



## Forum

# Dynamic Economic Thresholds for Insecticide Applications Against Agricultural Pests: Importance of Pest and Natural Enemy Migration

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## Abstract

In Integrated Pest Management programs, insecticides are applied to agricultural crops when pest densities exceed a predetermined economic threshold. Under conditions of high natural enemy density, however, the economic threshold can be increased, allowing for fewer insecticide applications. These adjustments, called ‘dynamic thresholds’, allow farmers to exploit existing biological control interactions without economic loss. Further, the ability of natural enemies to disperse from, and subsequently immigrate into, insecticide-sprayed areas can affect their biological control potential. We develop a theoretical approach to incorporate both pest and natural enemy movement across field borders into dynamic thresholds and explore how these affect insecticide applications and farmer incomes. Our model follows a pest and its specialist natural enemy over one growing season. An insecticide that targets the pest also induces mortality of the natural enemy, both via direct toxicity and reduced resource pest densities. Pest and natural enemy populations recover after spraying through within-field reproduction and by immigration from neighboring unsprayed areas. The number of insecticide applications and per-season farmer revenues are calculated for economic thresholds that are either fixed (ignoring natural enemy densities) or dynamic (incorporating them). The model predicts that using dynamic thresholds always leads to reduced insecticide application. The benefit of dynamic thresholds in reducing insecticide use is highest when natural enemies rapidly recolonize sprayed areas, and when insecticide efficacy is low. We discuss real-life situations in which monitoring of natural enemies would substantially reduce insecticide use and other scenarios where the presence of beneficial organisms may lead to threshold modifications.

**Key words:** grain storage, model, revenue, tomato, *Tuta absoluta*

Integrated Pest Management (IPM) strives to reduce pest damage to agricultural production by combining chemical, biological and cultural control methods. A key concept in IPM is the Economic Injury Level (*EIL*), which is the population density of pests above which control actions become economically profitable. Economic injury levels are pest- and crop-specific, as they depend on the extent of yield reduction due to the pest, the crop’s market value, and the monetary costs of control. They are calculated as:

$$EIL = \frac{C}{V ID I_p} \quad (1)$$

Where *C* is the cost of chemical control, *V* is the market value of the crop, *ID* is the yield loss due to each pest individual, and *I<sub>p</sub>* is the insecticide’s impact in reducing crop damage (Pedigo et al. 1986).

Agricultural crops are typically monitored for pests at regular (e.g., weekly) intervals by farmers or by trained inspectors. To account for both pest population growth between inspection rounds

and the time elapsed before a decision to apply pest control is implemented, Economic Thresholds (*ETs*) are often developed to use with *EILs*. An *ET* (often also called an Action Threshold) indicates the pest density at which an insecticide application is recommended, so as to prevent a pest from exceeding its *EIL* in the future. *ETs* are generally set lower than the corresponding *EILs*, and consider pest reproductive rates (Brown 1997). Lower *ETs* are set for rapidly reproducing pests to allow more time for preparing spray events (see, e.g., Ragsdale et al. 2007).

It has often been pointed out that *ETs* can, and ideally should, be adjusted to account for pest suppression by resident predators and/or parasitoids (e.g., Gonzalez and Wilson 1982, Hoffmann et al. 1990, Hollingsworth et al. 1995, Brown 1997, Giles et al. 2003, Conway et al. 2006, Hallett et al. 2014). Natural enemies can suppress pest population growth rates, which may allow farmers to reduce insecticide use (i.e., set higher thresholds for insecticide applications) when natural enemies are abundant (Ramsden et al. 2017). In addition, insecticides commonly have lethal or sublethal negative effects on natural enemies (e.g., Naranjo et al. 2002, Calvo-Agudo et al. 2021). These effects often lead to resurgence of the initial pest after spraying and/or to secondary pest outbreaks, namely infestation of the crop by a different pest species (Luck et al. 1977, Hardin et al. 1995, Heimpel and Mills 2017, Janssen and van Rijn 2021). Economic thresholds that consider natural enemies are termed ‘dynamic thresholds’ (*DTs*), because they are dynamically adjusted to the abundance of the natural enemies during the crop growing season. Dynamic thresholds have been estimated in several ways. Brown (1997) proposed the calculation of economic thresholds using the following equation:

$$ET = \frac{EIL}{1 + r} \quad (2)$$

where  $r$  is the instantaneous reproductive rate of the pest. To calculate the dynamic threshold, information about the natural enemy population density at time  $t$ ,  $NE_t$ , and the predation rate,  $\alpha$ , of each natural enemy is also needed.

Consider a single natural enemy species whose population dynamics do not track changes in pest densities. This may be the case if the natural enemy is limited by abiotic factors, or exploits additional prey/hosts (if the natural enemy’s population is coupled to the pest population, modified equations should be used, Brown 1997). In such cases, the dynamic threshold, *DT*, can be estimated using:

$$DT = \frac{EIL + \alpha NE_t}{1 + r} \quad (3)$$

Musser et al. (2006) used a modification of Brown’s (1997) framework to propose *DTs* for the control of the European Corn Borer (*Ostrinia nubilalis* Hübner [1796] [Lepidoptera: Crambidae]) in sweet corn in the presence of the egg parasitoid *Trichogramma ostriniae* Peng & Chen (Hymenoptera: Trichogrammatidae). An alternative approach was advocated by Zhang and Swinton (2009). These authors used discrete dynamic optimization to calculate the best timing for multiple spraying events, with the goal of maximizing the farmer’s revenue from a crop while accounting for loss of pest control due to damage to the natural enemy community. The optimization process, implemented through dynamic programming, considers the densities of both the pest and the natural enemies at each decision point. A third approach utilized field data that described the population growth of an economic pest (the pear psyllid, *Psylla pyri*), with and without its natural enemies (Sanchez et al. 2022). Gompertz growth functions, which represent growth rates that decline very gradually at high densities, were fitted to the population dynamics data series. The fitted curves were used to estimate *DTs*.

