Evaluation of predicted Medfly (*Ceratitis capitata*) quarantine length in the United States utilizing degree-day and agent-based models

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Keywords

biosecurity, Mediterranean fruit fly, eradication, invasive
pest, agriculture

TO REMOVE:
Take-homes:

1. There is significant variation in predicted quarantine length at different times and locations.

    (a) Captured by normals

    (b) Climate

2. Variation in prediction within time / location (across years) is important.

    (a) Captured by day-of-year (between-year) variation

    (b) Informs reliability of prediction

    (c) Influenced by rare events (eg. cold snaps)

    (d) Prediction based on normal temps vs normal of predictions based on measured temps

3. DD vs ABS comparison

    (a) ABS is better behaved

        i. Seasonal swings less dramatic; Much less discontinuity at beginning of autumn

        ii. Smaller overall range

        iii. Captures common-sense effects missed by DD: eg. extreme cold kills

    (b) Large disagreement between DD and ABS may indicate DD prediction is unreliable/broken

    (c) Variance in predictions should inform management and planning. ABS variance is easier to interpret (KFAT being a dramatic example).

Introduction

Invasions by insects, pathogens and pests increasingly appear to be a defining challenge of the 21st century, facilitated by global connectivity, climatic shifts, and other factors [1] (find paper on number of invasive species). Invasions by insects that do not become established are by their nature less likely to be detected than those that are "successful" from the point of view of the insect. However, when the invading species is of environmental, human health, or economic concern there is a greater chance that cases of invasion followed by extirpation would be detected and studied [2]. Eradication of such insects can be desirable and feasible [3] depending on several factors. One factor might be that the new environment is only marginally or seasonally suitable to the invading insect, facilitating its eradication. Another is that the high cost of allowing establishment leads to extensive efforts for eradication. The invasion of the malaria mosquito species *Anopheles gambiae* into Northeastern Brazil in the 1930's [4] is one example of an invasive insect that was successfully eradicated primarily due to the second of these reasons [5, 6]. In the case of *An. gambiae* there have been no reports of reinvasion, but there are examples of insects that recurrently invade areas outside their native range and are recurrently extirpated within relatively few genrations. The Gypsy moth *Lymantria dispar* in Canada [7] is one such species. Arguably, another example is the screwworm *Cochlyomyia hominivorax* along the current northernmost edge of its range in Panama[8] and more recently in Florida (add citation on Florida).

One of the most important instances of repeated invasion and extirpation by an economically important pest is that of the Mediterranean fruit fly *Ceratitis capitata* (Wiedemann), aka. Medfly, in California. The last four decades have seen a repeated pattern of invasion, detection, and response interspersed by periods of no detections [9, 10]. While it has been suggested that this pattern is the result of cryptic establishment of Medfly and other tephritids in California, Others have argued that Medfly in California is an example of a "metainvasion", consisting of multiple sequential or overlapping introductions [11]. Still other researchers have maintained that Medfly is repeatedly eradicated from the state [12] or for different situations in different regions of the state [13, 14]. Medfly is occasionally found in other parts of the mainland US such as Florida (cite), and in other countries or areas that are considered free of the pest such as New Zealand (CHECK), and (some free areas here).

The response plan to Medfly in California, and the other "free" regions mentioned above, is extensive and costly, including a quarantine [15]. A practical and important problem is how long to maintain the countermeasures and quarantine after flies are no longer detected. Predicting the likely duration of required quarantines would help with management decision making and planning, including potential cost savings by having sufficient but not excessive resources available.

Currently most programs determine quarantine lengths by calculating the amount of time required for a given number of generations to elapse under a thermal unit a accumulation ("degree day") physiological development model (CITE). Degree day based quarantine lengths have been codified in some legal regulations, including United States Federal (@TCC make ref:Title 7 Subtitle B Chapter III Part 301.32-10 Treatments) and California[16]. However, the procedure prescribed only defines when the end of a quarantine period has been reached after the fact. For planning and resource allocation, policy makers and managers typically attempt to predict the quarantine lengths by using normal temperatures for forward projection [?]. Although it frequently works fairly well, this approach is mathematically flawed and also provides no indication as to the variance or uncertainty of those predictions.

