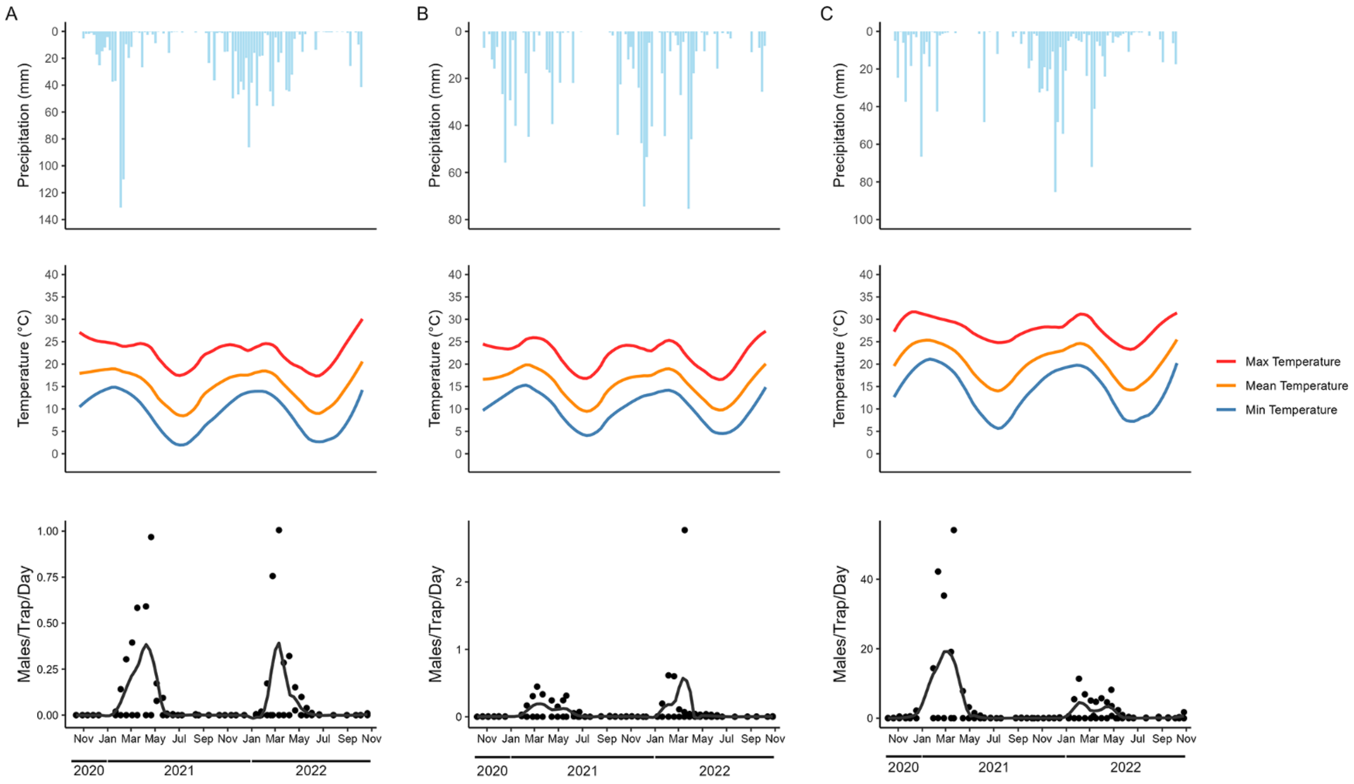

Figure 3. Phenological profile of *Bactrocera dorsalis* males catches across an altitudinal gradient in (A) Ermelo (high-altitude site), (B) Schoemanskloof (mid-altitude site), and (C) Mbombela (low-altitude site). The top row shows mean weekly precipitation trends (mm), the middle row illustrates smoothed temperature trends using loess lines for maximum (red), mean (orange), and minimum (blue) temperatures (°C). The bottom row presents male captures per trap per day (black dots) with loess smoothing (black line).