A key aspect that has not yet been incorporated into *DT* estimates is the migration of natural enemies and of pests in the agricultural landscape. Some insect predators and parasitoids disperse out of agricultural plots in response to insecticide treatment, and immigrate into the plots days or weeks later (Jepson and Thacker 1990, Duffield and Aebischer 1994, Schindler et al. 2022). We hypothesized that such dispersive natural enemies are more likely to complement chemical pest control than are natural enemies that do not move across field boundaries. This is because dispersive natural enemies can better migrate from the field when insecticides are applied, and can return to resume their pest control services more quickly after these spraying events are concluded. With such migratory natural enemies, population fluctuations between insecticide applications are expected to be high, and the farmers’ information gain from monitoring natural enemy densities would increase as well. We therefore also hypothesized that *DTs* would be more sensitive to the population densities of highly migratory than to more sedentary natural enemy species. Pests can also enter fields from off-field locations at rates that depend on their dispersal abilities (Dunley and Croft 1990), weather conditions (Ludwig et al. 2018), crop plant (Tillman et al. 2014) and landscape (Tscharnke et al. 2008) characteristics. We predicted that the rates of immigration of the pest and the natural enemy into the field would interactively affect *DTs*. Namely, *DTs* would be highest (and insecticide applications lowest) when pest immigration rates are low, but natural enemy immigration rates are high.

To evaluate these hypotheses, we developed a model addressing the use of an insecticide to suppress a single hypothetical pest species over one growing season, using Brown’s (1997) framework. In the ‘economic threshold’ (*ET*) scenario of the model, the insecticide was applied whenever the pest population exceeded a fixed threshold density. In the ‘dynamic threshold’ (*DT*) scenario, spraying decisions incorporated natural enemy densities. We tested different values of the parameters of the model related to the crop, to the pest, and to the natural enemy, to identify parameter values that markedly reduced the number of insecticide applications in the *DT* scenario. To use *DTs*, farmers and inspectors need to monitor the natural enemies in addition to monitoring the pests, which involves some extra costs. The model enabled us to identify circumstances that make these costs worthwhile – namely conditions where the use of a dynamic threshold would substantially reduce the need to apply insecticides in comparison to the use of a fixed *ET*. To illustrate the utility of the model we apply it to two test cases, control of *Tuta absoluta* in tomato fields, and control of grain beetles in wheat storage. We discuss the benefits and costs of using *DTs* in commercial cropping systems, and advocate crop protection approaches that consider population densities of pests and beneficial insects (natural enemies and pollinators) in decision-making.

## Methods

### The Basic Model

A deterministic model was built to follow the population dynamics of a pest and its specialized natural enemy over a 24-week crop growing season. For simplicity, the model does not include stage- or age-structure. Hence, all pest individuals induce identical damage to the crop, and are equally susceptible to chemical and biological control. The model also does not include selective (population genetic) changes in the traits of the crop plant, the pest, or the natural enemy, nor is there explicit spatial structure. The default variable values for the model and their ranges of values tested in the model runs are provided in Table 1.

**Table 1.** Default variable values for the model and their range of values tested in the computation. Several default values are based on the tomato-*Tuta absoluta*-*Nesidiocoris tenuis* Taxonomy: (Reuter, 1895) (Hemiptera: Miridae) system in Israel. We were unable to obtain realistic estimates for the remaining variables in this system, and then chose default values arbitrarily (bold font)

| Variable name                    | Interpretation  | Default value (and range of values explored in this work) |
|----------------------------------|---|---|
| Pest-related variables:          |   |   |
| <i>Cp</i>                        | Rate of pest immigration (individuals/plant/week)                           | 0.001 (0.0001–0.0015)                                     |
| <i>Ip</i>                        | Proportion of pests killed by insecticide                                   | 0.75 (0.4–1.0)  |
| <i>K</i>                         | Field carrying capacity for pests (individuals/plant)                       | 50  |
| <i>P</i>                         | Pest population size (individuals)  | 10  |
| <i>r</i>                         | Pest reproductive rate/week   | 1 (1–10)  |
| Natural enemy-related variables: |   |   |
| <i>α</i>                         | Natural enemy's predation rate (prey items/individual/week)                 | 2.2 (1–10)  |
| <i>β</i>                         | Natural enemy birth rate/week   | 4.9   |
| <i>NE</i>                        | Natural enemy population size   | 2   |
| <i>Cne</i>                       | Out-field natural enemy immigration rate (individuals/plant/week)           | 0.001 (0.000–0.003)                                       |
| <i>Ine</i>                       | Proportion of natural enemies killed by insecticide                         | 0.2 (0.0–1.0)   |
| <i>μ</i>                         | Natural enemy mortality rate/week   | 4.2   |
| Crop-related variables:          |   |   |
| Cost spray                       | Insecticide application cost (USD/ha)                                       | 120   |
| Crop value                       | Market price of crop (USD/kg)   | 0.12 (0.01–1.00)  |
| Planting density                 | Crop planting density (plants/ha)   | 30,000  |
| Yield reduction                  | Damage to yield per pest individual (proportion of yield of a single plant) | 0.0121 (0.0010–0.0500)                                    |

When the crop is unsprayed, the pest (*P*) population increases at rate *r* per week, and the natural enemy (*NE*) population's weekly rate of increase is  $\beta - \mu$  (birth minus mortality). Each individual in the natural enemy population consumes  $\alpha$  pest individuals per week. We consider a single-crop farming unit that we call a 'field', but which could also represent an orchard, section of forest plantation, greenhouse, or food-storage facility. Pests and natural enemies may immigrate into the field from areas outside the margins, which contain an unlimited pool of individuals. We assume that the number of pest individuals entering a field decreases linearly with pest density within the field, and reaches zero when field pest density attains the carrying capacity (*K*). Hence, pests colonize fields at a rate  $Cp(K - Pt)$  individuals/time step. This term increases with the pest's *per capita* immigration rate (*Cp*) and decreases with the pest's population density in the field at time *t* (*Pt*). Natural enemy colonization of fields, in contrast, increases with the density of pests in the field because pests represent the natural enemies' sole resource. The natural enemy's *per capita* rate of immigration into the field (colonization) is expressed as *Cne*. Thus, we assume that natural enemies are increasingly attracted by the pests as pest density increases (e.g., Schellhorn and Andow 2005). As the resources for the pests are concentrated within the agricultural field, the pests are assumed not to leave the field. Natural enemies, on the other hand, may migrate out of the field after spraying, in response to the decline in prey density.

