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Climatic and edaphic characteristics constrain the distribution of the quarantine pest *Anastrepha grandis*

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Abstract

The South American cucurbit fruit fly, *Anastrepha grandis* (Macquart) (Diptera: Tephritidae), is an economically important pest of cucurbits and is classified as a quarantine species in many countries. In Brazil, *A. grandis* has a limited distribution; it is absent from northern and northeastern Brazil and distributed discontinuously in other parts of the country. To indirectly evaluate the influence of climatic and edaphic variables on the occurrence of *A. grandis*, we used data based on 4 years of cucurbit fruit collections from all mesoregions of the state of São Paulo. Our results show evidence that *A. grandis* is constrained by a minimum air temperature above 12 °C, low (<20 °C) and high (>29 °C) maximum air temperature, and by low rainfall and relative humidity, occurring at altitudes from 520 to 780 m. More importantly, *A. grandis* was not collected in central to western São Paulo, where sandy soil and low soil water availability predominate and the climate is hot and dry. Our findings suggest that soil texture and moisture may be limiting factors for pupal survivorship of *A. grandis*, and consequently edaphic characteristics should be taken into account in studies on its geographical distribution. Based on our results, central to western São Paulo state can potentially be classified as an area of low pest prevalence. Moreover, in countries where cucurbit species are cultivated in such conditions, it is not likely that *A. grandis* could become established.

Introduction

Anastrepha grandis (Macquart) (Diptera: Tephritidae), the South American cucurbit fruit fly, is one of the main pests of Cucurbitaceae species in South America (Norrbom et al., 2012). The main hosts of *A. grandis* are squash (*Cucurbita moschata* Duchesne), pumpkins (*Cucurbita maxima* Duchesne), zucchini (*Cucurbita pepo* L.), melon (*Cucumis melo* L.), and watermelon (*Citrullus* spp.). *Anastrepha grandis* is considered a quarantine pest in several countries, including the USA, Mexico, Argentina, and Uruguay (COSAVE, 2011; CABI, 2020; EPPO, 2020).

Taxonomic, biological, and ecological studies must be performed for quarantine species as part of a 'pest risk analysis' (PRA) (EPPO, 1993), whose protocol aims to

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guarantee the biosecurity of imported vegetables. These studies are used to evaluate the risks and potential for a pest to establish in a certain region (FAO, 2019). For example, the life cycle of the pest species, its host range, biology, and geographical distribution must be determined. Therefore, for a certain cucurbit-producing region to be able to export to countries where *A. grandis* is considered a quarantine species, the commodities must be produced in a pest-free area (FAO, 2018a), such as melon and watermelon for export in Brazil; or growers must confirm that a systems approach is used in cucurbit crop production, according to the standards defined by ISPM No. 35 (FAO, 2018b). Studies of the biotic and abiotic factors that affect the establishment of *A. grandis* are essential to determine the risk of spread into or out of a country.

In South America, because of the interest ofmany countries in exportingmelon, watermelon, and other cucurbits, the studies necessary for PRA and classification of *A. grandis-free areas began in the mid-1980s (de Cabanilla & Escobar, 1993; Aguirre, 1997; Gonzalez & Troncoso, 2007; Guillen & Sanchez, 2007), including Brazil (Araujo et al., 2000). The biology (Silva & Malavasi, 1996; Bolzan et al., 2015, 2017), pest-free areas (Nascimento et al., 1993; Malavasi & Zucchi, 2000; Silva et al., 2019a), and regions using systems-approach crop production (Araujo et al., 2009; Montes et al., 2011; Rabelo et al., 2013; Silva et al., 2019b) are well defined. However, the factors limiting the distribution of A. grandis* in these regions are still unknown.

Anastrepha grandis has a restricted distribution in Brazil; it is present from central to southern Brazil and absent from the northern and northeastern regions (Uchôa & Nicácio, 2010). Moreover, even in Brazilian states where *A. grandis* is recorded, there are sites where it is not collected (Silva et al., 2019b). For example, in the state of São Paulo, *A. grandis* is present in the eastern half of the state and absent from the western half (Montes et al., 2011; Silva et al., 2019b). Although the reasons for the absence of *A. grandis* from these regions are still unknown, climatic characteristics could be a limiting factor, especially in the Brazilian northeast and in central to western São Paulo. However, both regions have thermal conditions suitable for the development of *A. grandis*, based on current knowledge of its biology (Bolzan et al., 2015, 2017). In fact, Silva et al. (2019a), based on thermal requirements, predicted that *A. grandis* would occur in the semiarid region of northeastern Brazil, a large region that could be classified as a pest-free area, including two officially registered pest-free areas in the states of Rio Grande do Norte and Ceará. Therefore, temperature cannot be solely responsible for the restricted distribution, and other abiotic factors are probably preventing *A. grandis* from establishing in certain regions.

The life cycle of *A. grandis* is similar to that of other tephritids; the female oviposits up to 110 eggs in the fruit (Bolzan et al., 2016), where the larvae develop feeding on the pulp and then leave it to pupate in the soil (Christenson & Foote, 1960; Silva & Malavasi, 1996). Studies with various tephritids have shown that soil texture and moisture content significantly affect pupal mortality (Fitt, 1981; Ahmed et al., 2007; Bento et al., 2010; El-Gendy & AbdAllah, 2019). In this study, we evaluated the possible influence of edaphic (soil group, texture, and water availability) and climatic characteristics on the distribution of *A. grandis* in the state of São Paulo. Based on studies with other fruit fly species (Neuenschwander et al., 1981; Milward-de-Azevedo & Parra, 1989; Eskafi & Fernandez, 1990; Hulthen & Clarke, 2006), we hypothesized that *A. grandis* is absent from the western half of the state of São Paulo, where soils are predominantly sandy, with a long-term water deficit, whereas in the eastern half of the state, where *A. grandis* occurs, clay and heavy clay soils predominate.

Materials and methods

Data collection

Fruit of cucurbits known as hosts of *A. grandis* (see Zucchi & Moraes, 2008) were collected at 98 sampling points, located in 51 municipalities in several mesoregions of São Paulo, from February 2009 to February 2012. The state of São Paulo is located in southeastern Brazil and has an area of 248.209 km^2. Fruit were collected mainly in crop fields, but also in urban and peri-urban areas, and were identified at the species or cultivar level by one of the authors (MFSF). The coordinates and altitude of each sampling point were determined at the time of fruit collection, using a global positioning system (GPS); therefore, all data were geo-referenced.