altitude site to 20 °C and below at the onset of winter may have potentially suppressed population development and reproduction. Additionally, reduced fruit availability in spring and early summer compared to mid-summer (table 1) may have further limited reproductive opportunities as conditions became more favourable. The presence of competitors for these fruit resources may also need to be factored in when considering reproductive opportunities (Clarke and Measham, 2022). One of these competitors, which was previously recorded in Ermelo (the high-altitude site), was *Ceratitis quilicii* De Meyer, Mwatawala and Virgilio (Grove *et al.*, 2019). *Ceratitis quilicii* was reared in one of the fruit species recorded in that area – *Acca sellowiana* (Grove *et al.*, 2019). The presence of *C. quilicii* was confirmed in traps baited with three-component Biolure placed in the highest altitude site. Other *Ceratitis* species were also identified in these traps in the same site. Although reproductive opportunities may have been limited, the winter temperatures could have extended the adult lifespan and lengthened the pre-oviposition period of the species, as observed in laboratory studies by Choi *et al.* (2020).

The temporal population abundances of *B. dorsalis* in this study were evaluated by means of catches in ME-baited traps. Males of *B. dorsalis* exhibit strong attraction and feeding responses to ME (Tan *et al.*, 2014). Grids of ME-baited traps at a density of 5 per 2.5 km^2 were found to be able to detect small populations of the pest species (Shelly *et al.*, 2010). In mark release recapture studies on wild live *B. dorsalis* in Penang, Malaysia, carried out under optimal climatic conditions for the pest, male captures in ME-baited traps were shown to provide reliable estimates of population sizes (Tan, 1985). However, low winter temperatures can influence captures by reducing fly movement to traps, which could in turn influence population estimates. This factor should be considered in models to predict its potential population distribution and growth. Flight performance of *B. dorsalis* was found to be optimal between 20 °C and 24 °C and limited at low temperatures (Makumbe *et al.*, 2020). More recently, it was demonstrated that *B. dorsalis* flight was negatively affected, at least temporarily, as adults acclimatise to 20 °C (Malod *et al.*, 2024) compared to when they are under constant optimal conditions at 25 °C. For *B. dorsalis*, this might imply that favourable conditions for prevalence after low temperatures in winter may not necessarily lead to an immediate improvement in flight performance and hence trapping rates.

The positive relationship between relative humidity and abundance observed in our study aligns with findings from some previous field research on *B. dorsalis* (Chen and Ye, 2007; Vayssieres *et al.*, 2009). However, other field studies have reported no significant correlation between relative humidity and *B. dorsalis* abundance (Jayanthi and Verghese, 2011; Tan and Serit, 1994). No studies to date have specifically examined the sole effects of relative humidity on *B. dorsalis*. Studies on the effects of relative humidity on adult survival and reproduction of another tephritid, *B. oleae*, showed that low relative humidity (12% and 33%) at an optimal temperature of 25 °C adversely impacted female longevity and reproductive maturation of this species (Broufas *et al.*, 2009). In this study, while relative humidity levels fluctuated continuously across time in all sites, the winter period (from June to August) was generally characterised by lower average relative humidity level of 66% compared to the summer period (from December to February), which had higher average relative humidity level