In the absence of insecticide application, pest population dynamics are influenced by reproduction, predation/parasitism by the natural enemy, and immigration from outside of the field. These processes are described, respectively, by the terms  $\alpha NE_t$ , and  $Cp(k - Pt)$  in Eq. 4. Natural enemy population dynamics are influenced by reproduction and colonization from outside the field (Eq. 5). Reproduction depends on the number of natural enemies born (which, in turn, increases linearly with the density of the pest,  $\beta Pt NE_t$  in Eq. 5), and dying (independent of pest density,  $\mu NE_t$  in

Eq. 5) in each time step. The number of colonizers from out-field locations is affected by pest densities within the field ( $CnePt$  in Eq. 5), but not by off-field natural enemy densities, since we assume infinite populations outside of the field.

$$P_{t+1} = P_t + rP_t - \alpha NE_t + Cp(k - P_t) \quad (4)$$

$$NE_{t+1} = NE_t + \beta Pt NE_t - mNE_t + CnePt \quad (5)$$

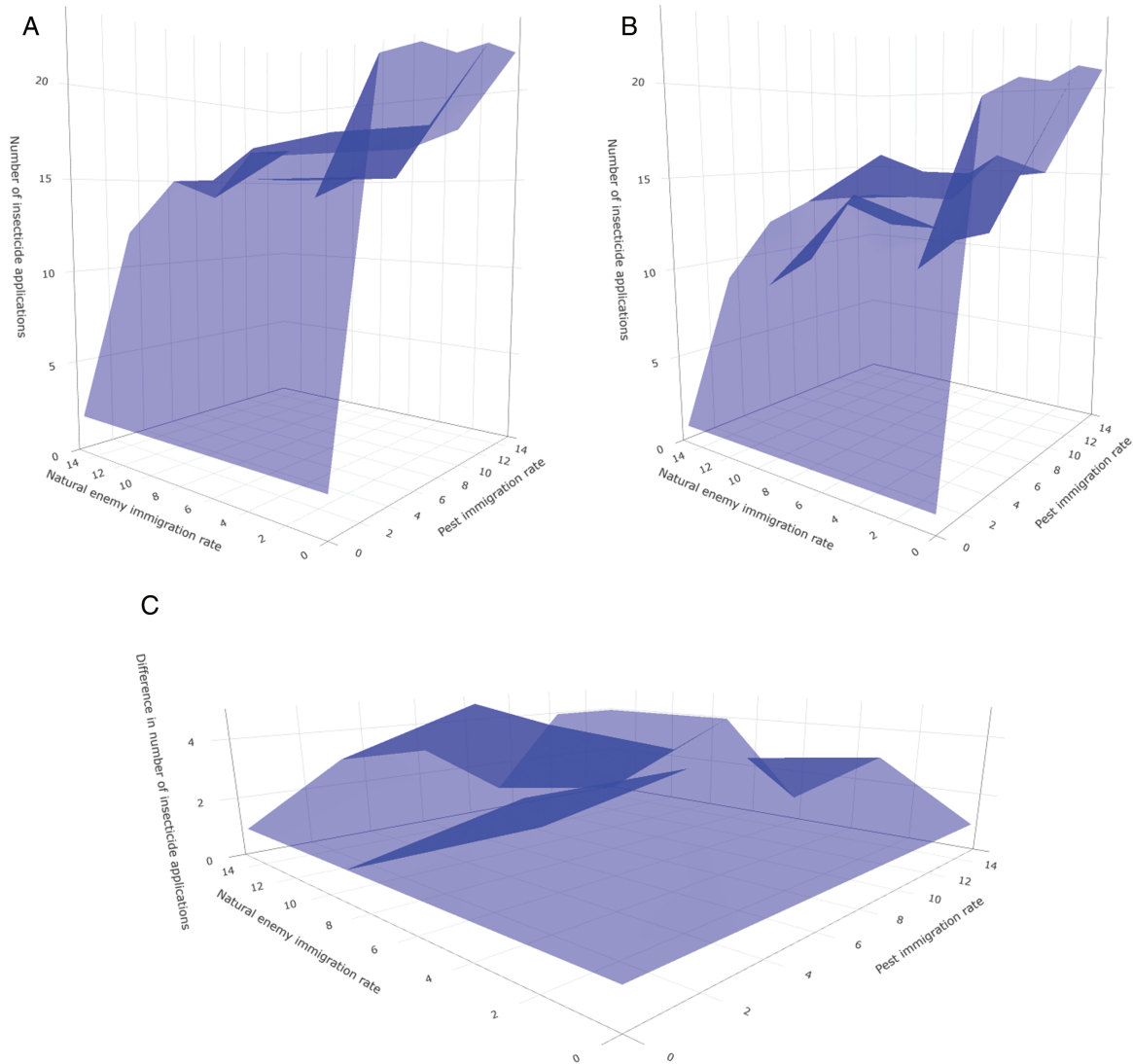
The pest and natural enemy dynamics after spraying are described by Eqs. 6 and 7, respectively. Application of the insecticide kills a fraction *Ip* of the pests and a fraction *Ine* of the natural enemies. Hence,  $IpPt$  pests (Eq. 6) and  $IneNE_t$  (Eq. 7) natural enemies die. It has no further (residual, longer-term) effect on either the pest or the natural enemy population. Following the spraying event, a fraction  $I_m$  of the natural enemies disperse from the field, resulting in  $I_m NE_t$  natural enemy individuals that leave the field (Eq. 7). Pests do not disperse from the field after spraying.

$$P_{t+1} = P_t + rP_t - \alpha NE_t - IpPt + Cp(k - P_t) \quad (6)$$

$$NE_{t+1} = NE_t + \beta Pt NE_t - mNE_t - IneNE_t - I_m NE_t + CnePt \quad (7)$$

The Economic Injury Level was calculated according to Eq. 1. We considered two model scenarios for each combination of parameter values. In the *ET* scenario, insecticide is applied when pest densities exceeded the Economic Threshold, calculated with Eq. 2. In the *DT* scenario, the field is sprayed when pests exceed the Dynamic Threshold (Eq. 3). The default values for the insect demographic parameters and for the crop-related parameters (Table 1) are based on one of the case studies that we consider in the Discussion section: the tomato pest *Tuta absoluta* and its natural enemy, the mirid bug *Nesidiocoris tenuis* (van Lenteren et al. 2021, L. Shaltiel-Harpaz, unpublished data).