Recently, another approach to determining effective quarantine durations was introduced via Agent-Based Simulations (ABS)[17]. The MED-FOES system simulates a population of individual medflies under inundative sterile insect technique (SIT) control, explicitly modeling extirpation as opposed to the degree day approach of just attempting to determine the time for a specific number of generations to elapse. MED-FOES also allows for the sampling of parameter space (temperature dependent mortality for each stage, fecundity, etc.) producing a distribution of possible outcomes.

In this paper, we analyzed the predicted quarantine length

(PQL for short) for 11 sites in the continental United States (figure 1 and table 1) based on both the standard thermal accumulation degree day method[18] as well as the MED-FOES[19] ABS under sterile insect technique (SIT)[**?**] eradication. Seasonal variations dominate the variation in quarantine length predictions, so we aggregated the PQL values for each day of the year (Jan. 1, Jan. 2, ect.) across a large number of years (65 for most of locations) to produce normals. This approach allows us not only to compare the standard degree day method to the MED-FOES ABS, but more importantly provide insight into seasonal and spatial variations, prediction uncertainties, and model reliability.

Figure 1. Location of sites analyzed.

Methods
Sites and Temperature Data
Hourly air temperature data for 11 sites was downloaded from NOAA's Integrated Surface Database (ISD) dataset[20, 21]. The airport sites shown in figure 1 were chosen for their biological relevance and availability of high quality hourly data over a long time frame.

Sites are referred to here by the last three letters of the callsign shown in table 1. For 8 sites (SFO, FAT, LAX, RIV, SAN, JAx, TPA, and MIA), temperature data starting on 1950-01-01 was used. The 3 other sites contained large (> 14 days) gaps or other problems in the early years of their data, so data starting on 1970-01-01 for IAH and 1973-01-01 for BUR and MCO was used. For all sites, temperature data from the start date through 2017-05-15 was used for quarantine length predictions for dates ranging from the start date for the site up to 2016-01-01. Data was fetched and parsed using the `Fetching and parsing ISH.ipynb` program. Records for the same station callsign were merged, since identification, format, and precise location of stations has changed over the years. The data was then cleaned using the `Cleaning temperatures.ipynb` program by removing outliers, identifying large gaps (> 3 hours), resampling to every hour on the hour using linear interpolation, and filling the large gaps using day-over-day linear interpolation (interpolating using values for the same hour of day from previous and following days). The processing programs and resulting temperature datasets are provided in the Supplemental Materials.

Degree-Day Calculation
Degree-days were computed by the single-sine method[18] using a base development temperature

of 12.39°C (53.3°F) and 345.56 degree-days Celsius (DDc; 622 DDf) per generation following the standard required by California Department of Food and Agriculture regulation 3406(b)[22, 16]. Since we have hourly temperature data, we also calculated degree-days by simple summation for comparison[23]. For each date, the number of days required to pass 3 generations of degree-day based life cycles was computed. These calculations are implemented in `Temperature functions.ipynb` in the Supplemental Materials.

Agent-based Simulations: MED-FOES
MED-FOES[19, 17] is an agent-based simulation explicitly modeling the eradication of a population of Medflies under inundative sterile male releases (aka: sterile insect technique or SIT). A MED-FOES simulation models a single non-spatial population starting from a given age distribution and number of individuals through the time the population experiences extirpation when the last potentially fertile female dies or mates with a sterile male. The simulation is parameterized on the initial population, additional mortality induced by control efforts, the effectiveness of SIT, and a large number of biological parameters for which ranges are known from the literature, including temperature-dependent development and mortality. The simulation is fed the same hourly timeseries of temperature values which was used for degree-day calculations and updated in hourly time steps.

Due to the fact that only ranges are known for many of the parameters, 2500 individual MED-FOES simulations were run for each given start date at each site sampling different regions of parameter-space using a Latin Hypercube Sampling[24] procedure. This set of simulations is referred to as a 'run'.

