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Landscape features determining the occurrence of *Rhagoletis mendax* (Diptera: Tephritidae) flies in blueberries

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ABSTRACT

Non-crop areas surrounding farms can support pest populations if they provide overwintering habitats or alternative hosts for them to feed and/or mate. Here we tested the hypothesis that a native North American pest of highbush blueberry, the blueberry maggot fly (*Rhagoletis mendax* Curran) is more abundant near forest habitats. For this, we monitored *R. mendax* adult occurrence using a trapping network across multiple farms and years (2009–2012) in New Jersey (USA), and then performed geospatial analysis on these data to determine whether traps in blueberry fields near forest habitats experience higher *R. mendax* adult captures than others. In addition, we conducted mark-release-recapture studies to determine the distance *R. mendax* flies can move into blueberry fields. Our results reveal that proximity to forest habitats positively affects *R. mendax* adult occurrence on traps. However, the type of forest was critical such that presence of flies on traps declined with increasing distance from upland forest while distance from wetland forest had no effect. We also showed that *R. mendax* flies can disperse up to 76 m into a blueberry field from adjacent wooded habitat within 48 h. In sum, our study identified landscape features important for *R. mendax* occurrence in blueberry fields, which can improve sampling methods and the development of precision-based pest management programs. Based on our findings, monitoring efforts and insecticide applications for *R. mendax* should be targeted mainly to fields close to upland forest and directed to the field borders within distances of less than 80 m from field edges.

1. Introduction

The landscape surrounding farms can be an important determinant of the abundance and distribution of insect populations and communities (Chaplin-Kramer et al., 2011). For instance, natural habitats around farms can have positive or negative effects on populations of insect pests. On one side, non-crop areas in the landscape can provide natural habitats for the enemies of insect pests and, consequently, may increase their services as biological control agents (e.g. Marino and Landis, 1996; Menalled et al., 1999; Landis et al., 2000; Bianchi et al., 2006; Landis et al., 2008; Gardiner et al., 2009; Chaplin-Kramer and Kremen, 2012; Veres et al., 2013). Conversely, non-crop areas may increase pest pressure if they provide suitable habitats for insect pests such as alternative hosts or mating and/or overwintering sites. For example, Bakken et al. (2015) identified non-managed plants (i.e., tree of heaven, catalpa, yellowwood, paulownia, cherry, walnut, redbud, and grape) along woodland edges as potential sources of brown marmorated stink bug, *Halyomorpha halys* (Stål), infestation in cultivated soybean fields. Rice et al. (2017) found that forest patches are positively correlated with the percent damage to tomato fields by stink bugs (including *H. halys*). Also, adults of the spotted wing drosophila, *Drosophila suzukii* Matsumura, appear earlier in the season at raspberry farms in landscapes with high amounts of woodland, but the overall risk to raspberry crops was similar across landscapes (Pelton et al., 2016). Thus, understanding the landscape features that influence the abundance and distribution of insect pests in agro-ecosystems can be critical for making accurate pest management decisions.

Landscape features surrounding agricultural farms are heterogeneous and may consist of forest, open fields, or neighboring farms having similar or different crops, which could serve as potential sources

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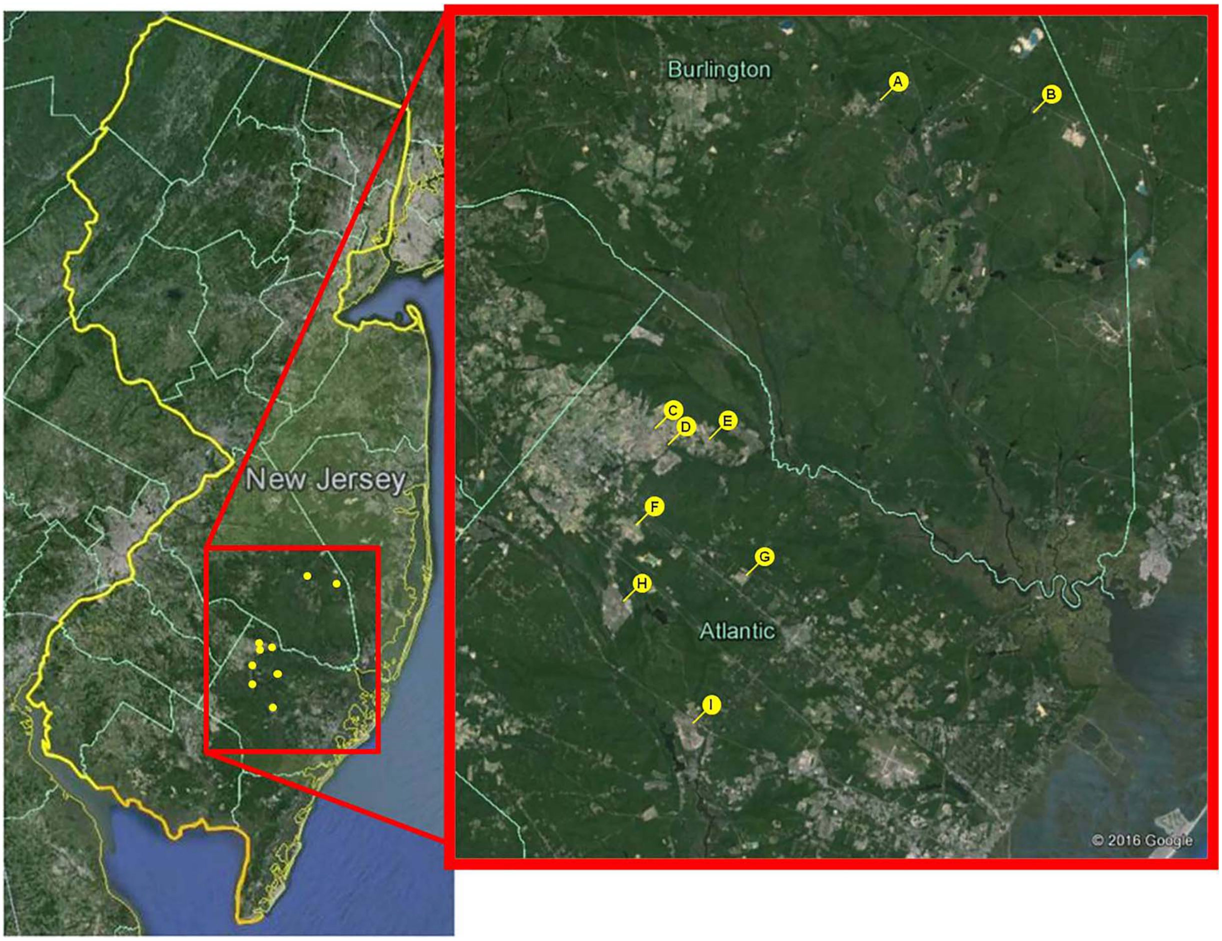