Fruit were taken to the Laboratory of Economic Entomology (LEE) at the Biological Institute of São Paulo, located in Campinas municipality. Fruit were sorted according to collection site, counted, weighed, and placed in plastic containers of various sizes, depending on the size of the fruit, with vermiculite at the bottom to facilitate pupation. Metal 2 × 2-cm mesh screens were used to support the fruit. The plastic boxes were covered with cotton cloth and kept in a room at ambient temperature. After 20–30 days, the vermiculite was sifted to collect the puparia, which were counted and transferred to Petri dishes in a 6-l glass container. The container was covered with voile, and moistened cotton wool was placed on the top to supply water to the emerged flies. Inside the container, a diet consisting of 1:3 parts sugar and yeast extract was available as food for the adult flies. The containers were transferred to a climate-controlled room under 25 ± 2 °C and 70 ± 10% r.h. After 30 days, the glass containers were placed in a freezer to kill the flies, which were sexed and counted. The species was identified by one of the authors (MFSF).

Climatic variables were obtained from the NASA Power database (Sparks, 2018). For each sampling point, we used its coordinates to record the daily minimum, maximum, and mean air temperature (°C) at a height of 2 m, air relative humidity (%) at 2 m, and total rainfall (mm).

The pedological map of the state of São Paulo (Rossi, 2017) was used to classify soil groups (Acrisols, Ferralsols, Cambisols, Fluvisols, and Nitisols) and soil texture (sandy, loamy, clay, and heavy clay soil) at each sample collection point. Soil water availability (SWA) was obtained from CIIAGRO (2020) for each sampling location. Soil water availability corresponded to the mean in the week that the collection was carried out.

Data analysis

All analyses were performed in the statistical software R v.3.6.2 (R Core Team, 2019). We recorded four response variables: total number of puparia, total fly abundance (females+males), infestation per fruit (number of puparia divided by number of fruit in the sample), and infestation per weight (kg) of fruit (number of puparia divided by the total weight of fruits in the sample). Principal components analysis (PCA) was applied to evaluate the correlation among the response variables. Abundance data were log (x + 1)-transformed and scaled to unit variance prior to the PCA.

A generalized additive model (GAM; Wood, 2017) was applied to evaluate the effect of explanatory variables on the distribution of the response variable, using the *mgcv* package (Wood, 2017). Generalized additive models are generalized linear models (GLM) that can account for possible non-linearity in the relationship between explanatory and response variables, employing smoother functions to the latter (Hastie & Tibshirani, 1986). The smoothers can manipulate a series of non-linear relationships. The main reason to use a GAM was the flexibility in modeling the spatial dependence in the data (Wood, 2017) and to select the variables (Marra & Wood, 2011). To select the variables that significantly affected the response, we used the double penalty approach (setting select = TRUE), which add an extra penalty to each term so that it can be penalized to zero (Marra & Wood, 2011).

The explanatory variables were host species, soil group, soil texture, and the interaction between soil group and soil texture, all entered as fixed effect. Years of collection were added to account for temporal trend and months to account for seasonal effect. Climatic variables, altitude, and water availability were added as a smoother variable using a thin plate spline. Spatial dependence was added to the statistical model as an interaction term between longitude and latitude, setting the smoother function as a Gaussian process. This method was employed setting bs = 'gp' in the smoother term. Due to differences in the sampling effort by months and years in the locations, we have added three interaction smoother terms to accommodate these sources of variability in our model. The first was an interaction between months and years, the second between month and location, and the third between years and location. These interactions were added as tensor product smoother using 'ti' smother. We fitted an error distribution of the quasi-Poisson type (a Poisson distribution corrected for overdispersion).

We used Quantum GIS (QGIS) free software v.3.12 (QGIS, 2020) to organize and represent the values for the number of puparia in shapefiles. Then, IDW (inverse distance weighting) interpolation was applied to the values for the number of puparia for each assessed location, providing a visual description of the number of puparia in the state of São Paulo.

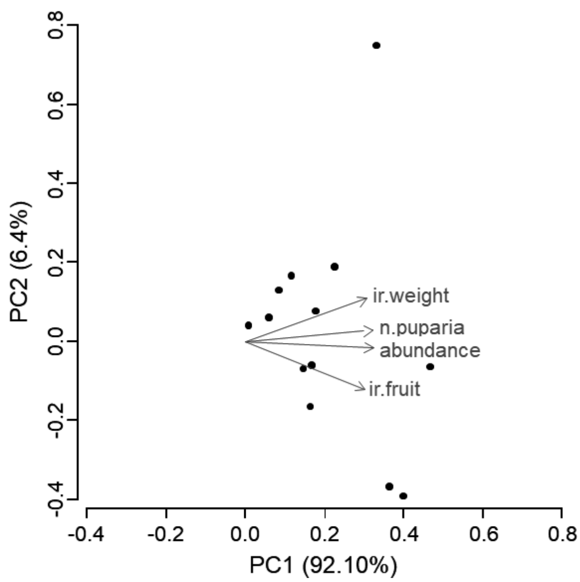

Figure 1 Biplot from the principal components analysis (PCA) displaying the ordination of the response variables: infestation rate by sampling weight (ir.weight) and by fruit (ir.fruit), and number of puparia (n.puparia) and abundance (i.e., sum of males and females) of *Anastrepha grandis* collected from cucurbits at 98 locations (black dots) in the state of São Paulo, Brazil, from 2009 to 2012.

Results

In total, 2 260 fruit from 15 cucurbit species, weighing 1 912 tons, were collected (Table S1). The total number of puparia was 8 297, of which 4 850 adults of *A. grandis* emerged (2 325 females and 2 525 males) (Table S1). Infestation per fruit ranged from 0 to 350 puparia, whereas infestation per weight ranged from 0 to 514 puparia kg^{-1} (Table S1).

The first two principal components (PCs) captured 98.5% of the variability of the data (Figure 1). PC1 accounted for 92.2% of the variation, revealing that the number of puparia and the infestation rate by fruit and by weight and abundance of *A. grandis* were highly and positively correlated (Figure 1). Therefore, we chose to analyze only the number of puparia, because it is the simplest parameter to record, reflects the insect's success in terms of development, and was not affected by mortality in the laboratory.

The results from the variable selection based on the double penalty method are shown in Table 1. The number of puparia was affected by year (Table 1), soil texture, rainfall, minimum and maximum air temperature, relative humidity, altitude, and SWA (Figure 2). Month (Table 1), host species, soil group, and mean air temperature at 2 m had no significant effect on the distribution of the number of puparia (Figure 3). The GAM accounted for 64.6% of the variance.

