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RESEARCH ARTICLE

The influence of landscape on insect pest dynamics: a case study in southeastern France

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Abstract Managing the spatial distribution of crop and non-crop habitats over landscapes could be used as a means to reduce insect pest densities. In this study, we investigated whether or not landscape characteristics affected the number of codling moths in commercial orchards. To do this, we collected overwintering larvae in 2006 and 2007 in 76 orchards over a 70 km^2 area in southeastern France. We analysed variations in the number of larvae using correlation tests and linear models. As independent variables, we took both characteristics of focus orchards (pear vs. apple, organic vs. conventional orchards) and of their surrounding landscape (orchard density and hedgerow network attributes) into account in buffers with widths varying from 50 to 500 m. Although the codling moth is specialised on orchards, the number of codling moths was lower in orchards within a high orchard density area. There was some indication that this effect was mostly due to the density of conventional orchards and thus to the intensity of insecticide treatments. Conversely, we found no particular effect of abandoned or organic orchards. In 2006, the number of codling moths was also significantly lower in a focus orchard when the hedgerow network acted as a protection against the prevailing wind. Finally, major effects of landscape variables on the number of codling moths were observed for distances of less than 150 m from the focus orchards, suggesting that codling moth management should be organised over areas of about 16 ha.

Keywords Codling moth · Correlation · *Cydia pomonella* · GIS · Habitat · Hedgerow · Orchard · Pest management · Tortricidae · Windbreak

Introduction

Alternatives are needed to the chemical control of agricultural pests. Although it generally makes it possible to maintain low levels of crop damage, chemical control has direct or indirect detrimental effects for human health (Lee et al. 2004) or biodiversity conservation (McLaughlin 1995; Letourneau and Goldstein 2001). Repeated use of insecticides frequently leads to the development of resistance in pests (McKenzie and Batterham 1998). The design of innovative environmentally-friendly crop protection strategies requires us to consider factors that affect pest population dynamics

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throughout their cycle, even if their effects are partial. One such factor is the landscape context of the crop, i.e. the composition and the configuration of the surrounding agricultural ecosystem, which could be managed to create an impact on the population dynamics of long-distance dispersing pests. The impact of landscape structure on population dynamics is well documented for many species (e.g. Wiegand 1999, for animal species in general, and Schmidt et al. 2005; Holzschuh et al. 2007, for non-pest insect species). However, studies are rare and results are not consistent when insect pest species are considered (Bianchi et al. 2006). One possible reason for this lack of observed effect is the direct impact of insecticides on pest dynamics, making it difficult to assess the effects of other factors on agricultural landscapes.

Insect species involved in active displacements at the landscape scale perceive agricultural areas as mosaics of more or less connected habitats of different qualities (Dennis et al. 2003). The spatial distributions of habitat quality and of the perturbation regimes strongly influence population dynamics (Hiebeler and Morin 2007). Good quality habitats provide favourable conditions that lead to a higher fecundity rate or a reduced mortality rate and, therefore, to population growth. Conversely, isolated populations normally decline in a poor habitat, but may persist thanks to migration from good habitats. For insects that specialise on crops, obvious landscape variables to be taken into account are crop distribution and pest management strategies over the landscape, although information is rarely provided about the latter (Valantin-Morison et al. 2007; Zaller et al. 2008). Furthermore, non-cultivated habitats are often considered as possible pest enemy pools (Elliott et al. 1998; Tscharntke et al. 2007).

Landscape structure impacts on pest population dynamics are generally investigated through empirical correlative approaches due to the difficulty of manipulating large landscapes. The main drawback of these correlative approaches is the difficulty of linking correlation levels to population dynamic processes such as local population growth or migration behaviour (Wiegand 1999). In some cases, however, correlations could be putatively interpreted in terms of mechanisms. For example, conventional cotton fields were shown to act as sources of pink bollworm for *Bt*-cotton fields located up to 2.25 km away (Carriere et al. 2004). Similarly, it was hypothesized that non-crop areas in the landscape harboured enemies of pollen beetles, an insect pest of oilseed rape (Thies et al. 2003).

Codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae), is a major insect pest in temperate regions, specialised on several domesticated host plants with a strong preference for apple and pear orchards (Shel'Deshova 1967). In early spring, adults produced from overwintering larvae emerge and reproduce. Free neonate larvae penetrate into fruits, causing damage. At the end of their development, the larvae leave the fruit and, depending on temperature and photoperiod conditions, either pupate to produce adults or enter into diapause. In southern France, codling moths complete two or three generations per year. Insecticide treatments are aimed at killing eggs or larvae before they reach the fruits and have less impact on adults (Reuveny and Cohen 2007). Because of the numerous treatments applied in orchards, codling moth has developed resistance to several chemical insecticides (Reyes et al. 2007). In addition, mark-release experiments indicate that the majority of codling moth individuals disperse within 150 m (Keil et al. 2001), although a few can fly up to 10 km (Mani and Wildbolz 1977). This is consistent with measurements of flight ability in flight mills (Schumacher et al.1997) and with a low genetic structure among codling moth populations (e.g. Franck et al. 2007). As a consequence, pest management strategies should be implemented over areas larger than single orchards (Calkins and Faust 2003).

Local populations of codling moth are likely to respond to conditions within orchards and to the spatial distribution of orchards over landscapes because of their specialisation on orchard plants (Tischendorf 2001). Furthermore, they may be directly or indirectly affected by hedgerow networks that affect both physical and biological flows and thus play a major role in agricultural landscapes (Baudry et al. 2000). In this study, we investigate the relative impacts of local agricultural practices and landscape characteristics on the dynamics of codling moth populations. To do this, we assess the influences of (1) orchard densities, and (2) hedgerow network design on codling moth population densities from 76 orchards in a 70 km^2 apple and pear production area in southeastern France.

Methods

Study area and landscape mapping

The study area (Fig. 1) is an agricultural landscape of approximately 70 km^2 in southeastern France (coordinates in WGS84 system from 43°46′27″N to 43°51′23″N and from 4°51′12″E to 4°57′34″E). The main agricultural production consists of fruits, mostly apples and pears. Apple and pear orchards are subsequently referred to as pomefruit orchards. All pomefruit orchards and all hedgerows were manually digitalised with ArcView (Version 9.1, ESRI) from an aerial photograph (BD ORTHO®, IGN, 2004–pixel size: 0.5 m). Pomefruit orchards were classified into three categories: abandoned, organic and conventional. Fruit attacks were actually ten times higher in abandoned orchards compared to organic ones, and twice as high in organic orchards compared to conventional orchards (data not shown). These three different categories of orchards may thus have different impacts on codling moth population dynamics. On the contrary, pear and apple orchards were not differentiated because they had similar population densities as estimated from sexual trapping of adults and monitoring of fruit damage (data not shown). Abandoned orchards (269 orchards) were identified by both photo interpretation and direct field observations. Field observations also confirmed that pomefruit orchards were correctly discriminated from other orchards (apricot, peach and olive trees), with an error rate of less than 5%. The locations of all organic orchards (74 orchards) were determined through regional surveys of the farmers, and the other non-abandoned orchards (2,881) were assumed to be conventional by default.