Varying the start date for different simulations was achieved by simply starting at different points in the input temperature file; for this study a run starting every 7 days over the range of dates available for each site. Each set of runs for a single site over a range of starting dates is referred to as a 'runset'. All runsets were conducted with the same input parameters aside from temperature. Initial population numbers were chosen as a standard outbreak based upon several real outbreaks modeled previously[17].

MED-FOES version 0.6.2 was run under OGS/Grid Engine 2011.11 on a CentOS 6.6 HPC cluster. The MED-FOES code, configuration files, and helper scripts are provided in the Supplemental Materials. Overall, we created 11 runsets (one for each site), each containing runs starting every 7 days over the input temperature data range for that site, where each run contained 2500 individual simulations sampling different regions of biologically plausible parameter space.

The MED-FOES data is summarized here by the number of days from the start date required for 95% of the simulations in a run to be eradicated, referred to as pe95.

Table 1. Weather station (NOAA ISD) sites used.

Callsign	Station Name	State	Latitude	Longitude	Elevation	Start year
KSFO	SAN FRANCISCO INTERNATIONAL A	CA	+37.620	-122.365	2.4	1950
KFAT	FRESNO YOSEMITE INTERNATIONAL	CA	+36.780	-119.719	101.5	1950
KBUR	BURBANK-GLENDALE-PASA ARPT	CA	+34.201	-118.358	236.2	1973
KLAX	LOS ANGELES INTERNATIONAL AIR	CA	+33.938	-118.389	29.6	1950
KRIV	MARCH AIR RESERVE BASE	CA	+33.900	-117.250	468.2	1950
KSAN	SAN DIEGO INTERNATIONAL AIRPO	CA	+32.734	-117.183	4.6	1950
KJAX	JACKSONVILLE INTERNATIONAL A	FL	+30.495	-81.694	7.9	1950
KIAH	G BUSH INTERCONTINENTAL AP/HO	TX	+29.980	-95.360	29.0	1970
KMCO	ORLANDO INTERNATIONAL AIRPORT	FL	+28.434	-81.325	27.4	1973
KTPA	TAMPA INTERNATIONAL AIRPORT	FL	+27.962	-82.540	5.8	1950
KMIA	MIAMI INTERNATIONAL AIRPORT	FL	+25.791	-80.316	8.8	1950

Statistical analysis

The main results reported here are 'normals' in a meteorological sense of term, but without the typical running mean smoothing which would complicate interpretation of the results. For a variable of interest (eg. temperature or PQL), all values for the same calendar day irrespective of year (eg. 20-July) are aggregated and summary statistics such as mean, minimum, maximum, and standard deviation are computed for each aggregation. Figure 2 shows the mean of the normal PQL based on 3 generation degree day accumulation and MED-FOES 95% extirpation along with the minimum and maximum of the normals for temperatures. Figures 4 and 5 show the standard deviations (σ) of the normals for the degree day and MED-FOES based PQL. `Temperature functions.ipynb` contains the code used to perform normal calculations, and the code generating these figures is `Summary Figures.ipynb`.

The results reported here are the normals of PQL computed using the full temperature time series as opposed to computing PQL from the normal of the temperature timeseries. While the latter is fairly common practice, it is not mathematically proper since, as with means, the normal of a function of X is not generally equal to the function applied to the normal of X. Additionally, by computing the normals of the predicted quarantine durations, we can investigate properties of the distribution of values as shown in figures 4 and 5 and the "supernorm" supplemental figures.

Results

There is significant variation in PQL across both time and location. The temporal variation in PQL is dominated by a yearly cycle which is characterized well by the normal values shown in figure 2. Table 2 shows the percentage of variance in quarantine length predictions which is captured by the mean of the normal yearly cycle (aka. R^2) for each site. At all but one site, greater than 75% of the variance in both degree day and MED-FOES based PQL is accounted for by the mean normal, and the majority ex-

Table 2. Percentage of PQL variance captured by the mean of the normal. DD PQL is the 3 generation single sine degree day based prediction, and pe95 is the MED-FOES agent-based simulation predictions.