Table 1 ANOVA test of significance from the quasi-Poisson-generalized additive model (GAM) evaluating the effects of explanatory variables on the number of pupae of *Anastrepha grandis* collected from several Cucurbitaceae species in the state of São Paulo, Brazil, from 2009 to 2012

	Explanatory variables	d.f.	F	P
Linear	Host species	5	0.904	0.54
	Soil group	1	0.005	0.94
	Soil texture	3	5.19	0.001
	Soil group*soil texture	2	0.80	0.45
		edf[1]		
Smooth	Month	0.46	0.02	0.062
	Year	0.39	3.93	<0.001
	Longitude*latitude	6.92	0.89	<0.001
	Tmin	2.67	1.88	<0.001
	Tmax	0.73	0.26	0.024
	T2m	0.02	0.00	0.23
	Rainfall (mm)	4.40	9.88	<0.001
	Relative humidity (%)	2.35	3.50	<0.001
	Altitude (m)	2.21	2.09	<0.001
	Soil water availability (SWA)	1.10	0.31	0.045
	Month*year	5.91	3.31	<0.001
	Month*longitude*latitude	1.80	0.09	0.001
	Year*longitude*latitude	0.16	0.08	0.002

Deviance explained = 64.6%.
[1]edf = effective degrees of freedom.

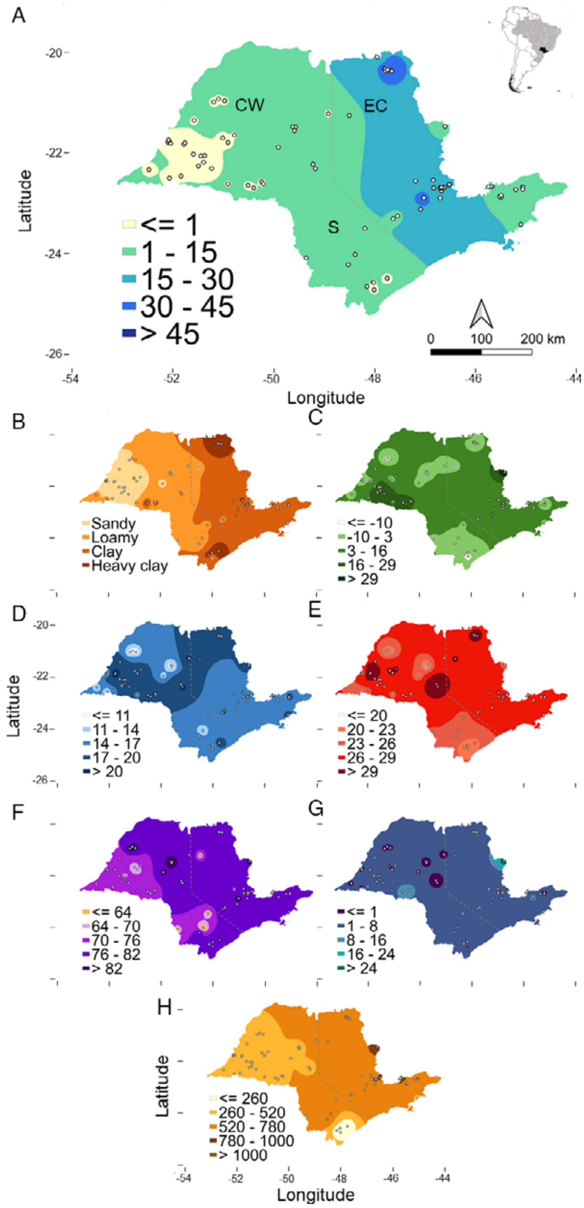

Figure 2 Maps of the state of São Paulo, Brazil: (A) map of South America highlighting Brazil (grey) and the state of São Paulo (back). The main plot displays the interpolated number of puparia of *Anastrepha grandis* collected from cucurbits from 2009 to 2012; (B) soil texture; (C) available soil water (mm); (D) minimum air temperature (°C); (E) maximum air temperature (°C); (F) relative humidity (%); (G) rainfall (mm); (H) altitude (m). The dots indicate sampling points. [Colour figure can be viewed at wileyonlinelibrary.com]

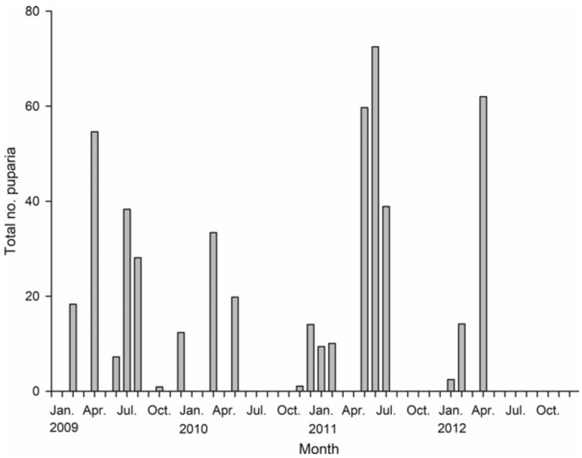

Figure 3 Total number of puparia of *Anastrepha grandis* by month in each year (2009–2012) collected from cucurbits in the state of São Paulo, Brazil.

Distribution of *Anastrepha grandis* in the state of São Paulo

The mapped distribution of the number of *A. grandis* puparia shows a distinct gradient of abundance (Figure 2A). *Anastrepha grandis* is restricted to a region extending approximately from 46° to 49°W and from 24° to 20°S (from the eastern to central part of the state, separated from the central-western and southern regions). In the eastern region, the number of puparia collected from cucurbit fruit ranged from 30 to >45, decreasing from 10 to 1 in the central-western part of the state (Figure 2A). No puparia were collected from fruit from the central-western region (49–52°W) or from the eastern part to the coast, from 45° to 46°W and from 23° to 24°S (Figure 2A).

Influence of edaphic characteristics on the distribution of *Anastrepha grandis*

The region with the highest number of puparia (46–49°W and 20–24°S) has clay to heavy clay soil (Figure 2B), whereas the region with no puparia has sandy to sandy-loam soil (Figure 2C).

Climatic, seasonal, and temporal variables influencing the distribution of *Anastrepha grandis*

The distribution of collected puparia of *A. grandis* was significantly affected by year, altitude, and certain climatic variables (Tmin, Tmax, rainfall, r.h., and SWA) (Table 1). There was no seasonal effect on the number of puparia (Table 1). More puparia were collected in 2009 and 2011 than in 2010 and 2012 (Figure 3) and a significant difference occurred in the sampling effort by months in each year and location and also in each location by year (Table 1).