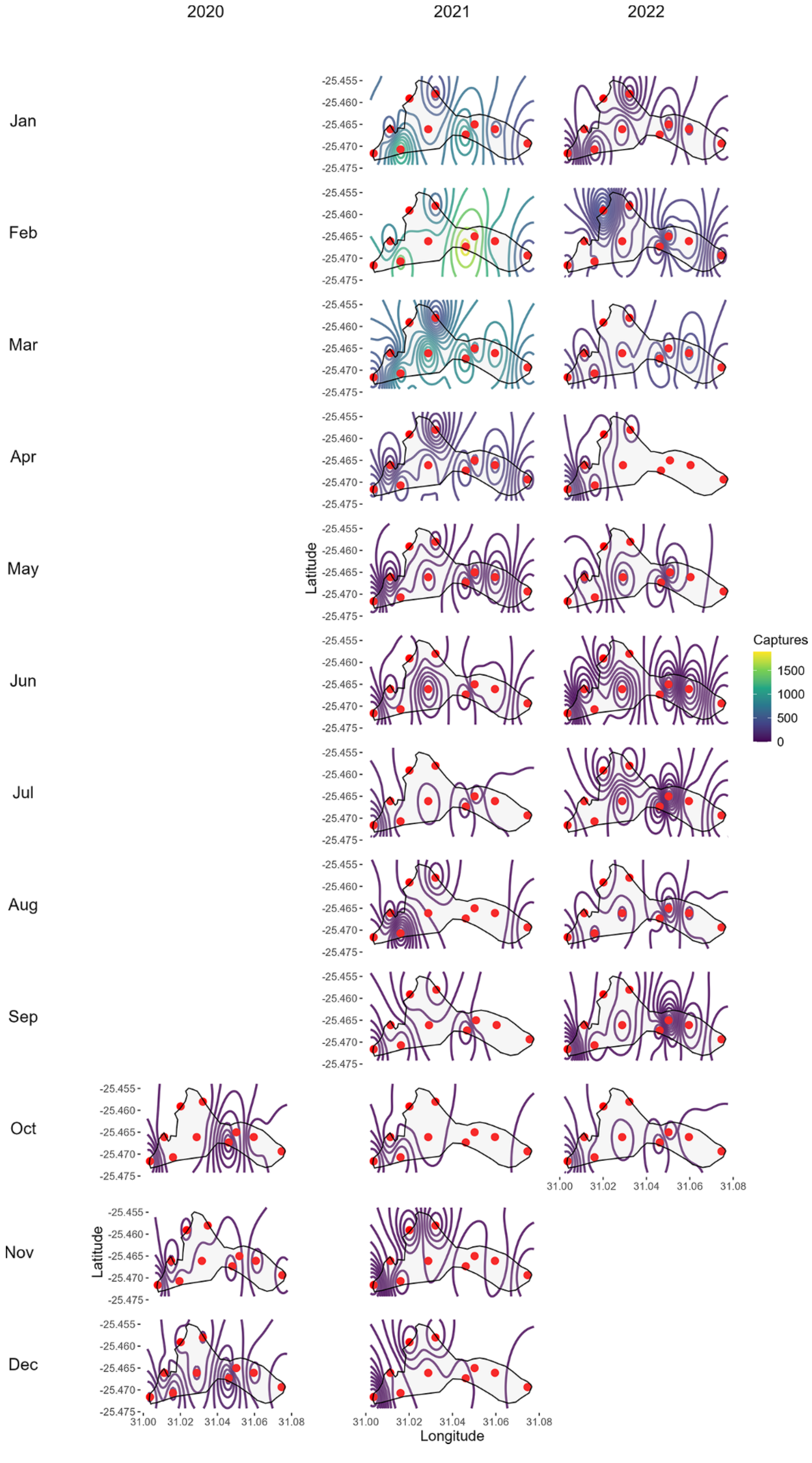

Figure 4. Contour plots illustrating *Bactrocera dorsalis* distribution in the Mbombela site (at the lowest altitude), across trapping months from October 2020 to October 2022. The red dots indicate locations of ME-baited traps.

of 82%. Whether *B. dorsalis* is affected in a similar way to *B. oleae* with low relative humidity remains to be investigated. For *B. dorsalis*, low humidity in combination with low temperature was found to reduce its tolerance to cold stress (Mutamiswa *et al.*, 2020).

The negative relationship between precipitation and *B. dorsalis* trap catch rates was unexpected, as other studies found either a positive direct relationship (Vayssieres *et al.*, 2009) or a positive lagged relationship (Theron *et al.*, 2017) between these variables. In the previous study on *B. dorsalis* population dynamics