	R^2	
Site	DD PQL	pe95
SFO	9.12%	28.01%
FAT	93.93%	75.68%
BUR	90.71%	90.88%
LAX	80.17%	83.07%
RIV	92.23%	81.89%
SAN	80.99%	80.91%
JAX	96.45%	94.78%
IAH	95.10%	91.80%
MCO	94.62%	95.77%
TPA	91.91%	94.40%
MIA	88.42%	92.00%

ceed 90%. SFO is an exception to the overall rule, with the mean normal accounting for only 9.1% of the variation in degree day based PQL and 28.0% of the MED-FOES based PQL. This is also shown in the respective 'supernorm' supplemental figures S?? and S??.

Seasonal dependence

The seasonal variation, evidenced by the general shape of the curves shown in figure 2, is doubtless familiar to anyone engaged in Medfly pest management. Outbreaks starting in the late summer, autumn, or early winter will extend through relatively cold periods where thermal dependent development will be slow and therefore extend the duration of quarantine required for 3 generations of degree days to accumulate (referred to as DD PQL hereafter). Similarly, outbreaks starting in the spring or early summer often lead to short quarantines due to the relatively high temperatures.
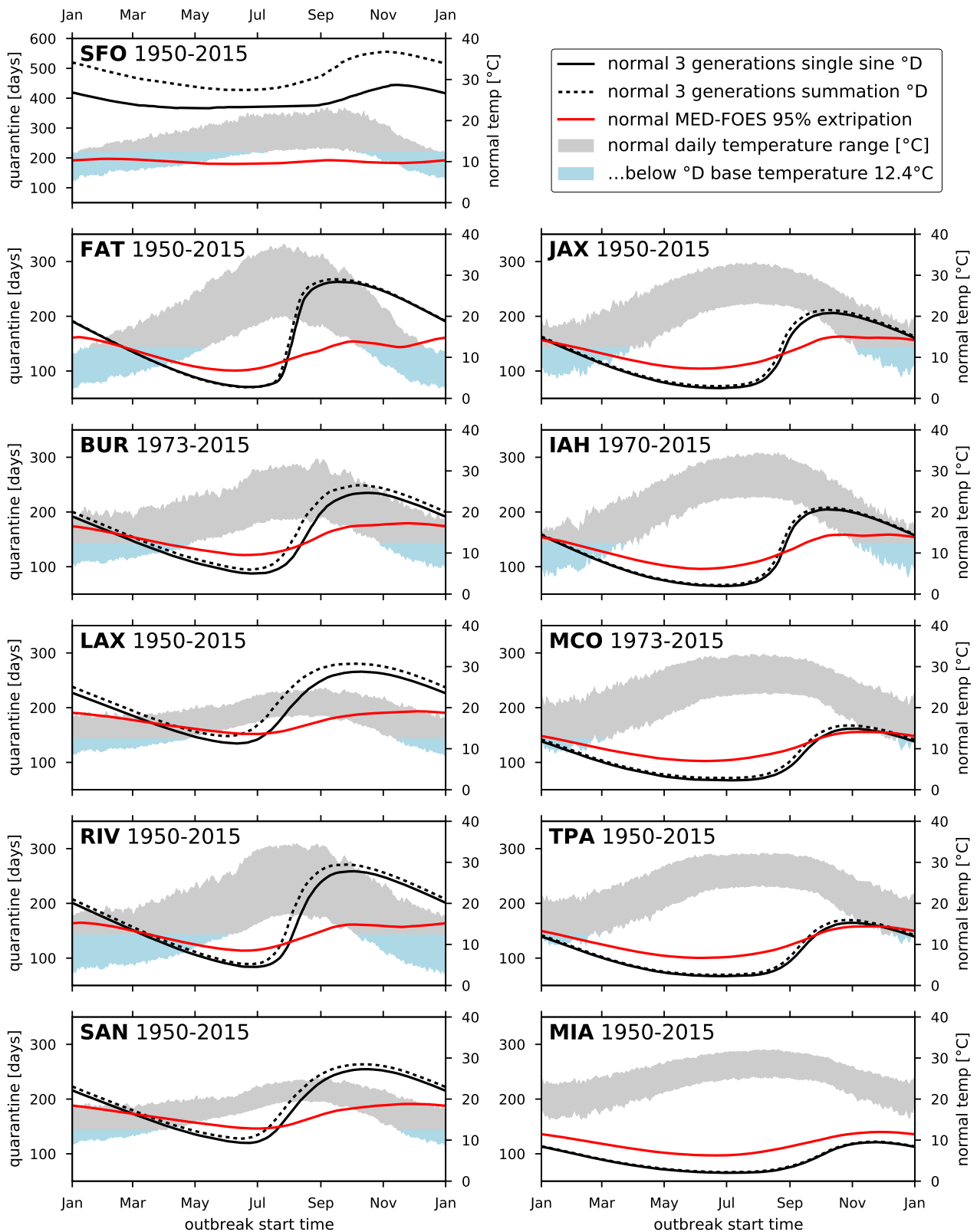
Figure 2. Summary of normal quarantine length predictions for each site. Year range of input temperature data used is inclusive. All panels have identical limits except SFO quarantine.