The region with the highest number of puparia had minimum air temperatures from 14 to 17 °C and maximum from 16 to 29 °C, whereas the region with no puparia had higher minimum temperatures, 17–20 °C (Figure 2D) and maximum temperatures below 20 °C and above 29 °C (Figure 2E). The preferred altitude for *A. grandis* was 520–780 m; in the region with no puparia, the altitude was lower than 520 m (Figure 2H). Relative humidity in the region with the highest numbers of puparia varied from 76 to 82%, whereas in the region with no puparia it ranged from 70 to 76% (Figure 2F). Rainfall was higher in the eastern region, with higher puparia abundance, and lower in the west (Figure 2G).

Discussion

Our results show a clear pattern in the distribution of *A. grandis* in the state of São Paulo, as the species was present from the eastern to central region and absent farther west. Flies were most abundant in autumn (April to July). As predicted, elevation, certain climatic conditions, and soil texture and moisture (SWA) constrained the distribution, as puparia were collected mainly at altitudes from 520 to 780 m, with minimum air temperatures from 14 to 17 °C, maximum air temperature with extremes of low (<20 °C) and high values (>29 °C), relative humidity from 70 to 76%, and higher rainfall. In accordance with our hypothesis, soil texture had a significant effect on the number of puparia and water availability. Puparia were most abundant in fruit collected on clay soils, whereas no puparia were found in fruit sampled on sandy to loamy soils. Accordingly, puparia were most numerous in fruit collected from soils with higher water availability and absent in fruit collected from soils with low water availability during the period of field sampling. Because larvae develop in fruit pulp and are therefore not directly affected by climatic conditions, we hypothesize that climate constrained the distribution of adults, and soil texture and moisture the pupal survivorship.

The monthly abundance of *A. grandis* corresponds to the period of cucurbit production in São Paulo, with the peak in the months with higher fruit availability and lower abundance when production is lowest (CEAGESP, 2020). The same pattern occurs in the state of Santa Catarina (Garcia & Lara, 2006; Alberti et al., 2012), where production occurs in the same period (EMBRAPA, 2010). In contrast, Lisbôa et al., (2020) found that in the colder seasons, the southern and southeastern regions of Brazil are inadequate for the development of the fly. In Switzerland, the expansion of the invasive species *Rhagoletis completa* Cresson was related to the low temperature (Aluja et al., 2011). The very low population of *A. grandis* during winter may be related to specific host requirements. Cucurbit crops are susceptible to chilling injury at temperatures below 7–10 °C (Maynard, 2007).

The response of insects to altitude gradients varies according to several factors that can act directly or indirectly (e.g., mediated through the host plant) on the insect (Hodkinson, 2005). In the present study, as only cucurbit fruit were sampled at all altitudes, the climatic conditions appeared to affect the distribution of *A. grandis*. This species occurs in moderate environmental conditions, unable to colonize neither areas at altitudes below 520 m, where the temperature is higher and relative humidity and rainfall are lower, nor areas at altitudes above 780 m, which exhibit the inverse climate. In Colombia, *A. grandis* was collected at altitudes above 800 m, which are considered suitable for *Anastrepha* species development in that country (Castañeda et al., 2010). In guava (Celedonio-Hurtado et al., 1995) and mango orchards in Mexico (Aluja et al., 1996), species richness was lower and the community was dominated by *Anastrepha obliqua* (Macquart) and *Anastrepha fraterculus* (Wiedemann) at altitudes up to 250 m; above that, *Anastrepha ludens* (Loew) dominated over *A. obliqua*. Moreover, several species showed different abundances at different altitudes (Celedonio-Hurtado et al., 1995; Aluja et al., 1996). Infestation of common walnut by *R. completa*, in Italy, was higher at lower altitudes and decreased linearly to 450 m; the fly did not occur above 700 m (Poggetti et al., 2019). Other tephritids have shown different responses to altitude. The invasive species *Bactrocera correcta* (Bezzi) was not limited by altitude in China, where it expanded its distribution from the lowlands to more than 1 000 m within a decade after invading (Liu et al., 2013). For *Ceratitis capitata* (Wiedemann), *Bactrocera oleae* (Rossi), *Bactrocera cucurbitae* (Coquillett), *Dacus ciliatus* Loew, and *Dacus demmerezi* (Bezzi), the altitudinal abundance is regulated by the weather. In warmer periods, these species are more abundant in higher areas, as the climate is more suitable; when the temperature decreases and the climate is no longer suitable, they migrate to lower altitudes (Vayssières & Carel, 1999; Kounatidis et al., 2008; Castrignanò et al., 2012; Krasnov et al., 2019). The range of occurrence of *A. grandis* in the state of São Paulo indicates that this species is not capable of surviving under harsh climate conditions, i.e., in hot dry regions (characteristic of the central to western part of the state, an unsuitable region) or in very humid regions (>84% r.h.).

The ability of adult fruit flies to survive in environments where water loss is high (desiccation resistance) depends mainly on the sex and also on the physiological characteristics of the species (Weldon et al., 2013, 2016, 2019; Tejeda et al., 2014, 2016). *Anastrepha ludens* males are more resistant to desiccation than females, despite being smaller (Tejeda et al., 2014), as also observed for *Bactrocera tryoni* (Froggatt) (Weldon et al., 2013). Adult flies with higher body lipid and water contents were more resistant to stress conditions than those with lower levels (Weldon et al., 2013, 2016; Tejeda et al., 2014).

Pupal survival is also affected by desiccation and therefore edaphic characteristics can be a limiting factor (Weldon et al., 2019). In agreement with several studies that have found higher mortality of tephritid pupae in sandy soils than in clay soils (Milward-de-Azevedo & Parra, 1989; Eskafi & Fernandez, 1990; Hulthen & Clarke, 2006; Bento et al., 2010), we also observed that *A. grandis* was absent from regions where sandy to loamy soils dominate, and the highest numbers of puparia were collected in clay soils. Therefore, it is possible to infer that the limiting effect of soil on the presence of *A. grandis* may be caused by the soil water content, which decreases progressively from the center to the west of the state of São Paulo (CIAGRII, 2020). Pupal mortality in sandy soils occurs due to lower capacity for water retention in these soils compared to clay soils (Brady & Weil, 2013). Several studies have demonstrated that drier soils have significant effects on fruit fly pupation, ranging from delayed adult emergence (Trottier & Townshend, 1979; Yee, 2013) to higher levels of malformed adults (Neilson, 1964; Yee, 2013) and mortality (Neuenschwander et al., 1981; Jackson et al., 1998; Hulthen & Clarke, 2006; Yee, 2013). The lower the moisture content in the first days of pupation, the higher the pupal mortality (McPhail & Bliss, 1933). Therefore, soil moisture content at the time of pupation is also crucial for fly survival. Water availability central to western São Paulo is lower than in the eastern to central region during the year, particularly in autumn and winter (March to September). In this period, due to lack of rainfall, there is a strong hydric deficit in this region (CIIAGRO, 2020), making the sandy soils even drier. As *A. grandis* is more abundant in this period, larvae that eventually move to pupate will find very dry soils, impeding their development. However, from the eastern to central regions, although rainfall is lower in the same period, the higher water-retention capacity of the clay soils ensures the necessary moisture for fly pupation.