Fig. 1. Locations of the nine commercial highbush blueberry farms (yellow circles) sampled for blueberry maggot flies (*Rhagoletis mendax*) within the Pineland National Reserve in southern New Jersey, USA (left panel). Right panel shows a more detailed map of the locations of each of the farms (farms A through I). Two farms were located in Burlington Co., while the other seven farms were located in Atlantic Co.; see Table S1 for details on geographic coordinates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of inter- and intra-field variability on pest pressure within farms (e.g. Banks, 1998; Zaller et al., 2008; Ruscha et al., 2013). For instance, the distance from forest edges can affect the intensity of pest invasion into fields in agricultural ecosystems (e.g. Altieri and Schmidt, 1986; Krauss et al., 2003; Krawchuk and Taylor, 2003). If woodland habitats affect insect pest populations, the abundance and spatial distribution of these pests within farms will likely depend on the proximity of fields to nearby natural habitats (e.g. Holland and Fahrig, 2000). Yet, there is limited information on the importance of proximity to, and the types of, natural habitats for insect pest abundance and distribution at whole farm scales (Sivakoff et al., 2013). In the present study, we addressed this issue using the blueberry maggot fly, *Rhagoletis mendax* Curran (Diptera: Tephritidae), a native insect pest of blueberries (*Vaccinium* spp., Ericaceae) in the United States of America (USA), by investigating whether habitat type and distance to forest affect the occurrence of *R. mendax* flies in highbush blueberry (*V. corymbosum* L.) fields.

In New Jersey (USA), highbush blueberries are grown in an ecologically-important forest region known as the Pinelands National Reserve (also known locally as the Pine Barrens). This region is characterized by upland and wetland forests with an understory dominated by several wild ericaceous species including *Gaylussacia* spp. (huckleberry) and *Vaccinium* spp. such as wild *V. corymbosum*, *V. macrocarpon* Aiton (large cranberry), and *V. vacillans* Kalm ex Torr. (lowbush blueberry) (Zampella, 1991). Many of these plant species serve as alternate hosts for several blueberry pests including *R. mendax* (Lathrop and Nickels, 1931, 1932; Lathrop, 1952; Smith et al., 2001; Rodriguez-Saona et al., 2015). *Rhagoletis mendax* is considered one of the most economically-important pests of commercially grown blueberries in New Jersey as well as in other eastern and mid-western states of the USA and some regions in Canada (Marucci, 1966; Prokopy and Coli, 1978; Smith and Prokopy, 1981; Vincent and Lareau, 1989; Rodriguez-Saona et al., 2015). From early June (fruit maturation) to early November, *R. mendax* flies disperse from wild hosts into commercial blueberry fields (Teixeira and Polavarapu, 2001; Collins and Drummond, 2004; Renkema et al., 2014). In this study, we provide information about key landscape features that influence the occurrence of *R. mendax* flies, as well as the potential risk of blueberry fields to its infestation, which will improve sampling methods and the development of precision pest management approaches.

The main objective of the present 4-year study was to investigate how proximity to forest and the type of forest (wetland versus upland) may contribute to differential *R. mendax* fly presence within blueberry farms. We hypothesized that there would be an increased occurrence of *R. mendax* adults in blueberry fields located near forest habitats. Specifically, we first asked: does proximity to forest affect the presence of *R. mendax* flies on monitoring traps? We addressed this question for upland and wetland forests. Second, we asked: how far do *R. mendax* fly from woods into blueberry fields and within blueberry fields?