This familiar pattern is also predicted by the MED-FOES ABS despite it being quite different in nature from simple degree day accumulation. However, the MED-FOES predictions (pe95) show a smaller seasonal swing. pe95 generally produces a smaller overall range of PQLs, with longer quarantines than DD PQL for spring and early summer outbreaks, and shorter quarantines for late summer through early winter.

A particular feature of interest, shown most dramatically at FAT in figure 2, is that MED-FOES PQL often flattens out or even dips for quarantines starting in the late autumn or early winter. This can be due to relatively rare and brief cold-snaps, normally lasting only a few hours, which increase mortality. Since DD PQL does not account for mortality, it misses the effect of cold-snaps entirely. This cold-snap effect is most clearly seen at more northern and more inland sites where cold-snaps are more likely: particularly FAT and RIV, but also BUR, LAX, JAX, and IAH.

Geographic dependence

PQL generally shows a positive correlation with latitude[**?**]. Sites are ordered by latitude in the figures and tables. As seen in figure 2, higher latitude sites tend to have longer PQL as well as larger seasonal swings for both DD and MED-FOES based predictions.

Figure 3 shows the relationship between PQL and latitude. An ordinary least squares fit to the median PQL at each site shows a significant slope for both DD (F=14.08, p=0.005) and MED-FOES (F=10.55, p=0.010), but the DD based predictions are more sensitive to latitude than MED-FOES (coefficients of 17.39 and 4.78 respectively). Additionally, MED-FOES predictions are better behaved for SFO, and to a lesser extent FAT, where the DD model for Medfly appears to break down.

In addition to the variation associated with latitude, large differences in PQLs computed for the same start date can exist between even relatively nearby sites. For example, the differences in both degree day and MED-FOES PQLs for the three sites in the Los Angeles region (LAX, BUR, RIV) (shown in the supplemental figure **??**) show a strong seasonal component with a spike in July and/or August. The difference in DD PQL between LAX and BUR is normally about a month (overall median=35 days; overall 25% & 75% quantiles are 28 & 45 days), but the median difference of the normal exceeds 75 days in August with some PQL differences up to 142 days. Differences in MED-FOES PQLs are more seasonally stable, with the LAX minus BUR difference not exceeding 42 days at its maximum.

Variance and uncertainty

Figures 4 and 5 report the standard deviation (σ) of the normal for DD PQL and MED-FOES PQL respectively. These indicate the year to year variability of the PQL for outbreaks starting at a given time of the year and can be used to gauge the uncertainty of quarantine length predictions relative to the actual quarantine length which will be required. Similar information is represented by the interquartile ranges shown in figure 3 and the 'supernorm' supplemental figures. Those 'supernorm' figures also show that the underlying distributions of PQL values are generally not highly skewed, making σ a relatively easy to interpret proxy for uncertainty.

Excluding SFO, the mean normal is a good predictor of DD PQL with values below 20 days except for the late summer and early autumn, where variance increases due to quarantines extending through the cold season. FAT

and, to a lesser extent, RIV show this increase more dramatically, presumably due to their more arid/inland climates where both daily and seasonal temperature ranges are larger (also see figure 2). The standard deviation generally decreases with latitude.