This is the first study using field collections showing that the distribution of *A. grandis* is constrained by environmental conditions. Further studies are needed to disentangle the mechanisms that limit the distribution of *A. grandis*.

Implications for *Anastrepha grandis* distribution in Brazil

Anastrepha grandis has a distribution limited to central and southern Brazil, with no records in the northern and northeastern regions (Uchôa & Nicácio, 2010), except for two reports in the state of Bahia (northeast), but the first report provided no sampling location (Bondar, 1950). The second report discussed seven adult flies collected in southern Bahia, in domestic orchards in areas of Atlantic Rainforest (Melo et al., 2016). Our results support the hypothesis that the absence of *A. grandis* from both regions is due to the extreme, although, opposite, climatic and edaphic conditions in those regions. The northeast is the hottest and driest region in Brazil, with a semi-arid climate and annual mean temperature >22 °C, maximum altitude of 600 m, and annual rainfall <1 000 mm (Köppen, 1936; Alvares et al., 2013). The northern region, which includes Brazilian Amazonia, is the warmest and wettest part of the country, a tropical zone with annual mean temperature >24 °C, altitude <400 m, and annual rainfall >2 500 mm (Köppen, 1936; Alvares et al., 2013). Therefore, the northeast and north have climatic conditions that do not support the survival of *A. grandis*. These same unfavorable climatic conditions for *A. grandis* are observed in the central to western region of the state of São Paulo.

Regarding edaphic characteristics, in the northeast region, sandy to loamy soils with low water availability dominate (Marques et al., 2014). In the northern region, in contrast, clay to heavy clay soils predominate (Teixeira et al., 2010), and the high rainfall and relative humidity throughout the year keep the soil moisture high (Falesi, 1986).

In addition to our findings, the hypothesis that edaphic characteristics, rather than temperature, constrain the distribution of *A. grandis* in the state of São Paulo is supported by two recent studies. Based only on a laboratory study of the biology of *A. grandis* at different temperatures (Bolzan et al., 2017) and the resulting data on its thermal requirements, Silva et al., (2019a) predicted up to 10 generations per year for *A. grandis* in northeastern Brazil, whereas Lisbôa et al., (2020) predicted that the annual number of generations would be highest (>2) in the north and northeast regions. However, the fly has never been collected in either of these regions (Uchôa & Nicácio, 2010), despite several fruit fly surveys carried out. Hence, soil characteristics are probably limiting the distribution of *A. grandis* in these regions.

More importantly, as previously shown for other tephritids (Kumar et al., 2016; van Klinken et al., 2019), our results suggest that an appropriate model for predicting establishment and number of generations of *A. grandis* needs to include the edaphic characteristics as explanatory parameters.

Implications for *Anastrepha grandis* management

Our results suggest that central to western São Paulo state may be classified as an area of low pest prevalence for *A. grandis*. In accordance with our results, in some municipalities of this region, a systems approach has been implemented to export cucurbit fruit to Argentina (Montes et al., 2011; Silva et al., 2019b). There are several specific requirements that a region must meet to be declared – and to maintain – the status of an area of low pest prevalence (FAO, 2017). These include the surveillance activities of trapping and fruit sampling, and official control of the movement of regulated products, among others. Fruit collection can be used to complement trap sampling, but not as the sole surveillance method for the presence/absence of the fly in an area. Therefore, there is a need for further studies in this region of the state of São Paulo, involving federal and state agencies to coordinate and fund the necessary activities (FAO, 2017). Once the region is declared an area of low pest prevalence, cucurbit crops such as melon, watermelon, squash, and cucumber can be exported to countries where *A. grandis* is classified as a quarantine species. This can have significant economic and social impacts for producers, the region, and the state.

In the pest-free zone in the states of Rio Grande do Norte and Ceará, farmers' income increased, unemployment rate decreased, and resource allocation was more efficient for those who adhered to the program (Sousa & Miranda, 2015a,b, 2018). In Ceará, every real (Brazilian currency) invested by farmers and the state government to maintain the status of pest-free area prevents the loss of three reais in exports and jobs (Sousa & Miranda, 2015b). Hence, the status of pest-free area in central to western state of São Paulo could have significant social and economic impacts in the region, particularly for the small farmers.

The constraints of soil texture and climate on *A. grandis* can be exploited to manage this pest. For example, where possible, cucurbits could be sown earlier in regions where the fly is abundant, to desynchronize the fruiting period with the months of higher fly abundance, and crop fields could be located in areas at lower altitudes. Also, our results suggest that irrigation can be used to reduce the fly abundance, if water is delivered in the appropriate amount and by more localized methods, such as micro-irrigation, lowering the local humidity and maintaining soil moisture as low as possible in the same region. In contrast, from central to western São Paulo, crops could be irrigated with less-expensive methods such as sprinklers year-round, enabling continuous production of cucurbits. Furthermore, any soil management technique that reduces water availability can be employed to diminish soil moisture, and consequently minimize the damage caused by *A. grandis*.

Implications for *Anastrepha grandis* as a quarantine species

The status of quarantine species means that the economic risk that *A. grandis* would establish in a region free of this pest is very high, increasing costs for producers due to the additional pest-management tactics necessary to overcome the problem and meet the requirements of importing countries (FAO, 2019). Sometimes, capturing a single specimen can reset the quarantine status and result in a temporary export ban. Based on our results we can infer that there is a very low probability that *A. grandis* would be able to establish in several countries where it is considered a quarantine species. For example, the climatic and edaphic characteristics of two important cucurbit-producing states in the USA, California and Arizona, are more extreme (hotter and drier) than those of the state of São Paulo (NOAA, 2020). Hence, the present study may be a useful resource for authorities to overcome the restrictions posed by countries on the importation of cucurbit fruits from Brazil. However, further studies are needed to evaluate the probability of establishment of *A. grandis* in cucurbit-producing regions worldwide, based on climatic and edaphic characteristics at each location.

In conclusion, our results showed that in addition to climatic conditions, soil texture and soil moisture availability must be taken into account in studies of insect pests that pass at least one stage of the life cycle in soil. For fruit fly species, our results agree with other studies (Hulthen & Clarke, 2006; van Klinken et al., 2019). More importantly, almost half of the total area of the state of São Paulo has potential for the establishment of *A. grandis-low prevalence areas, a status that would generate a positive socioeconomic impact. Finally, our results indicate that A. grandis* has a low probability of establishing in cucurbit-producing countries where the soil is sandy and the climate is hot and dry.