2. Methods

2.1. Study system

Blueberries are an important fruit crop in the USA, the largest producer in the world (Evans and Ballen, 2014). Our studies were conducted in the Pinelands region of Burlington and Atlantic counties in southern New Jersey (USA) in the summers of 2009–2012 in commercial and abandoned northern highbush blueberry (*V. corymbosum*) farms. Highbush blueberry is a native perennial deciduous shrub that is grown commercially in this region and harvested from early June until mid-August.

Rhagoletis mendax is a key direct pest of blueberries in this region (Marucci, 1966), with a single generation each year. Flies emerge around the second week in June, which corresponds to fruit maturation/harvest in commercial blueberry fields in New Jersey, and females oviposit inside mature fruit. They overwinter as pupae in the soil. Adult *R. mendax* are monitored using ammonium-baited yellow sticky traps (e.g. Wood et al., 1983; Gaul et al., 1995). In highbush blueberries, there is a low action threshold of 1 fly per trap and zero tolerance for larva-infested fruit in the fresh fruit market (Rodriguez-Saona et al., 2015). Thus, the presence/absence of flies on traps rather than their absolute numbers guide insecticide applications in this crop.

2.2. Landscape influence on R. mendax occurrence

To determine whether landscape features influence the presence of *R. mendax* flies, monitoring studies were conducted from 2009 to 2012 in nine commercial blueberry farms. These farms were located in Burlington and Atlantic Counties (7 farms in Atlantic Co. and 2 farms in Burlington Co.) in southern New Jersey, USA (Fig. 1), covering a total of ∼700 ha of blueberry plantings (Table S1). Farm size varied from 11.7 to 246.6 ha (mean ± SE = 77.1 ± 28.0 ha; Table S1), and contained at least one of three major blueberry cultivars: Duke, an early season cultivar; Bluecrop, a mid-season cultivar; and Elliott, a late season cultivar. Farms were selected to include a diversified habitat composition. High resolution orthophoto imagery for all farms and surrounding areas were downloaded from the New Jersey Department of Environmental Protection (NJDEP) Land Use/Land Cover information (http://www.nj.gov/dep/gis/lulc07shp.html); this is one of the best/most refined state datasets in the USA. This information was used to classify the land surrounding each farm into six main categories: 1. other blueberry fields; 2. upland forest; 3. wetland forest; 4. open fields (i.e., water reservoirs and other wetlands); 5. other crops (non- *R. mendax* hosts)/meadows/barrens; and, 6. industrial/residential areas (Fig. S1). Upland forest includes sites where drainage does not allow for soils to become saturated for an extended period of time, whereas wetland forest includes sites where soils may be inundated continuously or saturated for a few weeks per year (McCormick, 1979). The percent land in each category surrounding each farm was calculated by creating a buffer zone of ∼70 m, which corresponds to the farthest distance *R. mendax* can fly in 48 h (see Section 3), around the perimeter of each farm, and then superimposing the NJDEP Land Use/Land Cover within this buffer zone (http://www.nj.gov/dep/gis/lulc07shp.html) (Fig. S2). A minimum distance of 200 m separated the farms (i.e., closest distance between farms C and D; Fig. 1), and each field was digitally mapped using a GeoXT 2005 series GPS receiver (Trimble Navigation Ltd., Sunnyvale, CA, USA). Attribute tables were created with individual field information on their geographic coordinates, size, cultivar, surrounding landscape, and type of forest (e.g. upland or wetland). Digital maps with all trap positions were used to calculate the distance from each trap to the nearest forest patch (GPS Pathfinder Office 3.10; Trimble Navigation Ltd.).

Pherocon® AM-baited traps (Trécé Inc., Adair, OK, USA), baited with ammonium acetate, were placed approx. every 1 ha at each farm; we expected minimum interference between traps because preliminary field data showed that *R. mendax* can travel an average of 20 m every 24 h. A total of 531 traps were placed randomly across all farms (Fig. 2, Table S1); the number of traps per farm varied based on farm size. Traps were placed on a steel pole in the upper 15 cm of the canopy of blueberry bushes. One third of the traps were placed within the 1st rows or row end plants that bordered woods or other non-blueberry crop ecosystems, while the rest of the traps was placed inside individual plantings at least 100 m from the farm border (Ricci et al., 2009). Thus, farms with longer peripheral borders (especially smaller farms) had higher ratio of traps on border edges to the number of traps inside fields. The traps were monitored twice a week starting the 1st week of June until the 2nd week of September. Traps were changed every 15 days. Trap locations were mapped using a Trimble hand held GPS device and digitally marked as point source data with appropriate geographic coordinates (GPS Pathfinder Office 3.10; Trimble Navigation Ltd.). All farmers followed standard local pest management practices and insecticide records were collected after each growing season. Only insecticides used during fruit maturation to target fruit-feeding insects like *R. mendax* were used in data analysis and the records were used to determine the total kg of insecticide active ingredient applied per hectare during this period of the season, for each field in the sampled farms.