The standard deviation in DD PQL for SFO shows a inversion of the seasonal trend other sites exhibit. This is due to the colder temperatures leading to extremely long degree day based quarantine predictions frequently extending across two winter seasons.

The standard deviations of MED-FOES based PQL normals shown in figure 5 are generally about $1/2$ as large as for DD based PQL. This indicates that MED-FOES PQL not only shows less dramatic seasonal swings, but is also produces more consistent predictions across years. Values again generally decrease with latitude, but less consistently than DD PQL σ of normals. Also, unlike with the DD PQL, the results for SFO appear consistent with other sites.

A notable feature is that BUR, LAX, and SAN all show an increase in the year to year variation in MED-FOES PQL starting in July and extending through November, while that increase for all other sites starts in July or August but extends all the way to January or February. Additionally, results for FAT show a sharp increase in uncertainty starting in September, fitting with the more aird/inland climate. RIV shows a significant but more gradual increase.

Extrapolation from historical quarantines

A list of 34 Medfly quarantines in CA dating from 1975 to early 2017 was obtained from APHIS[**?**] and is shown in the supplemental table ??. All but two of these quarantines were declared in the latter half of the year (July through December) where DD PQLs are typically relatively long, with 68% (23/34) occurring in September through October where DD PQLs are longest. August, the month where uncertainty in DD PQL often spikes (see figure 4), accounts for 30% (7/34) of historic quarantines.

DD and MED-FOES based PQLs were computed using the start date for each historic quarantine and the temperature data from the closest site from the 11 analyzed here. MED-FOES vs DD PQLs ...

DD start date vs normal for DOY count 34.000000 mean -6.419693 std 25.900133 min -77.712121 255075max 36.106061

pe95 start date vs normal for DOY count 34.000000 mean -0.589953 std 8.224247 min -22.856247 255075max 16.445749

DD-pe95 start date count 34.000000 mean 64.480820 std 62.604590 min -40.071429 255075max 191.805556

Taking historical quarantine declaration dates as a guide, MED-FOES PQLs greater stability and shorter durations for quarantines spanning cold weather

Discussion

The principal contributions of this work can be broken down into three categories: 1) Comparison of PQLs as determined by the DD and ABS methods. 2) variation in av-
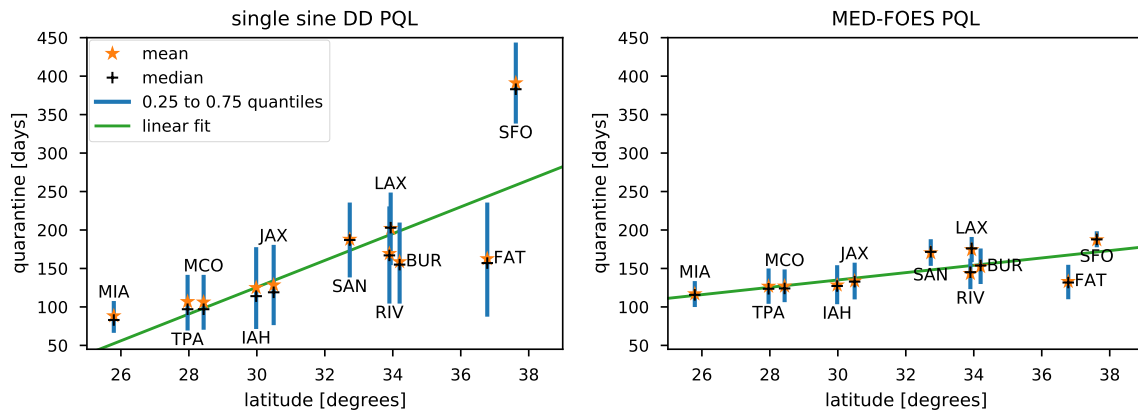
Figure 3. Predicted quarantine length dependence on latitude. For each site, the mean, median, and inter-quartile range are shown (similar to a boxplot). An ordinary least-squares linear fit to the median values is shown by the green lines. The left pane is for single sine degree day predictions, and MED-FOES based predictions (pe95) in the right pane.
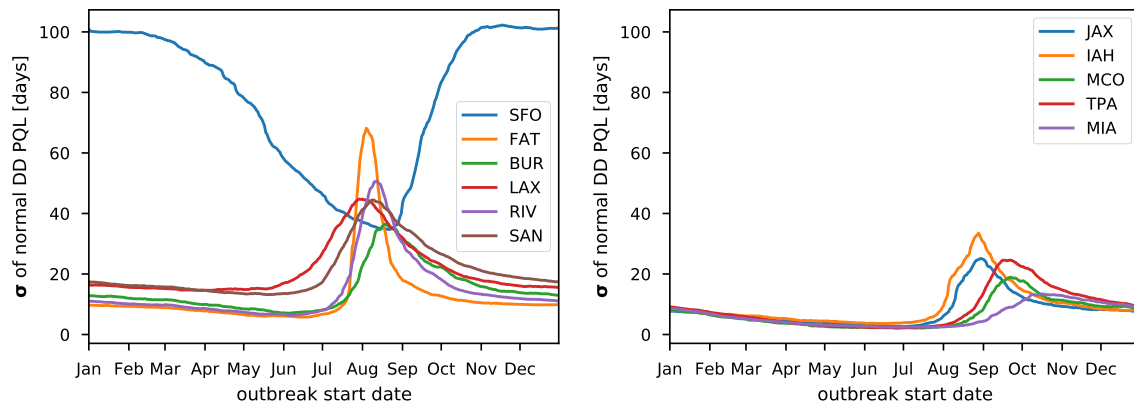