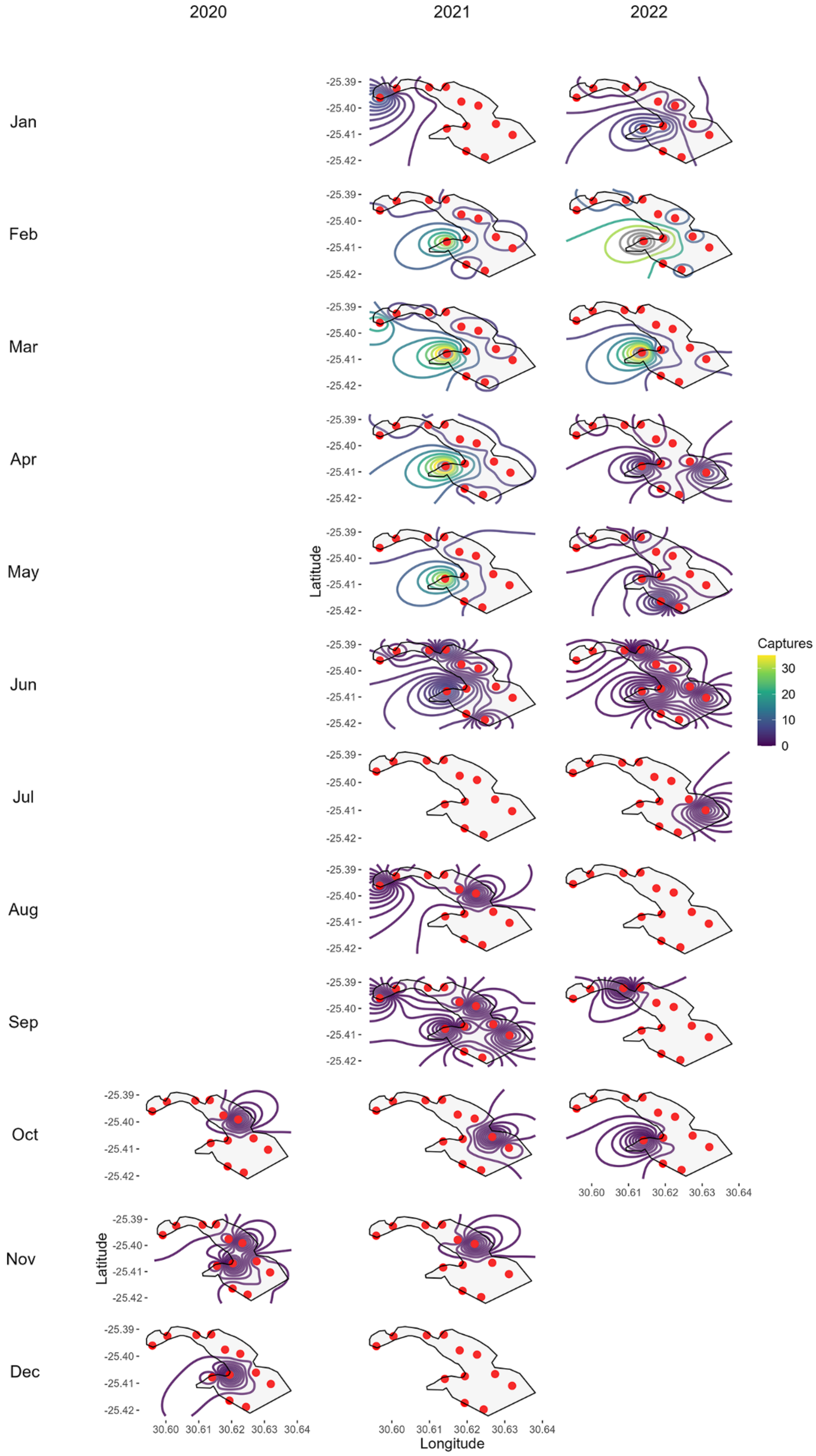

Figure 5. Contour plots illustrating *Bactrocera dorsalis* captures distribution in the Schoemanskloof site (at mid-altitude), across trapping months from October 2020 to October 2022. The red dots indicate locations of ME-baited traps.