2.3. In-situ dispersal of R. mendax

To determine the flight capacity of *R. mendax*, we conducted a mark-release-recapture experiment in an abandoned blueberry field in Chatsworth, New Jersey (latitude 39°47′33.97″N, longitude 74°32′4.68″W). This study was done in an abandoned field (different from the sites used in the landscape study) because of risks to the crop associated with releasing hundreds of flies in a commercial blueberry farm. To obtain *R. mendax* flies, we followed rearing procedures described in Barry and Polavarapu (2005). Infested blueberries were collected near Chatsworth, New Jersey, in the summer of 2009 and placed over moist sand for larvae to drop and pupate. Puparia were sifted from sand 3-to-5 weeks later, kept in a screen house, and then were transferred to an incubator on November 2009, at 6 °C with a photoperiod of 12:12 (L:D) to complete diapause. On March 2010, puparia were placed at 8 °C. Periodically groups of puparia were transferred from 8 to 15 °C for approximately 8 d and then transferred to an incubator at 25 °C with a photoperiod of 16:8 (L:D) until adult emergence, which occurred 25–45 d later. Flies were kept at 22 °C and were provided a diet of sucrose and water (i.e., protein-starved); flies used in the experiment were 6–10 d-old. On each release date, *R. mendax* flies were cooled down for 5 min to facilitate the marking process. Polyethylene bags were dusted with small amounts of ultraviolet Day-GLO powder (Day-Glo Color Corp., Cleveland, OH, USA); a common method for marking tephritid flies (Holbrook et al., 1970; Schroeder and Mitchell, 1981). Different color powders were used to mark the flies from each release, so that released and natural populations could be differentiated. Flies were placed inside the bags for a maximum of 10 min, and marked flies were released in the morning (8:30 am). A total of 900 *R. mendax* flies were marked and released in six different dates from 28 June through 10 July 2010.

The experiment, which investigated adult movement from wooded areas into blueberry fields (i.e., dispersing populations), was done inside a 36.5 m long × 5.0 m wide × 2.5 m high tunnel constructed of steel with a semicircular frame and covered with white polyethylene shade fabric (which blocks 50% of light) (Fig. S3). A single tunnel was installed in an abandoned blueberry field (see above). The tunnel, which was used to maximize recaptures of marked *R. mendax* flies while minimizing capturing feral flies, extended parallel to the blueberry rows, with one end of the tunnel located at the field's edge and near an upland forest, and the other end in the field interior (see Fig. S3). The end of the tunnel near the forest (where flies were released) remained closed at all times while the opposite (interior) end remained open to allow for air circulation and to monitor fly movement beyond the length of the tunnel. Because the presence of fruit (berries) can influence *R. mendax* movement within blueberry fields (e.g. Senger et al., 2009), flies were released at two different sites: outside (i.e. forest edge) and inside (i.e. field edge) the field (see Fig. S3). The release point

Fig. 2. Landscape features surrounding highbush blueberry farms and the occurrence of blueberry maggot (*Rhagoletis mendax*) flies on these farms. Each dot within farms represents the presence or absence of *R. mendax* flies on Pherocon® AM traps from 2009 to 2012. Each panel shows a sampled farm (farms A through I). Details on farm size and number of traps per farm are shown in Table S1.

outside the field was close to the forest edge and 3 m from the field's edge. These releases were made on 28 June (N = 100 *R. mendax* adult flies), 4 July (N = 200 flies), and 6 July (N = 200 flies). The other point of release was situated at the edge of the field. These releases were made on 30 June (N = 100 flies), 2 July (N = 200 flies), and 10 July (N = 100 flies). Inside the tunnel and beyond the length of the tunnel (see Fig. S3), two Pherocon® AM traps (Trécé Inc.), baited with ammonium acetate, were placed at 1–1.5 m above the ground on steel poles, every 9 m from the field's edge, and up to 72 m. Traps were inspected for *R. mendax* flies 2, 4, 6, 12, 24, and 48 h after being released. Preliminary laboratory and field data showed effective recognition of marked flies within this time period. This timing has practical management relevance as it can guide growers, once they find a captured fly on traps, to treat a buffer zone within the following 48 h after the first capture. This was also used to limit the amount of immigration of non-marked flies from outside that could have affected the behavior and measured distribution patterns of *R. mendax*. Captured flies were examined in-situ and in the laboratory using a hand lens and microscope, respectively, and those containing the ultraviolet dye were determined to be from the release rather than a wild population. In addition, weather information was obtained from a HOBO unit (Onset Computer Corporation, Pocasset, MA, USA) placed inside the tunnel and from the Oswego weather station located at the Rutgers Marucci Research Center in Chatsworth, New Jersey (http://www.njweather.org/). There were no differences in temperature between the interior and exterior air (data not shown); the temperature varied between 22 and 24 °C and no precipitation occurred during the experiment.

2.4. Statistical analysis

To determine whether distance from forest influenced the presence of *R. mendax*, we performed a generalized mixed model with a binomial error structure (R v.2.15; R Development Core Team, 2012). The response variable was presence or absence of *R. mendax* flies on an individual trap. Fixed effects were, for each trap, distance from upland forest and distance from wetland forest. Because insecticide applications can also influence *R. mendax* abundance, mean amount (kilograms) of active ingredient of applied insecticides per hectare during fruit maturation (June–August) was calculated for each field for each year and included in the model. Year was also designated as a fixed effect. Data were analyzed for each separate year as well as for across all years (2009–2012). Random effects were farm and trap. We used random slopes for each farm for distance metrics as well as the intensity of insecticide use [amount of insecticide (active ingredient) per hectare]. Using the *arm* package (Gelman and Su, 2015), we rescaled fixed effects to a mean = 0 and standard deviation = 0.5 as these parameters had large differences in scale. We used the lme4 package in R for generalized mixed models (Bates et al., 2015).