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References

Aguirre C (1997) Distribución y Registros de las Principales Especies de Moscas de las Frutas (Diptera: Tephritidae) en los Países Suramericanos. Instituto Interamericano de Cooperación para la Agricultura (IICA), Lima, Peru.

Ahmed A, Soltani N, Kellouche A & Mazouzi F (2007) Effects of the soil texture and the burying depth of the larvae on some biological parameters of *Ceratitis capitata* (Diptera: Trypetidae). African Journal of Agricultural Research 2: 105–106.

Alberti S, Bogus GM & Garcia FRM (2012) Flutuação populacional de moscas-das-frutas (Diptera, Tephritidae) em pomares de pessegueiro e maracujazeiro em Iraceminha, Santa Catarina. Biotemas 25: 53–58.

Aluja M, Celedonio-Hurtado H, Liedo P, Cabrera M, Castillo F et al. (1996) Seasonal population fluctuations and ecological implications for management of *Anastrepha* fruit flies (Diptera: Tephritidae) in commercial mango orchards in southern Mexico. Journal of Economic Entomology 89: 654–667.

Aluja M, Guillén L, Rull J, Höhn H, Frey J et al. (2011) Is the alpine divide becoming more permeable to biological invasions? – Insights on the invasion and establishment of the walnut husk fly, *Rhagoletis completa* (Diptera: Tephritidae) in Switzerland. Bulletin of Entomological Research 101: 451–465.

Alvares CA, Stape JL, Sentelhas PC, de Moraes Gonçalves JL & Sparovek G (2013) Köppen's climate classification map for Brazil. Meteorologisches Zeitschrift 22: 711–728.

Araujo EL, Cunha AA, Silva RK, Nunes AMM & Guimarães JA (2009) Espécies de moscas-das-frutas (Diptera: Tephritidae) na região do Baixo Jaguaribe, Estado do Ceará. Arquivos do Instituto Biológico (São Paulo) 76: 577–581.

Araujo EL, Lima FAM & Zucchi RA (2000) Rio Grande do Norte. Moscas-das-Frutas de Importância Econômica no Brasil: Conhecimento Básico e Aplicado (ed. by A Malavasi & RA Zucchi), pp. 223–226. Holos Editora, Ribeirão Preto, Brazil.

Bento FMM, Marques RN, Costa MLZ, Walder JMM, Silva AP & Parra JRP (2010) Pupal development of *Ceratitis capitata* (Diptera: Tephritidae) and *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae) at different moisture values in four soil types. Environmental Entomology 39: 1315–1322.

Bolzan A, Diez-Rodríguez GI & Nava DE (2016) *Anastrepha grandis*: Bioecologia e Manejo. Pelotas: Embrapa Clima Temperado (Documentos/Embrapa Clima Temperado), Brazil.

Bolzan A, Nava DE, Garcia FRM, Valgas RA & Smaniotto G (2015) Biology of *Anastrepha grandis* (Diptera: Tephritidae) in different cucurbits. Journal of Economic Entomology 108: 1034–1039.

Bolzan A, Nava DE, Smaniotto G, Valgas RA & Garcia FRM (2017) Development of *Anastrepha grandis* (Diptera: Tephritidae) under constant temperatures and field validation of a laboratory model for temperature requirements. Crop Protection 100: 38–44.

Bondar G (1950) Moscas de fruta na Bahia. Boletim do Campo 6: 13–15.

Brady NC & Weil RR (2013) Elementos da Natureza e Propriedades dos Solos, 3rd edn. Bookman, Porto Alegre, Brazil.

Cabanilla GC & Escobar J (1993) Free zone program of *Anastrepha grandis* in Ecuador. Fruit Flies (ed. by M Aluja & P Liedo), pp. 443–447. Springer, New York, NY, USA.

CABI (Centre for Agriculture and Bioscience International) (2020) Invasive Species Compendium: *Anastrepha grandis* (South American Cucurbit Fruit Fly). https://www.cabi.org/isc/datasheet/5649#5836DD94-0376-4F14-B370-B85B4E32FBE4. Accessed 5 April 2020.

Castañeda MDR, Osorio FA, Canal N & Galeano P (2010) Species, distribution and hosts of the genus *Anastrepha* Schiner in the Department of Tolima, Colombia. Agronomia Colombiana 28: 265–270.

Castrignanò A, Boccaccio L, Cohen Y, Nestel D, Kounatidis I et al. (2012) Spatio-temporal population dynamics and area-wide delineation of *Bactrocera oleae* monitoring zones using multi-variate geostatistics. Precision Agriculture 13: 421–441.

CEAGESP (Companhia de Entrepostos e Armazéns Gerais de São Paulo) (2020) Sazonalidade dos Produtos Comercializados no ETSP. http://www.ceagesp.gov.br/wp-content/uploads/2015/01/sazonalidade_de_produtos.pdf. Accessed 25 May 2020.

Celedonio-Hurtado H, Aluja M & Liedo P (1995) Adult population fluctuations of *Anastrepha* species (Diptera: Tephritidae) in tropical orchard habitats of Chiapas, Mexico. Environmental Entomology 24: 861–869.

Christenson LD & Foote RH (1960) Biology of fruit flies. Annual Review of Entomology 5: 171–192.

CIIAGRO (Centro Integrado de Informações Agrometeorológicas) (2020) Balanço Hídrico Atual e Cenários. http://www.ciiagro.sp.gov.br/blc_hidrico.html. Accessed 1 May 2020.

COSAVE (Comité de Sanidade Vegetal) (2011) Fichas Técnicas Cuarentenarias: *Anastrepha grandis* (Macquart, 1846). Comité de Sanidad Vegetal. http://www.cosave.org/ficha-tecnica-cuarentenaria/anastrepha-grandis-macquart-1846. Accessed 5 April 2020.

El-Gendy IR & AbdAllah AM (2019) Effect of soil type and soil water content levels on pupal mortality of the peach fruit fly [*Bactrocera zonata* (Saunders)] (Diptera: Tephritidae). International Journal of Pest Management 65: 154–160.

EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) (2010) Catálogo Brasileiro de Hortaliças. http://bis.sebrae.com.br/bis/download.zhtml?t=D&uid=C22F9A4962A6E2E68325771C0065A2E4. Accessed 25 May 2020.

EPPO (European and Mediterranean Plant Protection Organization) (1993) Guidelines on pest risk analysis. EPPO Bulletin 23: 191–198.