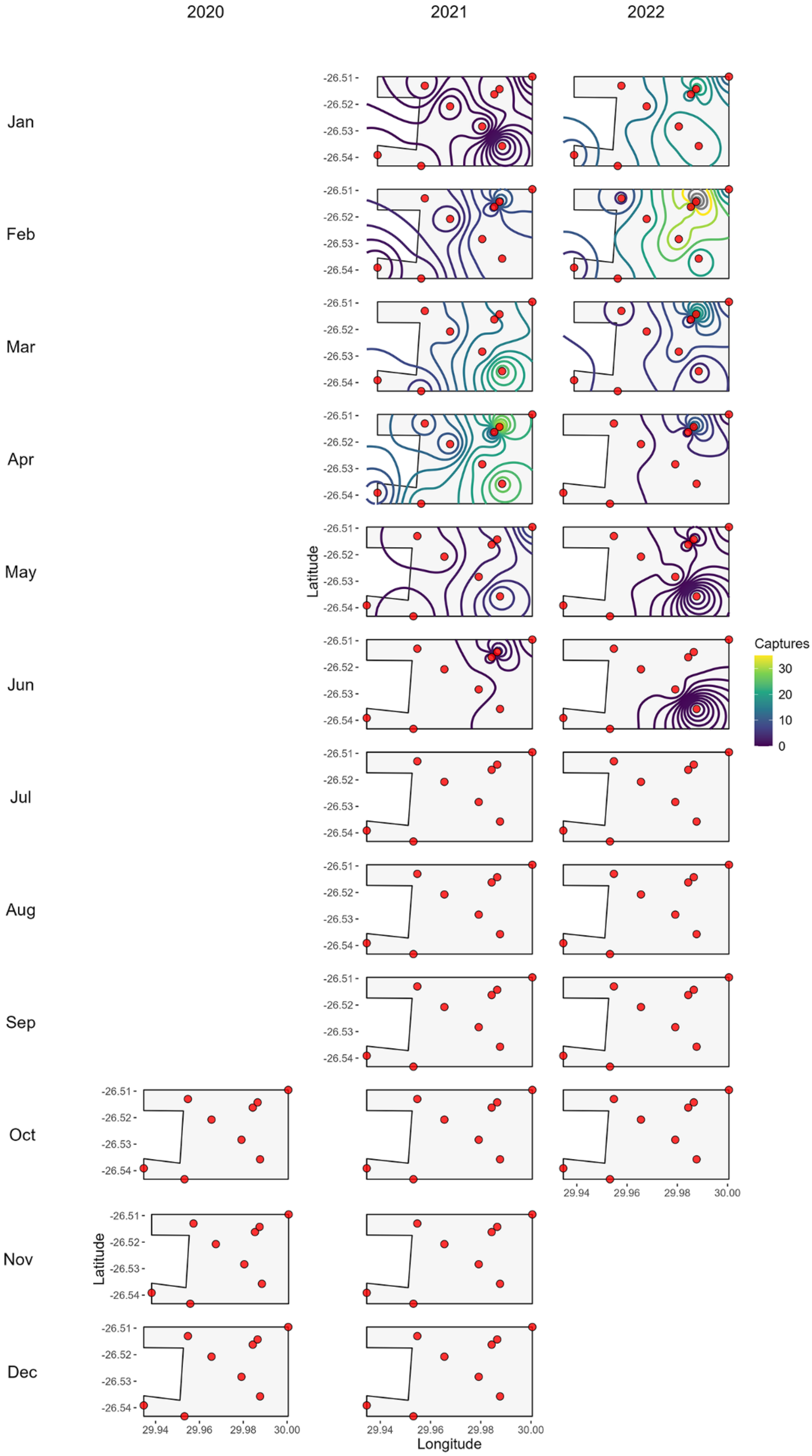

Figure 6. Contour plots illustrating *Bactrocera dorsalis* captures in Ermelo town (at the highest altitude), across trapping months, from October 2020 to October 2022. The red dots indicate locations of ME-baited traps.

Table 3. Global Moran's *I* spatial autocorrelation statistics for *Bactrocera dorsalis* male captures in methyl eugenol traps for all data, including data at minimum, median, and maximum trap distance intervals for each month of each study year from October 2020 to October 2022 at the low-altitude site of Mbombela. Probabilities in bold indicate significant spatial autocorrelation

