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Comments on the concept of ultra-low, cryptic tropical fruit fly populations

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Determining establishment of invasive species is crucial for developing policy for their management and/or eradication, but what if establishment is difficult to assess? Papadopoulos *et al*. [1] expand a line of reasoning [2] that posited the Mediterranean fruit fly (*Ceratitis capitata*, medfly) was established in California below measureable levels, and extended it to 17 tropical fruit flies detected in California during 1950–2012. This theory has statistical and biological limitations that we review. We suggest an alternative approach that addresses the biology of the invasive species.

To estimate the likelihood of establishment [1], statistic *N* was defined as the cumulative number of times a species was detected during two *proximal* years in the same 196 km^2 geographical lattice cell in California, skipping years with no captures. The values for *N* were compared with simulated values under the assumption of random yearly introductions to test the probability of obtaining by chance *N* as large as computed from the detection data. Sufficient detection data were available for *Anastrepha ludens*, *Bactrocera dorsalis* and *C. capitata* in the Los Angeles region and for the latter two species in the San Francisco Bay area. Observed *N* was significantly greater than random for the three species in the Los Angeles region but only for *B. dorsalis* in the Bay Area, and the authors inferred their establishment at *ultra-low, cryptic levels* [1] below those enabling estimates of population density. They further assert that '. . . several lines of evidence support the hypotheses that from five to nine tephritid species have become established' [1, p. 7]. Their test is anti-conservative [1] as differences in habitat suitability and trapping intensity influence capture probabilities.

While it is impossible to disprove their 'necessarily subjective' hypothesis [1, p. 8], projecting establishment of rare tropical fruit flies in temperate regions without considering the effects of weather is vexing, and inference about establishment based on recurrence data is neither explanatory nor provides confirmation. *N* may be a measure of recurrence that may be owing to multiple causes including multiple introductions without establishment (e.g. [3]) owing to increased international trade in the areas of the highest detection [4].

Cited paper [5] states that establishment requires the existence of a self-sustaining population over a period of time corresponding to multiple generations, and failure to establish (e.g. [6]) may be because of biotic and abiotic factors acting on any stage of the life history of the species. Papadopoulos *et al*. failed to explain why the polyphagous medfly, if established, did not develop measureable continuous populations despite more than 35 years of multiple introductions (e.g. [3]) and large numbers of detections [1], or why the olive fly (*Bactrocera oleae*) spread widely in California. Answering this requires the capacity to characterize the species' niche (e.g. [7,8]) so as to estimate its potential for establishment and population growth in time and place under current and climate change scenarios [6]. Papadopoulos *et al*. incorporated as part of their argument a series of projected fruit fly-friendly regions based on correlative ecological niche modelling (ENM) [9] and other less rigorous studies. ENM approaches attempt to characterize the climatic niche of a species in the area of recorded distribution using aggregate weather data assuming that the current distribution is the best indicator of its climatic requirements, the distribution is in equilibrium with current climate and climate niche conservatism is maintained [10]. ENM approaches have several limitations, make implicit mathematical assumptions and lack mechanistic underpinnings that limit their extension to new areas/novel climates [11,12]. More importantly, the use of tephritid detection records from California [1] to determine the ENM climatic correlates would yield results that are non-explanatory and untestable [13].

Our admitted bias is to use mechanistic physiologically based demographic models (PBDMs) that explicitly capture important aspects of the weather-driven biology and trophic interactions independent of distribution records [14–17]. The dynamics models and sub-model functions of PBDMs are largely the same across trophic levels and species, albeit with species-specific parameters, and when driven by daily weather or climate change scenarios predict prospectively the phenology and relative dynamics of a species' population across wide geographical areas [6,14,15]. Density is a state variable and is used to estimate the favourability of an area for a species, and to help us explain its establishment success or failure [6]. Distribution and field dynamics data can be used as independent tests of the model (e.g. [18,19]), and given appropriate data, PBDMs can be used to explore the invasion process itself [20]. PBDMs are useful for assessing how *fruit fly friendly* a region might be. For example, a PBDM for medfly showed that it has relatively narrow thermal limits, and predicted prospectively that its distribution in California is limited to coastal southern California where high detection occurred [1], while establishment in the San Francisco Bay area was deemed unlikely [18]. In Mexico, coastal northern Baja California is also moderately favourable with the highest average densities predicted in tropical areas [6] where containment efforts are ongoing. The same model was used to predict medfly's distribution in the Mediterranean Basin where the fly is endemic in many regions (e.g. Italy [18], western Morocco [21]). Predicted average annual density is inversely related to the coefficient of variation and is a measure of favourability of locations (A. P. Gutierrez & L. Ponti 2013, unpublished data). The fly is known to overwinter in fruit cellars (microclimates) in northern Italy and in warmer near-coastal areas of Israel from where it disperses inland during summer (see [18]).

In sharp contrast, the obligate olive fly is widely established in California (e.g. Berkeley) [19]. Its thermal limits are quite broad, but field and simulation studies confirm that it is limited by high temperatures in desert areas and by cold in northern areas of California [6,19]. The same model predicts the distribution of olive fly in the Mediterranean Basin [17] including the mesoclimate of Sardinia and areas around the northern lakes of Italy [19]. Eradication of olive fly failed in the Mediterranean Basin and was not attempted in California [19].

In summary, inference of establishment of fruit flies based on recurrence data is neither explanatory nor provides confirmation of establishment in California, and ENMs based on the detection data will overestimate the distribution. By contrast, PBDMs for medfly and olive fly accurately predicted their potential distribution in California and elsewhere. PBDMs provide explanation for species phenology and dynamics that can be tested against independent field data (e.g. coffee [22] and other crops), and can be used to assess the risk of establishment in new areas relative to known areas of establishment under current climate and climate change scenarios [6]. This capacity is critical for risk assessment and policy development (see references in [6]).

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