The maximum distances a recaptured fly traveled inside the tunnel were determined using logarithmic decay equations with trap captures (y-axis) and the distance between the trap and the release point (x-axis); the x intercept where $y = 0$ corresponded to the maximum distance traveled by *R. mendax*. Differences in proportion of flies captured at each distance were analyzed using 2-way analysis of variance (ANOVA), with distance from the release point and point of the release (forest or field edge) as predictor variables using Minitab 16 software (Minitab, Inc., State College PA, USA). Response variable was the proportion of flies captured over the total number of flies released at each trapping distance and was arcsine square-root-transformed prior to analysis to meet the assumptions of normality and homoscedasticity. A significant ANOVA was followed by Tukey's HSD post hoc test. For simplicity, only 24 and 48 h captures were analyzed statistically and are presented here (see Fig. S4 for 2, 4, 6, and 12 h capture data). Data for each time duration were analyzed separately and only marked flies were used in the analyses.

3. Results

3.1. Landscape influence on R. mendax occurrence

The occurrence (presence or absence) of *R. mendax* adult flies on Pherocon® AM traps is shown in Fig. 2 for all sampled years. The surrounding landscape features varied among farms: percent of upland forest (range across farms) = 3.6–61.9%, wetland forest = 0–41.6%, open fields = 0–22.6%, other crops = 0–27%, and other blueberry fields surrounding the farms = 2.1–53.7% (Fig. S1).

Across all sampled years (2009–2012), the probability of *R. mendax* occurrence on a trap declined as distance to upland forest increased (Fig. 3; Table 1). In contrast, distance to wet forest did not affect *R. mendax* presence on traps (Table 1). The mean amount of insecticide (active ingredient) applied was also not related to *R. mendax* presence on the traps. The year did, however, have a large effect (Table 1). In particular, *R. mendax* was highest in 2009, lower in both 2010 and 2011, and lowest in 2012 (Fig. S5). In 2009 and 2010, a mean of 59% and 48% of traps captured *R. mendax* in highbush blueberry New Jersey farms, respectively. In 2011, on average, 40% of traps had at least one *R. mendax* adult fly present; while less than 25% of the traps caught *R. mendax* flies in 2012 (Fig. S5).

When each year was analyzed separately, distance from upland forest negatively affected the probability of *R. mendax* occurrence on a trap in 2009 and 2010, when fly abundance was highest, but not in 2011 or in 2012 (Table 1). The amount of insecticide used was positively correlated with *R. mendax* occurrence on traps in 2009 and 2010, indicating that farmers applied more insecticides in fields with greater

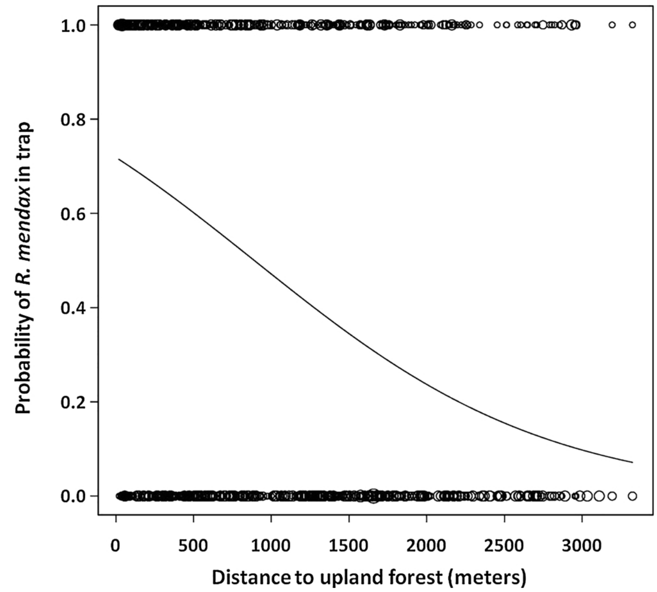

Fig. 3. Relationship between the probability of catching a blueberry maggot (*Rhagoletis mendax*) fly on a Pherocon® AM trap and the distance from upland forest. Each dot represents an individual trap and whether *R. mendax* was present ($y = 1$) or absent ($y = 0$). The regression line is the result of a model output using distance from upland forest scaled by 2 standard deviations and centered on a mean of zero.

Table 1
Model output for the effects of landscape features on blueberry maggot, *Rhagoletis mendax*, occurrence on Pherocon® AM traps in highbush blueberry fields in New Jersey (USA). The response variable was presence/absence of *R. mendax* flies on traps. Fixed effects included distance from upland forest, distance from wetland forest, intensity of insecticide use [mean amount (active ingredient) of insecticides per hectare], and year, while random effects were farm and trap.