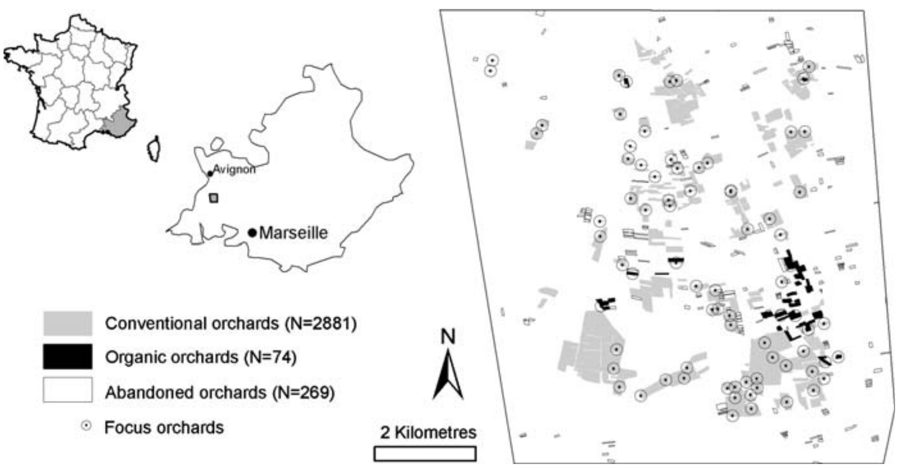
Choice of focus orchards

A first set of 66 orchards (45 apple orchards and 21 pear orchards) was selected by a random draw of spatial coordinates in order to ensure a correct representation of all classes of pairwise distances between focus orchards. We thus also expected to obtain a sample of farmers not particularly influenced by specific technical advisers. However, no organic orchard was selected from the random draw because of the small proportion of organic orchards over the area. We then further selected ten organic orchards (five apple orchards and five pear orchards) from all of the organic farmers over the area, thus reaching a total of 76 orchards subsequently referred to as "focus orchards". The mean orchard area in this sample was 0.85 ha (± SD = 0.56 ha) and the mean distance to the nearest focus orchard was 295.6 m (± SD = 147.5 m). On average, 12.9 (± SD = 3.9) treatments with granulosis virus were applied against codling moth during the growing season in the organic orchards. Conventional orchards received an average of 10.7 (± SD = 4.5) insecticide applications against codling moth.

Landscape variables

Landscape descriptors were calculated in 50, 100, 150, 250 and 500 m wide concentric buffers around

Fig 1 Map of the study area showing the positions of the 76 focus orchards and the distribution of the different categories of pear and apple orchards. The number of each type of orchards is given in parentheses



focus orchards using ArcView. The maximal distance was set at 500 m to avoid artificially large correlations due to overlapping of buffers. Six landscape descriptors were calculated in each buffer. Four of these describe the proportion of buffer areas covered by different categories of pomefruit orchards, including all pomefruit orchards, abandoned orchards, organic orchards and conventional orchards. For clarity, these variables are subsequently referred to as the "proportion" of each type of orchard.

The two other descriptors concern the hedgerow network. The hedgerow network length index, was calculated as the ratio of hedgerow length over buffer area. A second index considered the hedgerow orientation since strong winds blow from north to south in the study area. It was calculated as:

$$\text{Hedgerow network orientation index} = \frac{\sum_i L_i \times A_i}{90 \times \sum_i L_i}$$

(dimensionless) where L_i is the length of hedge i, and A_i its angle in degrees from the non-oriented north-south direction. A_i assumes a value ranging from 0 (north-south orientation) to 90 (east-west orientation). Hedgerows situated on the border of focus orchards were included in the buffers. Distributions and variances of landscape descriptors are provided in supplementary material S1.

In addition, we calculated two indicators of the connectivity of focus orchards: (1) d, the distance to the nearest pear or apple orchard, and (2) C, the area covered with orchards within easy reach of codling moths (Winfree et al. 2005). This second indicator was calculated for each focus orchard k as:

$$C_k = \sum_{j \neq k} S_j.\exp(-d_{jk}/D)\ (\mathrm{m}^2)$$

where S_j is the area of orchard j, d_{jk} the distance between the focus orchard k and orchard j, and D is a mobility constant that corresponds to the order of magnitude of the species movement distance. There are no consensual data about the value of such a parameter for the codling moth. However, several studies (Mani and Wildbolz 1977; Schumacher et al.1997; Tyson et al. 2007) indicate that this pest is mostly a short-distance disperser. D was thus considered to be equal to 100 m that represents the order of magnitude of the codling moth dispersal distance.

To assess correlations among descriptors, we also computed raster maps that provide information about the proportion per hectare (in a 100 × 100 m cell) of area covered by each type of orchard (pomefruit, conventional, organic or abandoned) and about hedgerow network length and orientation in each cell.

Codling moth sampling

In each focus orchard, 30 corrugated cardboard band traps (10 cm wide) were wrapped around tree trunks to collect overwintering codling moths. Ten of the 30 bands were placed on the border row of the orchard and the 20 others were evenly placed within the orchard. Bands were installed in mid-July and were collected in mid-October of 2006 and 2007. The population density of each focus orchard was quantified by averaging the number of codling moths of the 30 band traps.

Statistical analyses

Correlations between landscape descriptors

To address possible confusing effects due to correlations between landscape descriptors, we computed pairwise Spearman correlations between landscape variables calculated over raster maps using values in each 100 × 100 m cell.