EPPO (2020) European and Mediterranean Plant Protection Organization Global Database. http://gd.eppo.int/taxon/ANSTGR. Accessed 5 April 2020.

Eskafi FM & Fernandez A (1990) Larval–pupal mortality of Mediterranean fruit fly (Diptera: Tephritidae) from interaction of soil, moisture, and temperature. Environmental Entomology 19: 1666–1670.

Falesi IC (1986) Estado atual de conhecimento de solos da Amazônia brasileira. Proceedings of the 1st Symposium on the Humid Tropics, Vol. I: Climate and Soil. 12–17 November 1984, pp. 168–191. Belém, Pará, Brazil.

FAO (Food and Agriculture Organization of the United Nations) (2017) ISPM 30: Establishment of Areas of Low Pest Prevalence for Fruit Flies (Tephritidae). FAO/IPPC, Rome, Italy.

FAO (2018b) Systems Approach for Pest Risk Management of Fruit Flies (Tephritidae) (ISPM 35), International Plant Protection Convention (IPPC). https://www.ippc.int/en/publications/635/. Accessed 8 April 2020.

FAO (2018a) Establishment of Pest Free Areas for Fruit Flies (Tephritidae). International Standards for Phytosanitary Measures (ISPM 26), International Plant Protection Convention (IPPC). https://www.ippc.int/en/publications/594/. Accessed 8 April 2020.

FAO (2019) Guide for Establishing and Maintaining Pest Free Areas. FAO/IPPC, Rome, Italy.

Fitt GP (1981) Pupal survival of two northern Australian tephritid species and its relationship to soil conditions. Australian Journal of Entomology 20: 139–144.

Garcia FRM & Lara DB (2006) Análise faunística e flutuação populacional de moscas-das-frutas (Diptera, Tephritidae) em pomar cítrico no município de Dionísio Cerqueira, Santa Catarina. Biotemas 19: 65–70.

Gonzalez J & Troncoso P (2007) The fruit fly exclusion programme in Chile. Area-Wide Control of Insect Pests: From Research to Field Implementation (ed. by MJB Vreysen, AS Robinson & J Hendrichs), pp. 641–651. Springer, Dordrecht, The Netherlands.

Guillén D & Sánchez R (2007) Expansion of the national fruit fly control programme in Argentina. Area-Wide Control of Insect Pests: From Research to Field Implementation (ed. by MJB Vreysen, AS Robinson & J Hendrichs), pp. 653–660. Springer, Dordrecht, The Netherlands.

Hastie T & Tibshirani R (1986) Generalized additive models. Statistical Science 1: 297–310.

Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews 80: 489–513.

Hulthen AD & Clarke AR (2006) The influence of soil type and moisture on pupal survival of *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae). Australian Journal of Entomology 45: 16–19.

Jackson CG, Long JP & Klungness LM (1998) Depth of pupation in four species of fruit flies (Diptera: Tephritidae) in sand with and without moisture. Journal of Economic Entomology 91: 138–142.

van Klinken RD, Murray JV, Garcia JN & Clarke AR (2019) Scale-appropriate spatial modelling to support area-wide management of a polyphagous fruit fly (Diptera: Tephritidae). Annals of Applied Biology 175: 350–362.

Köppen W (1936) Das geographische System der Klimate. Handbuch der Klimatologie (ed. by W Köppen & R Geiger), pp. 1–44. Borntraeger Science Publishers, Berlin, Germany.

Kounatidis I, Papadopoulos NT, Mavragani-Tsipidou P, Cohen Y, Tertivanidis K et al. (2008) Effect of elevation on spatio-temporal patterns of olive fly (*Bactrocera oleae*) populations in northern Greece. Journal of Applied Entomology 132: 722–733.

Krasnov H, Cohen Y, Goldshtein E, Mendelsohn O, Silberstein M et al. (2019) The effect of local and landscape variables on Mediterranean fruit fly dynamics in citrus orchards utilizing the ecoinformatics approach. Journal of Pest Science 92: 453–463.

Kumar S, Yee WL & Neven LG (2016) Mapping global potential risk of establishment of *Rhagoletis pomonella* (Diptera: Tephritidae) using MaxEnt and CLIMEX niche models. Journal of Economic Entomology 109: 2043–2053.

Lisbôa H, Grutzmacher AD, Wrege MS, Garcia FRM & Nava DE (2020) Impact of global warming on the distribution of *Anastrepha grandis* (Diptera: Tephritidae) in Brazil. Arquivos do Instituto Biológico 87: 1–10.

Liu X, Jin Y & Ye H (2013) Recent spread and climatic ecological niche of the invasive guava fruit fly, *Bactrocera correcta*, in mainland China. Journal of Pest Science 86: 449–458.

Malavasi A & Zucchi RA (2000) Moscas-das-Frutas de Importância Econômica no Brasil: Conhecimento Básico e Aplicado. Holos Editora, Ribeirão Preto, Brazil.

Marques F, Nascimento A, Araújo Filho J & Silva A (2014) Solos do Nordeste. EMBRAPA, Recife, Brazil.

Marra G & Wood SN (2011) Practical variable selection for generalized additive models. Computational Statistics and Data Analysis 55: 2372–2387.

Maynard L (2007) Cucurbit crop growth and development. Indiana Certified Crop Adviser Conference Proceedings 83: 495–505.

McPhail M & Bliss CI (1933) Observations on the Mexican Fruit Fly and some Related Species in Cuernavaca, Mexico, in 1928 and 1929. United States Department of Agriculture, Washington, DC, USA.

Melo EASF, dos Santos OO, Rocha RB, Strikis PC & Bittencourt MAL (2016) Diversity of frugivorous flies (Tephritidae e Lonchaeidae) in three municipalities in southern Bahia. Arquivos do Instituto Biológico 83: e0402014.

Milward-de-Azevedo EMV & Parra JRP (1989) Influência da umidade em dois tipos de solo, na emergência de *Ceratitis capitata*. Pesquisa Agropecuária Brasileira 24: 321–327.

Montes S, Raga A & Souza-Filho MF (2011) Levantamento de espécies de *Anastrepha* (Diptera: Tephritidae) em áreas de cucurbitáceas sob sistema de mitigação de risco. Arquivos do Instituto Biológico 78: 317–320.

Nascimento AS, Morgante JS, Malavasi A & Uramoto K (1993) Occurrence and distribution of *Anastrepha* in melon production areas in Brazil. Fruit Flies (ed. by M Aluja & P Liedo), pp. 39–42. Springer, New York, NY, USA.