Year[a]	Variable[c]	Estimate (z-score)	Standard error	P value
All[b]	Intercept	−0.33	0.27	.22
	Distance to Upland Forest	**−1.39**	**± 0.63**	**.03**
	Distance to Wetland Forest	−0.58	± 0.35	.10
	Intensity of Insecticide Use	0.42	± 0.29	.15
	Year: 2010	−0.06	0.18	.72
	Year: 2011	**−0.99**	**0.19**	**< .001**
2009	Intercept	0.05	± 0.14	.74
	Distance to Upland Forest	**−0.73**	**± 0.29**	**.01**
	Distance to Wetland Forest	0.05	± 0.33	.88
	Intensity of Insecticide Use	**0.59**	**± 0.24**	**.01**
2010	Intercept	−0.20	± 0.025	.43
	Distance to Upland Forest	**−1.51**	**± 0.41**	**< .01**
	Distance to Wetland Forest	−0.44	± 0.30	.15
	Intensity of Insecticide Use	**0.67**	**± 0.29**	**.03**
2011	**Intercept**	**−0.97**	**± 0.32**	**< .01**
	Distance to Upland Forest	−0.78	± 0.48	.10
	Distance to Wetland Forest	−0.65	± 0.46	.15
	Intensity of Insecticide Use	0.34	± 0.96	.34
2012	**Intercept**	**−1.88**	**± 0.21**	**< .01**
	Distance to Upland Forest	−0.70	± 0.93	.45
	Distance to Wetland Forest	0.05	± 0.56	.93
	Intensity of Insecticide Use	0.18	± 0.55	.58

[a] Data were analyzed for all years together and each year was analyzed separately. Each year used separate models.
[b] Model for all years included fixed effect of year. The *P*-values associated with year represent differences in each year from 2009.
[c] Variables in bold are significant at $P \leq .05$.

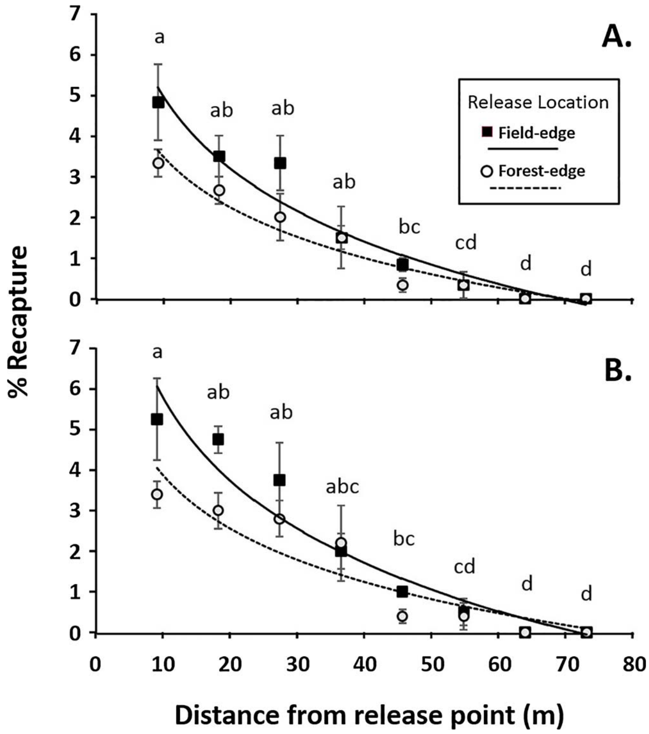

Fig. 4. Percent recovery (means ± SE) within 24 h (A) and 48 h (B) of color-marked blueberry maggot, *Rhagoletis mendax*, flies on Pherocon® AM traps. Flies were released on three different dates inside a high tunnel either at the edge of an abandoned blueberry field or at the forest edge near the field (see Fig. S3). Different letters indicate differences in recaptures among distances from the release point. Best fit equations and R-squared values are as follows: Forest edge (24 h): $y = -1.84 \times \ln(x) + 7.88$, $R^2 = 0.92$; Field edge (24 h): $y = -2.71 \times \ln(x) + 11.42$, $R^2 = 0.94$; Forest edge (48 h): $y = -1.91 \times \ln(x) + 8.27$, $R^2 = 0.84$; Field edge (48 h): $y = -2.94 \times \ln(x) + 12.55$, $R^2 = 0.93$.

R. mendax abundance (Table 1). Moreover, the amounts of insecticides used were lower in 2010 and 2011 than in 2009 and 2012 (Fig. S6).

3.2. In-situ dispersal of *R. mendax*

Distance from the release point had a significant effect on *R. mendax* fly recaptures on Pherocon® AM traps 24 h ($F_{7,32} = 27.97$, $P < .001$) and 48 h ($F_{7,32} = 28.75$, $P < .001$) after their release (Fig. 4). As expected, fly recaptures declined with increasing distance from the release points. Based on the equations in Fig. 4, the maximum distance *R. mendax* flew in 24 and 48 h when released at the edge of the field was 67.6 m and 71.4 m, respectively, while the maximum distance *R. mendax* flew in 24 and 48 h when released outside the field (forest edge) was 72.6 m and 75.9 m, respectively. There was also a marginal (after 24 h) and significant (after 48 h) effect of the point of release (i.e., forest edge versus field edge) on flies recaptured on traps (24 h: $F_{1,32} = 3.81$, $P = .06$; 48 h: $F_{1,32} = 5.68$, $P = .023$); however, there was no a distance-by-site interaction (24 h: $F_{7,32} = 0.39$, $P = .9$; 48 h: $F_{7,32} = 0.39$, $P = .903$). In general, fly recaptures on traps were higher when released at the field edge than when released at the forest edge (Fig. 4).