	Global Moran's *I*							
	Distance threshold (m)							
	2°000		4°000		6°000		7°000	
Month-year	Statistic	*p*-value	Statistic	*p*-value	Statistic	*p*-value	Statistic	*p*-value
Oct-20	−0.04	0.333	−0.20	0.329	−0.18	0.155	−0.10	0.394
Nov-20	0.07	0.193	−0.01	0.239	−0.10	0.388	−0.11	0.488
Dec-20	0.11	0.161	−0.13	0.488	−0.04	0.146	−0.07	0.090
Jan-21	−0.05	0.356	−0.21	0.274	−0.08	0.272	−0.14	0.090
Feb-21	0.00	0.288	−0.20	0.313	−0.12	0.496	−0.14	0.149
Mar-21	−0.09	0.415	−0.12	0.489	−0.06	0.215	−0.13	0.288
Apr-21	−0.24	0.310	−0.13	0.482	−0.10	0.435	−0.13	0.275
May-21	−0.28	0.173	−0.10	0.411	−0.13	0.435	−0.15	0.093
Jun-21	−0.33	0.185	−0.20	0.315	−0.18	0.162	−0.14	0.218
Jul-21	–	–	–	–	–	–	–	–
Aug-21	0.06	0.218	−0.10	0.411	0.02	0.051	−0.07	0.111
Sep-21	0.19	0.087	0.00	0.207	0.01	0.062	−0.08	0.111
Oct-21	0.04	0.230	−0.21	0.280	−0.17	0.210	−0.10	0.335
Nov-21	−0.17	0.454	−0.19	0.343	−0.10	0.392	−0.02	**0.009**
Dec-21	0.18	0.094	−0.04	0.261	−0.04	0.137	−0.07	0.062
Jan-22	−0.20	0.363	−0.34	**0.046**	−0.08	0.275	−0.14	0.164
Feb-22	−0.23	0.344	−0.36	**0.027**	−0.09	0.310	−0.14	0.242
Mar-22	−0.09	0.407	0.04	0.175	−0.13	0.419	−0.13	0.211
Apr-22	−0.23	0.288	−0.19	0.349	−0.15	0.291	−0.12	0.278
May-22	0.08	0.167	0.11	0.090	−0.05	0.151	−0.10	0.224
Jun-22	−0.34	0.159	−0.23	0.222	−0.12	0.483	−0.11	0.401
Jul-22	−0.16	0.495	−0.19	0.346	−0.07	0.211	−0.10	0.329
Aug-22	−0.26	0.285	−0.29	0.113	−0.18	0.134	−0.11	0.462
Sep-22	−0.06	0.346	−0.12	0.452	−0.18	0.150	−0.15	0.106
Oct-22	0.01	0.289	−0.10	0.420	−0.01	0.079	−0.06	0.055

completed in the earlier years of its establishment in Mpumalanga and Limpopo provinces, correlation lags between precipitation and abundance of *B. dorsalis* adults were as high as 4 months (Theron *et al.*, 2017). The soil-inhabiting stages of *B. dorsalis* may be particularly sensitive to precipitation and its resultant effect on soil moisture. It was found that *B. dorsalis* larvae prefer to pupate in moist soils as compared to dry soils (Alyokhin *et al.*, 2001). However, development of the pupal stage could be compromised if soil moisture is too high – above 80% as found in another study (Hou *et al.*, 2006).

Going back to the interesting phenology of *B. dorsalis* observed in the highest altitude site in this study, two hypotheses can be proposed: (1) The population of *B. dorsalis* dies out annually between June and December, with reinvasion in the region occurring by mid-summer (around January) through natural dispersal or movement of infested fruit from warmer, lower-altitude regions and (2) *B. dorsalis* overwinters in the region, with populations remaining undetectable until conditions become favourable, leading to detectability from mid-summer onwards. By applying the lower developmental thresholds of eggs, larvae and pupae of the Kenyan populations of *B. dorsalis* (Rwomushana *et al.*, 2008) alongside the daily minimum and maximum temperatures recorded between the last detections of *B. dorsalis* at the onset of winter and the first detections of *B. dorsalis* at the onset of summer at the highest altitude site, it was possible to estimate at least five generations of this species per season based on accumulated degree days. The conditions therefore would have been favourable for development of generations if suitable breeding sites were available. Because we did not include fruit sampling in this study, we are unable to confirm the presence of hypothesised overwintering generations. In future studies, fruit sampling coupled with trapping in the high-altitude site could provide key information on the overwintering ability of *B. dorsalis*. For *C. capitata*, some earlier studies in Northern Greece indicated that the overwintering stage

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Table 4. Global Moran's *I* spatial autocorrelation statistics for *Bactrocera dorsalis* male captures in methyl eugenol traps for all data, including data at minimum, median, and maximum trap distance intervals for each month of each study year from October 2020 to October 2022 at the mid-altitude site of Schoemanskloof. Probabilities in bold indicate significant spatial autocorrelation