Neilson WTA (1964) Some effects of relative humidity on development of pupae of the apple maggot, *Rhagoletis pomonella* (Walsh). Canadian Entomologist 96: 810–811.

Neuenschwander P, Michelakis S & Bigler F (1981) Abiotic factors affecting mortality of *Dacus oleae* larvae and pupae in the soil. Entomologia Experimentalis et Applicata 30: 1–9.

NOAA (2020) National Oceanic and Atmospheric Administration. https://www.climate.gov/ (accessed 7 May 2020).

Norrbom AL, Korytkowski CA, Zucchi RA, Uramoto K, Venable GL et al. (2012) *Anastrepha* and *Toxotrypana*: Descriptions, Illustrations, and Interactive Keys. https://www.delta-intkey.com/anatox/index.htm (accessed 2 April 2020).

Poggetti L, Raranciuc S, Chiabà C, Vischi M & Zandigiacomo P (2019) Altitude affects the distribution and abundance of two non-native insect pests of the common walnut. Journal of Applied Entomology 143: 527–534.

QGIS (2020) Quantum Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.org

R Core Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rabelo LRS, Veloso VRS, Rios ADF, Queiroz CS & Meshima FHS (2013) Moscas-das-frutas (Diptera, Tephritidae) em municípios com sistema de mitigação de risco para *Anastrepha grandis* Macquart. Arquivos do Instituto Biológico 80: 223–227.

Rossi M (2017) Mapa Pedológico do Estado de São Paulo: Revisado e Ampliado. Instituto Florestal, São Paulo, Brazil.

Silva JG & Malavasi A (1996) Life cycle of *Anastrepha grandis*. Fruit Fly Pests: A World Assessment of their Biology and Management (ed. by BA McPheron & GJ Steck), pp. 347–351. CRC Press, Boca Raton, FL, USA.

Silva MA, Bezerra-Silva GCD, Vilanova ES, Cunha MG & Santos MGS (2019a) Establishment probability of *Anastrepha grandis* and *Zeugodacus cucurbitae* (Diptera: Tephritidae) in Brazilian semiarid based on thermal requirements. Neotropical Entomology 48: 853–862.

Silva MA, Bezerra-Silva GCD & de Bolzan OJJD (2019b) Area-wide management of *Anastrepha grandis* in Brazil. Area-Wide Management of Fruit Fly Pests (ed. by D Pérez-Staples, F Díaz-Fleischer, P Montoya & MT Vera), pp. 301–314. CRC Press, Boca Raton, FL, USA.

de Sousa EP & de Miranda SHG (2015a) Eficiência na produção de melão na área livre de *Anastrepha grandis* no Nordeste brasileiro. Revista Econômica do Nordeste 46: 9–25.

de Sousa EP & de Miranda SHG (2015b) Análise do impacto econômico e social da área livre de mosca das frutas no estado do Ceará. Economia do Ceará em Debate (ed. by FAFD Barreto, ASB de Menezes, DNC de Assis & FJ de Sousa), pp. 165–191. IPECE, Fortaleza, Brazil.

de Sousa EP & de Miranda SHG (2018) Competitividade dos produtores de melão na área livre de *Anastrepha grandis* no Nordeste brasileiro. Revista de Ciências Agrárias 41: 199–208.

Sparks AH (2018) Nasapower: NASA POWER Global Meteorology, Surface Solar Energy and Climatology Data Client for R. Journal of Open Source Software 3: 1035.

Teixeira WG, Arruda W, Shinzato E, Macedo RS, Martins GC et al. (2010) Solos. Geodiversidade do Estado do Amazonas (ed. by MAM Maia & JL Marmos), pp. 73–86. CPRM, Manaus, Brazil.

Tejeda MT, Arredondo J, Pérez-Staples D, Ramos-Morales P, Liedo P & Díaz-Fleischer F (2014) Effects of size, sex and teneral resources on the resistance to hydric stress in the tephritid fruit fly *Anastrepha ludens*. Journal of Insect Physiology 70: 73–80.

Tejeda MT, Arredondo J, Liedo P, Pérez-Staples D, Ramos-Morales P & Díaz-Fleischer F (2016) Reasons for success: rapid evolution for desiccation resistance and life-history changes in the polyphagous fly *Anastrepha ludens*. Evolution 70: 2583–2594.

Trottier R & Townshend JL (1979) Influence of soil moisture on apple maggot emergence, *Rhagoletis pomonella* (Diptera: Tephritidae). Canadian Entomologist 111: 975–976.

Uchôa MA & Nicácio J (2010) New records of Neotropical fruit flies (Tephritidae), lance flies (Lonchaeidae) (Diptera: Tephritoidea), and their host plants in the south Pantanal and adjacent areas, Brazil. Annals of the Entomological Society of America 103: 723–733.

Vayssières J-F & Carel Y (1999) Les Dacini (Diptera: Tephritidae) inféodés aux Cucurbitaceae à la Réunion: gamme de plantes-hôtes et stades phénologiques préférentiels des fruits au moment de la piqûre pour des espèces cultivées. Annales de la Société Entomologique de France 35: 197–202.

Weldon CW, Boardman L, Marlin D & Terblanche JS (2016) Physiological mechanisms of dehydration tolerance contribute to the invasion potential of *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae) relative to its less widely distributed congeners. Frontiers in Zoology 13: 15.

Weldon CW, Díaz- Fleischer F & Pérez-Staples D (2019) Desiccation resistance of tephritid flies: recent research results and future directions. Area-Wide Management of Fruit Fly Pests (ed. by D Pérez-Staples, F Díaz-Fleischer, P Montoya & MT Vera), pp. 27–43. CRC Press, Boca Raton, FL, USA.

Weldon CW, Yap S & Taylor PW (2013) Desiccation resistance of wild and mass-reared *Bactrocera tryoni* (Diptera: Tephritidae). Bulletin of Entomological Research 103: 690–699.

Wood SN (2017) Generalized Additive Models: An Introduction with R, 2nd edn. CRC Press, Boca Raton, FL, USA.

Yee WL (2013) Soil moisture and relative humidity effects during post-diapause on the emergence of western cherry fruit fly (Diptera: Tephritidae). Canadian Entomologist 145: 317–326.

Zucchi RA & Moraes RCB (2008) Fruit flies in Brazil - *Anastrepha* Species, Their Host Plants and Parasitoids. http://www.lea.esalq.usp.br/anastrepha/ accessed 20 May 2020.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Data set used in the analysis. Table contains the total abundance of *Anastrepha grandis* (female + male) in each location in several municipalities in the state of São Paulo, Brazil, from 2009 to 2012. Soil characteristics and mean values of climatic variables are also given.