4. Discussion

Natural habitats near agricultural fields can have negative or positive effects on insect pests. Here we showed that proximity to natural habitats, i.e. upland forest, has a positive effect on the abundance of a frugivorous insect pest of blueberries. Occurrence of the blueberry maggot fly, *R. mendax*, on traps declined with increasing distance from upland forests in commercial highbush blueberry farms in New Jersey (USA). Although the difference is small, based on a mark-release-recapture study, we also showed that *R. mendax* flies move farther when released in surrounding woods than in crop fields. Once inside a blueberry field, they move up to 76 m from the edge of the field within 48 h. This information can be used by farmers to make more precise management decisions based on the risk of blueberry fields to *R. mendax* infestation, such that control efforts (monitoring and insecticide use) should be intensified in fields near upland forest and within 80 m from the field edges, which will ultimately improve *R. mendax* management programs and reduce insecticide inputs in blueberry farms.

Studies on the effects of landscape heterogeneity on insect populations in agro-ecosystems have focused mainly on their positive effects on biological control agents (e.g. Chaplin-Kramer et al., 2011; Veres et al., 2013); however, less is known on the potential positive effects that natural habitats may have on insect pests. In this study, we provide support to our hypothesis that higher populations of *R. mendax* in highbush blueberry farms are found near forest habitats in the Pinelands region of southern New Jersey. Not all types of forest provided this benefit to *R. mendax* as the distance from upland forest, but not wetland forest, positively influenced the presence of *R. mendax* adults on traps. There are two possible explanations for the observed differences in abundance of *R. mendax* in blueberry fields near upland versus wetland forests. First, *R. mendax* survival may be greater in upland as compared with wetland forest. Because *R. mendax* overwinters as pupae in the soil, it is likely that pupal survival differs between upland and wetland forests. Wetland forests have poorly drained, frequently flooded soils (McCormick, 1979; Zampella, 1991), which may increase *R. mendax* pupal mortality in the soil due to anoxia. Eskafi and Fernandez (1990) reported 17% pupal survival of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann), when submerged under water for 9 and 12 h daily. Similarly, Hulthen and Clarke (2006) showed 30% pupal mortality of the Queensland fruit fly, *Bactrocera tryoni* (Froggatt), at 100% soil moisture, while low levels of mortality occurred below 90% soil moisture. Soil moisture levels can also affect pupation depth in *R. mendax* (Renkema et al., 2011), which in turn could affect their exposure to natural enemies (Renkema et al., 2012). Future field studies need to be conducted to determine the effects of upland and wetland soils and their moisture status on *R. mendax* pupal survival.

Second, the number and availability of alternative hosts for *R. mendax* may differ between upland and wetland forest habitats. For instance, Renkema et al. (2014) reported that the presence of certain vegetation such as the bunchberry, *Cornus canadensis* L., in forested habitats influences the distribution of *R. mendax* in nearby lowbush blueberry, *Vaccinium angustifolium* Aiton, fields in Nova Scotia, Canada. Zampella (1991) provides a comprehensive list of the flora in the Pinelands, reporting that dwarf huckleberry (*Gaylussacia dumosa* (Andrews) Torr. & A. Gray), dangleberry (*Gaylussacia frondosa* (L.) Torr. & A. Gray ex Torr.), and highbush blueberry (*V. corymbosum*) frequently occur in upland forest but that they are more abundant in wetland forest; while black huckleberry (*Gaylussacia baccata* (Wangenh.) K. Koch) is usually the dominant shrub species in upland forest. Both wild *Gaylussacia* spp. and *Vaccinium* spp. serve as alternative hosts for *R. mendax* (Smith et al., 2001). Thus, although the data from Zampella (1991) do not support the idea that upland forest provides *R. mendax* with more alternative hosts than wetland forest in the Pinelands of New Jersey, additional research is needed to determine if there are differences in susceptibility among these various hosts to *R. mendax* infestation that could explain our findings.