	Global Moran's *I*							
	Distance threshold (m)							
	1°000		2°000		3°000		4°000	
Month-year	Statistic	*p*-value	Statistic	*p*-value	Statistic	*p*-value	Statistic	*p*-value
Oct-20	−0.08	0.441	−0.11	0.262	−0.11	0.163	−0.10	0.336
Nov-20	−0.02	0.146	−0.12	0.454	−0.14	0.230	−0.10	0.206
Dec-20	−0.23	**0.045**	−0.13	0.142	−0.11	0.132	−0.10	0.342
Jan-21	0.10	0.201	−0.05	0.307	−0.06	0.189	−0.07	0.115
Feb-21	−0.10	0.489	−0.17	0.273	−0.15	0.098	−0.09	0.471
Mar-21	−0.16	0.450	−0.29	**0.035**	−0.12	0.271	−0.09	0.385
Apr-21	0.12	0.188	−0.15	0.341	−0.11	0.389	−0.09	0.470
May-21	0.23	0.120	−0.07	0.389	−0.17	0.036	−0.12	0.099
Jun-21	−0.09	0.492	−0.24	0.107	−0.10	0.480	−0.08	0.360
Jul-21	–	–	–	–	–	–	–	–
Aug-21	−0.14	0.457	−0.17	0.257	−0.06	0.233	−0.07	0.179
Sep-21	−0.24	0.371	−0.24	0.120	−0.10	0.428	−0.10	0.298
Oct-21	−0.14	0.132	−0.10	0.380	−0.09	0.380	−0.10	0.343
Nov-21	−0.08	0.469	−0.11	0.251	−0.11	0.179	−0.10	0.342
Dec-21	–	–	–	–	–	–	–	–
Jan-22	0.40	**0.040**	0.02	0.166	−0.06	0.240	−0.09	0.490
Feb-22	0.13	0.205	−0.16	0.305	−0.13	0.202	−0.09	0.358
Mar-22	−0.02	0.390	−0.24	0.059	−0.11	0.410	−0.08	0.313
Apr-22	−0.35	0.186	−0.19	0.218	−0.11	0.385	−0.08	0.379
May-22	−0.31	0.236	−0.17	0.269	−0.12	0.333	−0.09	0.497
Jun-22	−0.03	0.463	−0.13	0.428	−0.10	0.492	−0.07	0.259
Jul-22	–	–	–	–	–	–	–	–
Aug-22	−0.03	0.130	−0.07	0.151	−0.08	0.276	−0.08	**0.036**
Sep-22	−0.09	0.454	−0.14	**0.049**	−0.09	0.469	−0.10	0.335
Oct-22	−0.02	**0.037**	−0.11	0.253	−0.11	0.166	−0.10	0.330

in open fields can occur primarily as young larvae within fruit, while adults and pupae are particularly susceptible to cold, especially at sub-zero temperatures (Papadopoulos *et al.*, 1996, 1998). In a more recent study conducted at a higher latitude in Vienna in Austria, Wernicke *et al.* (2024) found that all life stages of *C. capitata* were able to survive the winter conditions in protected environments, while none of them survived these same conditions in open-field trials. In Wuhan which represents the northern marginal populations of *B. dorsalis* in China, outdoor experimental trials suggested that *B. dorsalis* may overwinter as pupae, although survival depended on the timing of pupation (Han *et al.*, 2011). In a study conducted in China on both immature and adult stages of *B. dorsalis*, individuals from populations originating from the northern marginal temperate regions were more tolerant of a short-term cold stress than those originating from the southern tropical regions (Wang *et al.*, 2014). In the latter study, these physiological differences were correlated with variations in enzyme activities and concentration of biochemicals indicative of physiological adaptation to cold which could support the range expansion of this fruit fly species in the future (Wang *et al.*, 2014). Further work is required to fully understand the overwintering potential and mechanism of *B. dorsalis* in temperate areas.

Bactrocera dorsalis male catches were found to be clustered in the site with the lowest prevalence. Recognising the potential for such aggregation is important for optimising trap placement for early detection of *B. dorsalis*, particularly in warm temperate regions that are free of this pest. It was also clear that land use was important in influencing *B. dorsalis* trap catches. Catches of *B. dorsalis* were higher in commercial orchards and home gardens compared to abandoned orchards. The abandoned orchards in this study lacked irrigation which could have resulted in drier conditions known to be less suitable for *B. dorsalis* (De Villiers *et al.*, 2016). Aggregated distributions and significant effects of landscape factors have been previously reported for other fruit fly species,

Table 5. Global Moran's *I* spatial autocorrelation statistics for *Bactrocera dorsalis* male captures in methyl eugenol traps for all data, including data at minimum, median, and maximum trap distance intervals for each month of each study year from October 2020 to October 2022 in Ermelo town at the high-altitude site. Bold probabilities indicate significant spatial autocorrelation