Population densities of the pest and natural enemies during the growing season were calculated for each combination of variables,



**Fig. 1.** Number of insecticide applications needed to remain below the *ET* (A) or the *DT* (B) throughout the crop season, for varying immigration rates by the pest and the natural enemy. The immigration rate units are individuals $\times 10^{-3}$ /plant/week. The difference between the *ET* and the *DT* scenarios (C) represents the reduction in insecticide use if *DTs* are applied instead of *ETs*.

as were the number of insecticide applications and the seasonal revenue to the farmer. The ranges of tested variables were restricted to values that generated a positive seasonal revenue from the crop in both the *ET* and *DT* scenarios. The revenue calculation includes the economic value of the crop that was not damaged by the pest, minus the season-wide costs of insecticide applications. These costs include the pesticide, as well as the machinery and labor needed for its application. The costs of monitoring the pests and the natural enemies (e.g., manpower, traps, pheromones) were not added to the model.

The model was implemented in R version 4.2.0 (R Core Team 2022). The figures were produced using the library plotly (Sievert 2020), with no smoothing of the interpolated 3D-surfaces. The model code is available at <https://tamarkeasrmlab.weebly.com/data-sets.html>.

## Results

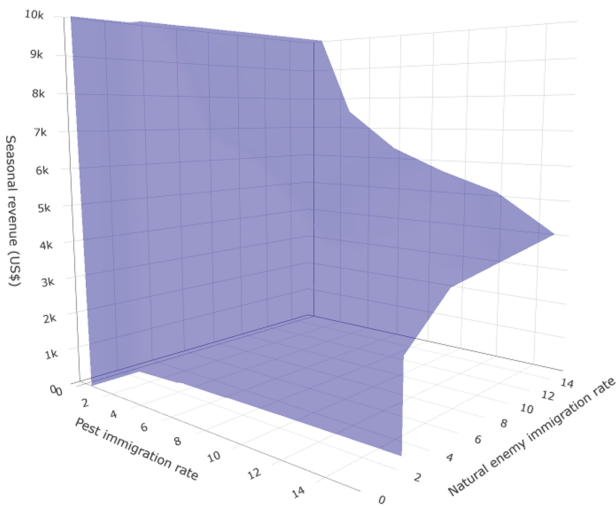
### Effects of Pest and Natural Enemy Immigration (Colonization) Rates ( $C_p$ and $C_{ne}$ )

The number of insecticide applications needed to control the pest increases with the rate of pest immigration and decreases with the

natural enemy's immigration rate (Fig. 1). More sprays are applied under the standard economic threshold scenario (*ET*, Fig. 1a) than under the dynamic threshold scenario (*DT*, Fig. 1b). The difference in the number of insecticide applications between the two scenarios increases with higher immigration levels by the natural enemy and by the pest (Fig. 1c). Since both scenarios operate under the same economic constraint (the *EIL*), they result in identical revenues to the farmers. Revenues decline with increasing pest immigration rates, and increase with natural enemy immigration (Fig. 2).

### Effect of Insecticide Toxicity ( $I_p$ and $I_{ne}$ )

In both model scenarios, the number of insecticide applications increases with the insecticide's toxicity to the pest (Fig. 3a, b). This is directly due to the inverse relationship between *EIL* and insecticide effectiveness originally envisioned by Pedigo et al. (1986; Eq. 1). It reflects the rationale that low-efficacy insecticides increase the effective cost of control and that farmers should tolerate higher pest damage under these conditions. Spraying is thus recommended at lower pest densities when the insecticide is highly effective than when the insecticide is less effective. In addition, increased pest mortality