We also performed pairwise correlations between landscape variables calculated in buffers for each buffer width (correlation matrix provided in supplementary material S2).

Correlations between landscape variables and the number of codling moths

To investigate effects of landscape composition on the number of codling moths and the scale of influence of landscape variables, we analysed correlations between the number of codling moths in focus orchards and landscape descriptors in buffers. We computed Spearman correlations for each of the 2 years between the number of codling moths and landscape variables in successive buffers, providing an overview of the descriptors most highly correlated with the number of codling moths and of the evolution of the correlation with distance from the focus orchard. We also computed Spearman correlations between the number of codling moths and the two indicators of orchard connectivity. Since the number of codling moths significantly differed between pear and apple focus orchards (see “Results”), all correlation analyses were performed for all focus orchards and separately for pear and apple focus orchards.

Effects of local and landscape variables on the number of codling moths

Because of the very large number of local and landscape variables that could influence codling moth populations and of their inter-correlations, we did not include all variables at once in a single model. First, we selected the local variables that significantly affected the number of codling moths (transformed as log (number of codling moths + 1)) without considering any landscape variables, using a linear model (proc MIXED, SAS Version 9.1, SAS Institute Inc., Cary, NC, USA). Second, codling moth numbers were analysed with linear models including both the selected local variables and each landscape variable separately, to select the most relevant landscape variables and the distance at which each variable has the strongest effect. Finally, we combined the selected local and landscape variables in a last set of nested linear models to identify the best model using the Akaike Information Criteria (AIC). Details of models are provided below.

Local variables On the basis of fruit damage data, we suspected that organic orchards hosted larger codling moth populations. Further band traps supposedly have a reduced yield on pear compared to apple trees because of indented bark that provides natural shelters for larvae. We tested for these effects on the number of codling moths at the field scale with a linear model, including the plant species (pear vs. apple), the type of pest management (organic vs. conventional) and their interaction, using the 2 years as replicates. Orchard area was further included as a covariate. We selected significant local variables and their interactions.

Landscape variables We performed one model per landscape variable and per distance. Each of these models contained the local variables selected before, one landscape variable calculated at each buffer width (50, 100, 150, 250 or 500 m), and the interaction between this landscape variable and each local variable. Since interactions other than those with the year were never significant, they were discarded in further analyses. Combining the six variables calculated in five successive buffers, we therefore obtained 30 models. We compared all models to the model including only the selected local variables using AIC. Only variables that improved the model for at least one buffer width were kept for further analyses. For these variables, we considered that the most relevant distance corresponded to the model with the lowest AIC among all models including this variable.