	Global Moran's *I*					
	Distance threshold (m)					
	3°000		5°000		8°000	
Month-year	Statistic	*p*-value	Statistic	*p*-value	Statistic	*p*-value
Oct-20	–	–	–	–	–	–
Nov-20	–	–	–	–	–	–
Dec-20	–	–	–	–	–	–
Jan-21	−0.10	0.463	−0.09	0.345	−0.15	0.323
Feb-21	0.49	**0.001**	0.21	**0.001**	−0.07	0.052
Mar-21	0.56	**0.001**	0.17	**0.003**	−0.09	0.096
Apr-21	−0.03	0.372	0.04	**0.049**	−0.10	0.233
May-21	0.44	**0.014**	0.06	**0.041**	−0.11	0.332
Jun-21	–	–	–	–	–	–
Jul-21	–	–	–	–	–	–
Aug-21	–	–	–	–	–	–
Sep-21	–	–	–	–	–	–
Oct-21	–	–	–	–	–	–
Nov-21	–	–	–	–	–	–
Dec-21	–	–	–	–	–	–
Jan-22	−0.07	0.258	−0.12	0.277	−0.13	0.424
Feb-22	0.17	0.113	−0.01	0.082	−0.18	0.082
Mar-22	0.16	0.101	0.07	**0.036**	−0.14	0.120
Apr-22	−0.08	0.386	−0.17	0.263	−0.13	0.463
May-22	−0.01	0.263	−0.05	0.130	−0.13	0.325
Jun-22	−0.02	0.144	−0.12	0.294	−0.13	0.375
Jul-22	–	–	–	–	–	–
Aug-22	–	–	–	–	–	–
Sep-22	–	–	–	–	–	–
Oct-22	−0.10	0.456	−0.13	0.461	−0.13	0.383

including *B. dorsalis* (Bota *et al.*, 2020; Papadopoulos *et al.*, 2003; Puche *et al.*, 2005; Sciarretta *et al.*, 2018; Zalucki *et al.*, 1984). These aggregation patterns, which were more evident at low pest densities, may be as a result of foraging activities of the flies for resources such as food and breeding sites (Sciarretta *et al.*, 2018; Zalucki *et al.*, 1984).

The seasonal phenology and spatial dynamics of *B. dorsalis* characterised in this study reveal interesting core-periphery relations across the altitudinal/temperature gradsect. In broad terms, these patterns were to be expected but raise an interesting question regarding the dynamics at Ermelo, the high-altitude site, on population overwintering or annual reinvasion. Another question raised from the findings in Ermelo is on the meaning of zero-trap catches for *B. dorsalis* and other invasive fruit flies particularly when it comes to the management of outbreaks of these pests. In areas free of these pests, response actions to their outbreaks could be in the form of eradication. Once eradication is rolled out and completed, the declaration of eradication and reinstatement of pest freedom in the affected area, usually delineated by the biology and ecology of the pest, are guided by the international standards for the establishment of pest-free areas for fruit flies (IPPC Secretariat, 2018). According to the international standards (IPPC Secretariat, 2018), a specific period of zero captures (equivalent to three life cycles) in a defined trapping array is required to declare eradication. Here, we found zero catches of *B. dorsalis* for up to six months, periods which were estimated to be equivalent to more than three life cycles based on accumulated degree days. Meats and Clift (2005) introduced the concept of non-viable trap density, which is the fly density within a trapping array below which a population is no longer sustainable. The authors proposed the non-viable trap density as a basis for determining the fly-free period needed to achieve a critical probability level for confirming eradication (Meats and Clift, 2005). Incorporating this concept into management strategies could improve the development and implementation of action plans for invasive fruit fly species, enhancing their effectiveness and supporting the achievement of eradication goals. However, repeated detections of invasive fruit flies in areas where eradication campaigns were considered successful may raise the question of residual populations persisting at low, sub-detectable levels, as previously explored by Papadopoulos *et al.* (2013).

While the findings of this study raised important questions, they also provided useful information to refine and test model parameters on the population dynamics of *B. dorsalis*. These improved models would be particularly relevant for warm temperate areas in the northern hemisphere that are experiencing frequent outbreaks of *B. dorsalis*. Improved models on the potential distribution and growth of this invasive pest would provide important information for designing early detection and control strategies.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485325100230.

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Competing interests. The authors declare no conflicts of interest.

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