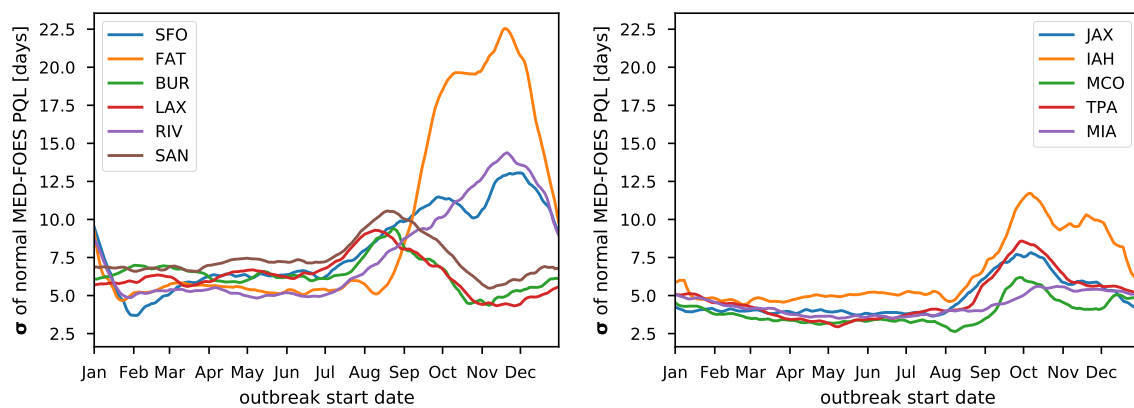**Figure 4.** Variation in quarantine length prediction based on 3 generations of single-sine degree day accumulation.

Figure 5. Variation in quarantine length prediction based on 95% of MED-FOES simulations showing extirpation.

erage PQLs across time of year and space, and 3) variation in PQLs within a time of year and location. Consideration of all three of these by program managers, planners and other decision makers is likely to improve quarantines by informing resource allocation ahead of outbreaks, reduc-

ing quarantine costs in some cases, and reducing risk from premature quarantine suspension in others. The results presented cover most of the latitudinal range of Medfly suitability within the United States as well as many sites of probable introduction, and will hopefully find use as a

general guide.

Extirpation models are extremely difficult to test for accuracy given the impracticality of experimental introductions and the sparse and idiosyncratic nature of historic outbreaks.