Although the landscape factors that drive *R. mendax* abundance in blueberry farms were previously unknown, this insect had been reported to aggregate along field edges when moving from neighboring habitats. For instance, Collins and Drummond (2004) reported aggregation of *R. mendax* flies within the first 30 m into edges of lowbush blueberry, *V. angustifolium*, fields. Renkema et al. (2014) also showed that male fly captures and fruit infestation levels in lowbush blueberries were higher at 5 m than at 30 m from field edges. In the present study, we report that *R. mendax* flies can fly a maximum distance of 76 m within 48 h, moving 4.5 m farther within blueberry fields when released from forest edges than from field edges. These results are similar to those from a pilot mark-release-recapture study done in an open blueberry field (data not shown), indicating that the tunnel did not influence *R. mendax* movement. More flies were recaptured on traps when released in the interior (field edge) than the exterior (forest edge) of fields, which suggests that more flies tended to stay in the field when exposed to fruit-bearing bushes. Our data show that most (75–80%) of the flies were recaptured within the first 30 m into fields (Fig. 4), as previously reported by Collins and Drummond (2004). Low dispersal capacity of less than 5 m within a cherry orchard was also reported for a closely related species, the European cherry fruit fly (*Rhagoletis cerasi* (L.)) (Daniel and Baker 2013). Renkema et al. (2014) indicated that *R. mendax* fly captures are predicted by densities of ripe lowbush berries, which may cause the aggregation of flies within field edges. Fruit availability also increases movement to and residence time of two related fruit flies, the Western cherry fruit fly, *Rhagoletis indifferens* Curran, and apple maggot, *Rhagoletis pomonella* (Walsh) (Prokopy et al., 1994; Senger et al., 2009). As compared with lowbush blueberries, highbush blueberries have a lower threshold for number of maggots per trap (1 versus 10; Rodriguez-Saona et al., 2015). Combined with a zero tolerance for maggots in fruit (Rodriguez-Saona et al., 2015), this meant that farmers treated fields as soon as traps indicated the presence of flies. For this reason, unlike the study done by Renkema et al. (2014) in lowbush blueberries, we did not assess fruit infestation, as there was very little chance of finding maggots in them–also note that throughout the course of this study none of the participating farmers reported fruit infested by *R. mendax* during their regular scouting. Our findings, together with those previously reported (e.g. Collins and Drummond, 2004; Renkema et al., 2014), support the use of border applications of insecticides to manage *R. mendax* in blueberry fields. Indeed, numbers of *R. mendax* flies on traps were reduced after a perimeter application of phosmet (Imidan) 70 WP (Collins and Drummond, 2004) or GF-120 Naturalyte Fruit Fly Bait (Rodriguez-Saona et al., 2008). Altogether, our data can be used to define border insecticide applications to manage *R. mendax* in highbush blueberries, which should be targeted to fields close to upland forest and directed to the field borders at distances between 30 and 80 m from field edges. Moreover, because of the low *R. mendax* fly captures in field interiors, the fact that only 20–25% of flies traveled more than 30 m in 2 days inside fields, and the intensity of management practices in these fields, it is unlikely that flies would gradually disperse further and further into the field each year or move long distances in a high resource-rich environment like a commercial blueberry field. The significance of areas without host plants or periods of host-deprivation for *R. mendax* dispersal would, however, need to be the subject of future research to further explore dispersal in this species.

The results from our weekly trapping data were shared with the participating farmers who made management decisions accordingly. This is reflected in our multi-year data on the amount of insecticide use. In 2009 and 2010, farmers used greater amounts of insecticides in fields with higher chance of catching *R. mendax* flies on traps. This indicates that farmers were using our spatial data to manage *R. mendax* populations more precisely by applying insecticides to fields with greater risk of infestation. This resulted in a decrease in the amounts of insecticides applied across all blueberry farms in 2010 and 2011 (Fig. S6), and was likely a key factor responsible for the observed steady decline in *R. mendax* populations in these farms from 2009 to 2011 (Fig. S5). A decrease in insecticide use in 2010 and 2011 led also to lower management costs (C.R-S., D.P., P.V.O., unpublished data). In 2011, a newly invasive pest from Asia, the spotted wing drosophila, *D. suzukii*, was detected for the first time in New Jersey (Michel et al., 2015), as well as in most other states in the Northeast USA (Asplen et al., 2015). *Drosophila suzukii* is a pest of soft, thin-skinned small fruits including blueberries (Walsh et al., 2011; Kinjo et al., 2013; Asplen et al., 2015), and has now become the primary driver of insecticide applications during fruit maturation in New Jersey blueberry farms. After arrival of this pest, blueberry farmers in New Jersey changed their pest management practices by switching to a more intense (i.e. calendar-based) insecticide program that involves weekly applications of insecticides in all susceptible fields regardless of the landscape features surrounding these fields. This has resulted in a ~45% increase in insecticide use in blueberry farms in the state of New Jersey since 2012 (D.P., unpublished data), which is also reflected in our data by the more than 2-fold increase in insecticide use in 2012 as compared with 2011 (Fig. S6).

5. Conclusions

Knowledge of the distribution of insect pests in agro-ecosystems can provide information for more precise pest management practices by targeting insecticide applications only to locations where needed (i.e., exceed an economic threshold). The present 4-year study shows that the landscape surrounding highbush blueberry farms influences the abundance of a native frugivorous pest of blueberries, the blueberry maggot fly (*R. mendax*). Captures of this fly on traps decline with increasing distance from upland forest, which suggests that upland forest provides suitable overwintering and feeding/mating habitats for this pest. We also demonstrated that once the flies reach a blueberry field, 50% of flies move only about 30 m while 0% move > 80 m into the interior of the field from the field or forest edges within 48 h. Altogether, based on these data, blueberry farmers should focus their monitoring and management efforts for *R. mendax* to those fields near upland forest habitats and within 80 m from the field edge. Farmers participating in this study followed these recommendations in the first two years after the start of the study (2010 and 2011), resulting in lower *R. mendax* abundance in farms and less insecticide use. These pest management practices for *R. mendax* were disrupted in 2012 after the invasion of *D. suzukii*, which resulted in an increase in insecticide use while keeping low populations of *R. mendax*. This pattern has continued for the past five years causing *R. mendax* populations to remain at very low levels (C.R.-S., D.P., personal observation). Future studies need to identify features of upland forests, such as alternative hosts and soil conditions, that facilitate *R. mendax* populations and the new invasive pest *D. suzukii* to promote wider adoption of more targeted pest management approaches. This study highlights the importance of understanding the landscape ecology of insect pests to improve pest management practices in agro-ecosystems.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.agee.2018.02.001.

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