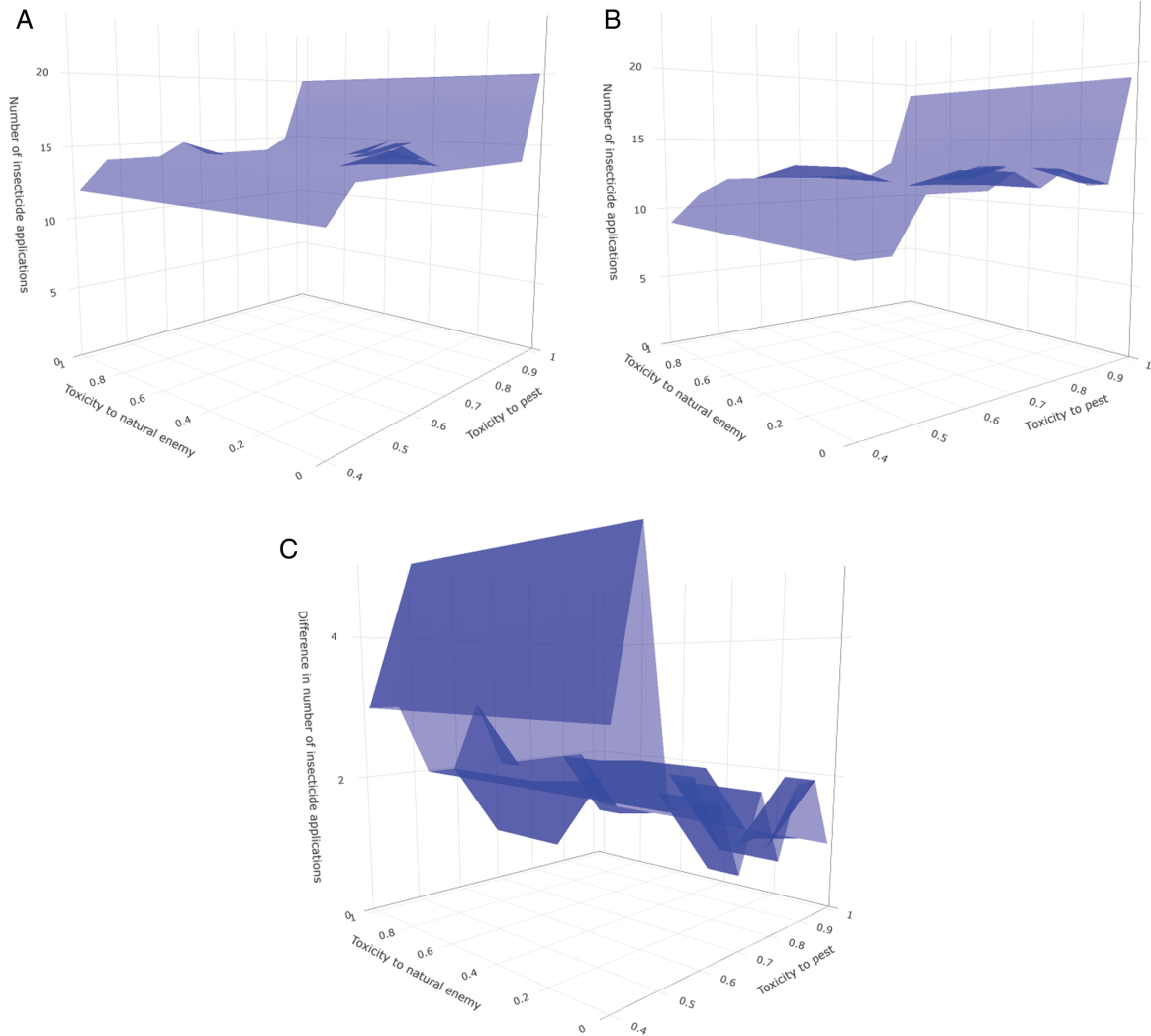


**Fig. 2.** Seasonal revenues from the crop at varying rates of pest and natural enemy immigration into the field.

also reduces natural enemy populations in the field because of resource limitation. This indirectly reduces pest control, which leads to pest resurgence and further spraying. The insecticide's direct toxicity to the natural enemy, on the other hand, does not affect the number of sprays applied during the crop season in either scenario (Fig 3a, b). This indicates that, in our model, pest availability limits natural enemy populations more strongly than insecticide toxicity. *DTs* generate the highest benefit, in terms of reduced chemical control, when the insecticide's toxicity to the pest is low (Fig. 3c). Insecticides that have low toxicity to the pest also generate lower seasonal revenues than more effective insecticides (Fig. 4).

**Effects of Pest Reproduction (*r*) and Natural Enemy Feeding Rate (*α*)**

The number of insecticide applications proposed by the model is rather insensitive to the reproductive rate of the pest and to the voracity of the natural enemy (Fig. 5a, b). For most combinations of *r* and *α*, the *ET* scenario predicts about three more sprays than does the *DT* scenario. The difference between the scenarios is smallest at low values of *r* and high values of *α* (Fig. 5c).



**Fig. 3.** Number of insecticide applications needed to remain below the *ET* (A) or the *DT* (B) throughout the crop season, for varying toxicity levels of the insecticide to the pest and to its natural enemy. The difference between the *ET* and the *DT* scenarios (C) represents the reduction in insecticide use if *DTs* are applied instead of *ETs*.