Requiring a fixed number (typically 3) generations of degree days to pass is a "tried and true" method, but not explicitly an extirpation model. It may overestimate required quarantine length through cold weather[**?**] and may underestimate length when growth conditions are very favorable, which somewhat paradoxically leads to quicker extirpation under SIT. However, the simplicity of degree day and the "has worked so far" nature means it will likely continue to be the regulatory benchmark.

ABS results may be used to inform and modulate responses and treatments which are under the discretion of managers. In situations where DD PQL greatly exceed those from MED-FOES, it is likely that DD is missing important effects such as cold snaps which may justify shortening quarantine periods. On the other hand, in cases where MED-FOES predicts longer times to extirpation, it is plausible that the DD model is overly generous and it is critical that eradication treatments and SIT releases be conducted aggressively.

A few specific results arising from overall comparisons of different locations are worth highlighting. In general, DD PQL for Medfly around San Fransisco are almost certainly too long for the entire year. The ABS PQLs are flatter and seem more realistic at around 200 days for San Fransisco compared with the 400-550 days of DD PQLs. For several other California locations (typified by Fresno and Riverside) DD PQLs are in close alignment with those from the ABS for the first half of the year, but go significantly longer in the cooler months. For three of four Florida locations analyzed, DD PQLs are significantly shorter than the ABS results (Miami, Tampa, and Orlando). The extent of the difference in those Florida locations is smaller in the later months of the year, but the generality of this pattern suggests that the margin of safety for quarantines as calculated by DD in those locations may be smaller than expected.

Other systematic comparisons of (PQLs? development?) include .. (PLUG Davis paper here)

As expected, there is significant variation in PQL depending on the location of the outbreak, with the extremes in our study sites represented by Miami and San Fransisco. These geographic results could be compared directly to previous efforts to model climatic suitability of different parts of the US for Medfly, by equating longer PQLs with higher climatic suitability. One of the early studies on the subject focused on Medfly found higher climatic suitability in Florida locations (Fort Pierce and Orlando) compared with California sites [25]. Within California, however, those authors found a higher number of suitable months in coastal areas such as Oceanside compared with Riverside and Fresno, roughly paralleling our findings (compare Los Angeles or San Diego with Fresno or Riverside). A more recent analysis of climatic suitability likewise concludes that coastal S. California is the most favorable area of the state for Medfly, but favora-

bility drops inland in the south due to desert conditions. Suitability in central and northern California is limited by cold temperatures and freezes [26].

Seasonal variation within locations revealed WORDS ON SEASONAL HERE

An important aspect of PQLs from the ABS is variation within particular times of years and locations. Rare events like cold snaps can increase mortality in the ABS, and thereby lead to shorter PQLs than expected based on historical averages, or DD PQLs. The specificity of the ABS is particularly useful in determining when quarantines might be safely suspended due to a rare event, something that would not be captured by the DD model. The DD model includes only development for generating PQLs, and development is halted at low temperatures, extending quarantine lengths. The ABS, however, also includes mortality for generating PQLs, which means that low temperatures can significantly reduce estimates.

By expanding on previous work [17], this study suggests that an improved approach to setting quarantine lengths would include estimates from the DD method and from the ABS.

The initial quarantine length estimate could be quickly produced based on the distribution of PQL values generated using historical temperatures. This would generate not just a single 'typical' value as the current method of projecting using historical average/normal temperatures does. The median 'most likely' value may be used for official estimates, while the variance and extremes would provide managers and affected parties additional information vital for planning.

Once the eradication program is underway, weekly simulations via the ABS could indicate the likelihood that extirpation has been achieved. If the threshold 95% extirpation is observed the decision to end quarantine early could be made, or in the case where the ABS has not reached the 95% threshold at the end of the DD PQL additional measures could be considered to reduce the risk of redetection.

Conclusions

Please state what you think are the main conclusions that can be realistically drawn from the findings in the paper, taking care not to make claims that cannot be supported.

Author contributions

In order to give appropriate credit to each author of an article, the individual contributions of each author to the manuscript should be detailed in this section. We recommend using author initials and then stating briefly how they contributed.

Competing interests

All financial, personal, or professional competing interests for any of the authors that could be construed to unduly influence the content of the article must be disclosed and will be displayed alongside the article.

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