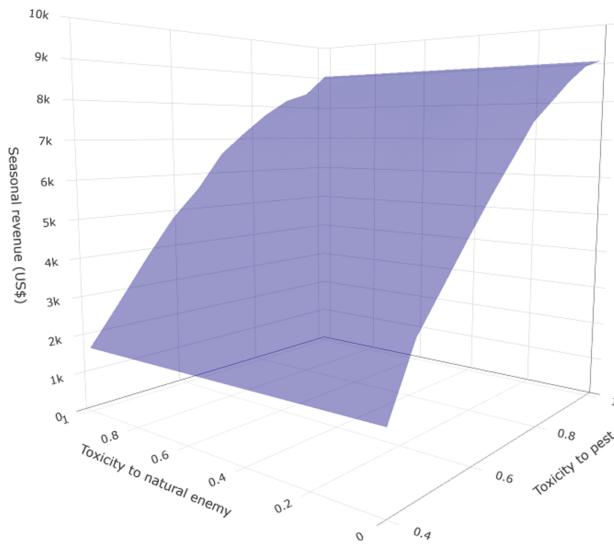


## Effects of Crop-Related Variables

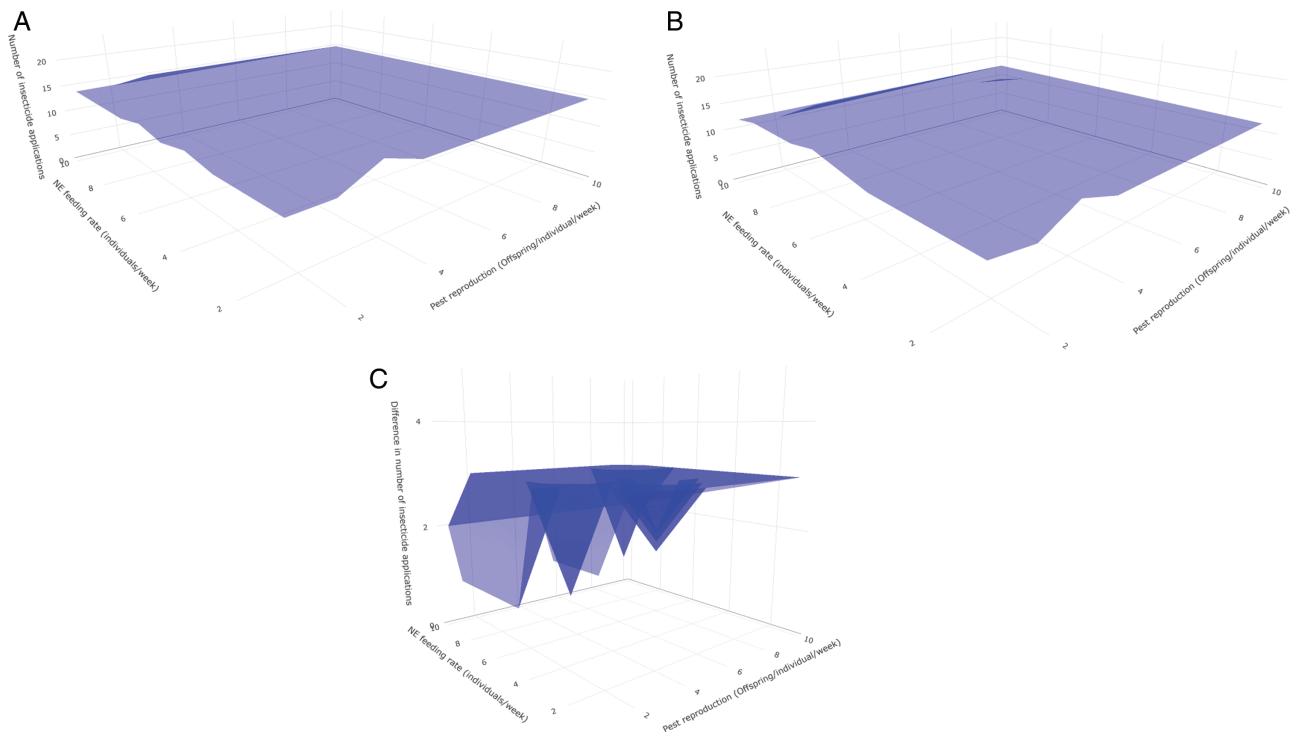
More insecticide applications are expected with increasing crop value and pest-induced yield loss under both scenarios (Fig. 6a, b). The *ET* scenario consistently predicts more sprays than the *DT* scenario, except for cases of minimal damage in low-value crops. Under these conditions, both scenarios advise against any insecticide application (Fig. 6c).

## Case Studies

Our model presents a general framework for estimating the benefits of dynamic thresholds, and is not tailored to any specific cropping



**Fig. 4.** Seasonal revenues from the crop at varying proportions of pests and of natural enemies killed by the insecticide.



**Fig. 5.** Number of insecticide applications needed to remain below the *ET* (a) or the *DT* (b) throughout the crop season, for varying pest reproductive rates and natural enemy feeding rates. Fig. (c) depicts the difference between the *ET* and the *DT* scenarios.

system. To illustrate the extent to which adopting *DTs* might influence pest management practices in real-life agroecosystems, we present below two case studies from Israel in some detail.

## Developing *EILs*, *ETs*, and *DTs* to Control *Tuta absoluta* in Tomato Fields

The invasive moth *Tuta absoluta* is a major economic pest of tomatoes around the world (Santana et al. 2019). In Israel, it is often effectively controlled by indigenous natural enemies, most importantly the predatory bug *Nesidiocoris tenuis* (Shaltiel-Harpaz et al. 2016). Insecticides are applied during the fruit growth and ripening stages, based on weekly counts of the pest's larval galleries. Using the crop's current local economic parameters (Table 1) and insecticide efficiency (75%), the *EIL* (Eq. 1) is calculated at 0.92 larvae/plant (L. Shaltiel-Harpaz, unpublished information). The pest's weekly reproductive rate ( $r$ ) is  $\sim 1.00$  (van Lenteren et al. 2021), and the *ET* is thus  $\sim 0.46$  larvae/plant (Eq. 2). To estimate *DTs* based on Eq. 3, we use published data on *N. tenuis*' pest kill rate  $\alpha$  ( $\sim 2.20$ /week; van Lenteren et al. 2021), and two realistic population densities of the natural enemy (1.0 or 2.5 individuals/plant; Shaltiel-Harpaz et al. 2016). The *DTs* are 1.56 and 2.66 pest larvae/plant when natural enemy density is 1.0 or 2.5 larvae/plant, respectively. In other words, the tolerable pest densities are 3-5-fold higher in the presence of their natural enemies than without them. To illustrate the potential effects on insecticide application, we consider an insecticide-free field in Israel where *T. absoluta* and natural enemies were monitored weekly over a growing season (Shaltiel-Harpaz et al. 2016). Pest densities exceeded the *ET* (0.46 larvae/plant) in 7 out of 11 weekly counts in this field, but exceeded the *DT* only once.

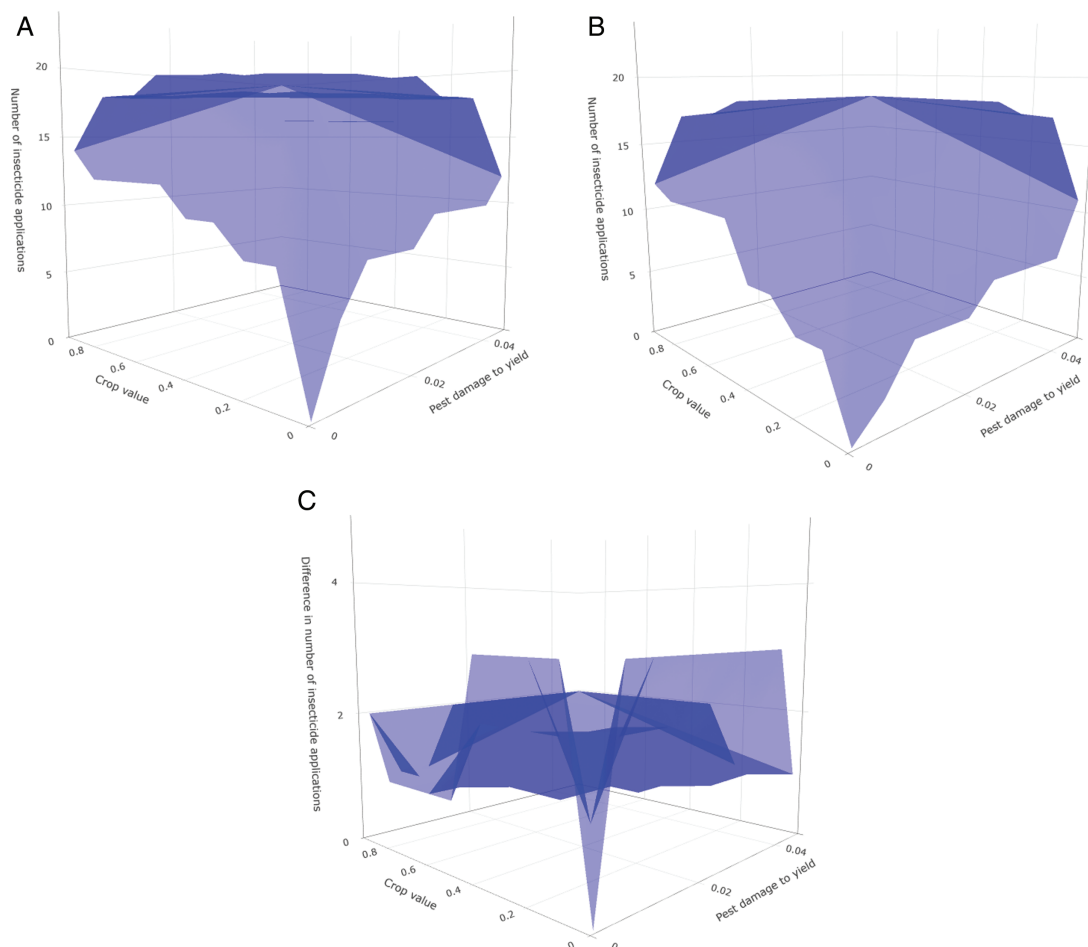
Insecticide resistance develops quickly in *T. absoluta* and is a major concern for the management of this pest (Guedes et al. 2019). As insecticides become less cost-effective for controlling resistant

pests, the economic thresholds and dynamic thresholds increase. Suppose, for example, that the success of *T. absoluta*'s chemical control declines from the current 75.0 to 37.5% (a 50% decrease) due to pest resistance. This would set the *DTs* at 2.02 and 3.67 pests/plant for natural enemy densities of 1.0 and 2.5 per plant, respectively. Adoption of *DTs* can greatly reduce insecticide use in such cases, compared with reliance on *ETs*.

### Developing *EILs*, *ETs*, and *DTs* to Control Grain Beetles in Wheat Warehouses

Stored grain is attacked by multiple beetle and moth pests which are treated, globally, using phosphine as a fumigant. Phosphine can have negative environmental effects, consumers are concerned with insecticide residuals, and pest resistance to this insecticide is quickly evolving worldwide (Nayak et al. 2020). In Israel there are four common pest beetle species associated with stored wheat, and five additional species are considered minor pests. Warehouses are generally fumigated with phosphine once per year (Vidan et al. 2020). The pests support a community of several species of naturally occurring parasitoid wasps (Harush et al. 2021). Based on local economic parameters (Supp Table 1 [online only]), and local insecticide efficiency of 99%, the *EIL* (Eq. 1) is calculated as 47 beetles/kg of stored wheat, and the *ET* (Eq. 2) as 20 beetles/kg. We calculated this *ET* using published demographic data (Driscoll et al. 2000) and a reproductive rate of 1.35 individual beetles per month. There is some

variation in reproductive rates between the four main beetle pest species (Driscoll et al. 2000). However, given the relative insensitivity of the *ET* to a range of  $r$  values (Fig. 5), a single intermediate value of  $r$  appears to be sufficient. The monthly rather than weekly rate was used because the time interval monitoring and fumigation is about one month. To estimate *DTs* (Eq. 3), we used published data on the most abundant parasitoid species in this system, *Cephalonomia tarsalis* Ashmead, 1893 (Hymenoptera: Bethyridae) (Eliopoulos 2019), setting  $\alpha$  at 3.09 individuals/month. At the average natural enemy population density of 1.5 individuals/kg grain that was recorded in the storage facilities, the *DT* is estimated at 22 beetles/kg. This value provides very little advantage of using *DTs* for choosing when to fumigate: in monthly pest monitoring done in four storages over four seasons, total pest density exceeded the *ET* of 20/kg grain in 30% of the samples, whereas the threshold of 22/kg grain was exceeded in 28% of the cases (D. Gottlieb, unpublished data). Thus, using *DTs* rather than *ETs* would change spraying decisions only in 2% of the cases. Nevertheless, by monitoring for natural enemies, farmers could take advantage of those times when their densities are greater than average to postpone insecticide use. Moreover, if the population density of the natural enemies is increased to 10/kg infested grain then the *DT* would be 36 beetles/kg, which would greatly increase the benefits from monitoring the natural enemy density. In such a situation, the frequency of insecticide use could be reduced from 30 to 15% (a twofold reduction). Populations of



**Fig. 6.** Number of insecticide applications needed to remain below the *ET* (a) or the *DT* (b) throughout the crop season, for varying levels of pest damage to the yield and the crop's cash value. Fig. (c) depicts the difference between the *ET* and the *DT* scenarios.

natural enemies could potentially be boosted through augmentative biological control. Furthermore, assuming a future 50% decline in the insecticide efficacy (from 99.0 to 49.5%) and 10 natural enemies/kg infested grain, the *ET* and *DT* values would increase to 39 and 56 beetles/kg, respectively.

These two case studies illustrate that farmers can considerably diminish insecticide use in some real-life cropping systems through monitoring of natural enemies and implementation of dynamic thresholds. The rapid ongoing evolution of insecticide resistance in many pest species provides an additional incentive for developing dynamic thresholds.

## Discussion

The production and use of chemical insecticides involve hazards to human health, negative impacts on biodiversity, and considerable greenhouse gas emissions (Geiger et al. 2010, Heimpel et al. 2013, Wyckhuys et al. 2022). Extensive insecticide use also selects for the evolution of resistance in pest populations, which reduces the effectiveness of the insecticides and increases their costs to farmers (Heckel 2012). Furthermore, insecticides interfere with pest control by local natural enemies, and this often leads to pest resurgence over the course of the cropping season (Janssen and van Rijn 2021). The use of dynamic thresholds (*DTs*) can reduce insecticide use and provide economic and environmental benefits compared to the use of economic thresholds (*ETs*) and less sophisticated approaches such as fixed-interval or prophylactic insecticide applications. Case studies where *DTs* reduced, or even eliminated, the need for chemical pest control include the monitoring of predators and of pollen resources for *Frankliniella occidentalis* Pergande (1895) (Thysanoptera: Thripidae) thrips in strawberries *Fragaria × ananassa* (Duchesne) (Rosales: Rosaceae) (Shakya et al. 2010); the assessment of parasitism levels on *Helicoverpa* Hübner (1808) (Lepidoptera: Noctuidae) eggs and larvae in tomatoes (Hoffmann et al. 1990, Walker et al. 2010); and sampling of predators, parasitoids, and pathogens of cotton aphids (Conway et al. 2006).

Despite their apparent advantages, *DTs* have not been widely adopted in Integrated Pest Management (IPM) programs. We are aware of only a handful of field studies that used *DTs* to guide insecticide applications, and that were adopted as commercial-scale protocols (Table 2). A likely reason is that such protocols necessitate the monitoring of natural enemy populations in addition to the monitoring of pests. This requires farmers and field entomologists to invest extra labor (and acquire the associated expertise), which thereby increases the costs of monitoring procedures (Giles et al.

2017). To popularize the use of thresholds among farmers, simple and standardized sampling protocols for pests and natural enemies should be developed, combined with user-friendly software to support spraying decisions. Our model can help to identify cropping systems where both of these endeavors are important and timely.

The predictions of our model point to conditions under which the impact of *DTs* on farming practices are maximal. Monitoring of natural enemy densities is expected to be most beneficial (in terms of reduced spraying) under these conditions, especially if the monitoring protocol is simple and rapid. For example, monitoring for egg parasitoids is especially feasible because they are visible on the plant as parasitized eggs. Further, where hosts are monitored at the egg stage it does not take extra effort to assess the fraction parasitized. In line with our working hypothesis, the model forecasts large benefits of *DTs* when natural enemies immigrate rapidly into the fields after spraying. This is realistic when natural enemies are highly dispersive and can be supported in off-field locations near agricultural crops (Blitzer et al. 2012). Also, in IPM-managed crops, chemical and augmentative biological control are often combined. Since farmers regularly release biological control agents into their fields (augmentative biological control), immigration rates for natural enemies are high. Our model predicts high gains from using dynamic thresholds in such cropping systems. The model further predicts that the potential of dynamic thresholds to reduce insecticide application increases when chemical control is relatively ineffective (i.e., when its toxicity to the pest is low). Insecticide resistance may provide farmers with an added incentive to adopt *DTs* for some crops. Finally, while insecticide use is generally high for high-value crops, *DTs* can reduce the number of sprays in high-cash cropping systems. If crop value is low then the incentive to spray is low with or without *DTs*.

The uncertainty around parameter estimation is a further barrier to the adoption of *DTs* in IPM programs: The pests' reproductive rate (*r*) must be estimated to calculate *ETs*, and to calculate *DTs*, the natural enemies' feeding rates (*α*) should also be known. It is typically much more straightforward to measure these rates in the laboratory than under field conditions. However, the insects' demography and behavior greatly depend on abiotic conditions (such as temperature, humidity, photoperiod) that fluctuate in the field and thus laboratory estimates may not accurately represent field reality. Also, spraying decisions often influence several pest and natural enemy species, each of which differs in demography and voracity. Thus, *DTs* should ideally combine information from multiple species. Moreover, the proportions of feeding and reproducing life-stages in insect field populations are often unknown, complicating

**Table 2.** Studies that used dynamic thresholds to guide insecticide use decisions, listed in chronological order. '+' indicates evidence for field testing and commercial use of dynamic threshold in a particular cropping system

| Crop       | Pest   | Natural enemy                  | Field validation and commercial adoption | References   |
|------------|--------|--------------------------------|--|--|
| Tomato     | Moth   | Parasitoids                    | +  | Hoffman et al. (1990), M. Hoffman and F. Zalom, unpublished data |
| Cotton     | Aphid  | Predators, parasitoids, fungus | +  | Conway et al. (2006), Steinkraus (2007)                          |
| Corn       | Moth   | Predators                      | -  | Musser et al. (2006), F. Musser, unpublished data                |
| Tomato     | Moth   | Parasitoids                    | +  | Walker et al. (2010)   |
| Strawberry | Thrips | Predators                      | +  | Shakya et al. (2010)   |
| Soybean    | Aphid  | Predators                      | +  | Hallett et al. (2014), C. Bahlai and T. Baute, unpublished data  |
| Wheat      | Aphids | Parasitoids                    | +  | Giles et al. (2017)  |



the estimation of population-wide rates of feeding and reproduction. We thus used a sensitivity analysis to explore how different values of  $r$  and  $\alpha$  would influence the model's spraying recommendations, and found that the recommendations were quite robust (Fig. 5). These findings support the use of laboratory-collected data for developing IPM thresholds, even though they derive from simplified environments.

### Synthesis: Beyond ETs and DTs

Dynamic thresholds (DTs) are extensions of economic thresholds (ETs) that take into account the density of beneficial natural enemies, as well as the density of pests, in integrated pest management (IPM). As such, they are similar to the concept of considering the density of beneficial crop pollinators, as well as of pests, in integrated pest and pollinator management (IPPM: Egan et al. 2020), which seeks to minimize trade-offs, and to maximize co-benefits and synergies between pest and pollinator management (Lundin et al. 2021). As IPPM represents a combination of IPM and integrated crop pollination (ICP: Isaacs et al. 2017), so DTs represent a combination of 'simple' IPM and a process that we tentatively term 'integrated natural enemy management' (INEM). The advantages of using DTs over ETs will be associated with greater complexity of implementation just as implementing IPPM will be more challenging than either IPM or ICP alone. Moreover, the overarching challenge will be to develop approaches that combine threshold information on pests, beneficial natural enemies, and beneficial pollinators to provide truly integrated decision-based management of future agro-ecosystems.

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### Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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