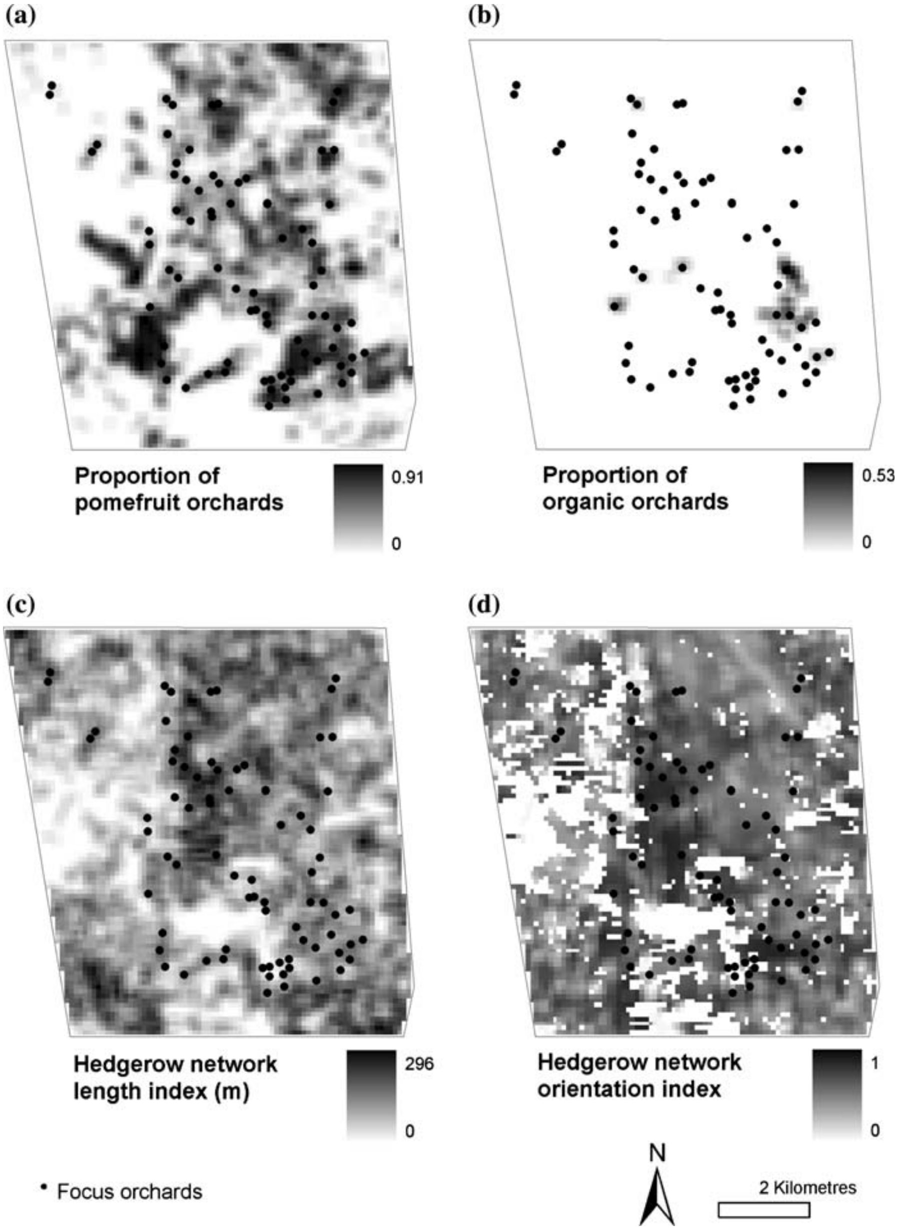
Final model selection We included (1) all selected local variables, (2) the combination of the selected landscape variables calculated at their most relevant distance, and (3) their interactions with the year in a single “full” model. We then selected the final best model by AIC comparison of all possible sub-models of this full model.

Results

Descriptive statistics of the study area

The average area of pomefruit orchards in the study area was 0.60 ha ± SD 0.46 ha. The mean proportion of area covered by pomefruit orchards in a 100 × 100 m cell was 0.22, ranging from a very high density of 0.91 to no orchards (Fig. 2a). Organic orchards were clustered together in four spots with a main group in the southeast of the study area (Fig 2b). The hedgerow network (Fig 2c) was dense in most of the study area with a mean hedgerow length of 110 m per hectare. The highest value of the hedgerow network orientation index (indicating windbreak hedgerows) was in the central part of the area (Fig 2d). The hedgerow length was positively correlated with the hedgerow network orientation index ($r = 0.462$, $P < 0.0001$), meaning that most hedges were planted as windbreaks (Table 1). The proportion of pomefruit orchards was also positively correlated to both hedgerow length ($r = 0.260$, $P < 0.0001$) and hedgerow orientation ($r = 0.266$, $P < 0.0001$), meaning that map cells with numerous orchards also had numerous hedges that were mostly east-west oriented (i.e. perpendicular to the winds).

Fig 2 Maps of study area components: proportion of area covered by **a** pomefruit orchards and **b** organic orchards; **c** hedgerow network length and **d** hedgerow network orientation in 100 × 100 m cells. *Black dots* represent focus orchards



Number of codling moths

The number of codling moths varied with the year and the characteristics of focus orchards. On the average, we found 1.29 codling moth larvae per band trap in 2006 and 0.73 in 2007. We caught approximately twice as many larvae per trap in organic than in conventional orchards and about ten times more in apple than in pear orchards both years (Table 2).

Correlations between spatial distribution of orchards and the number of codling moths

Density of orchards

Orchards surrounded by higher proportions of pomefruit orchards had lower codling moth populations in 2006 and 2007. Correlation patterns were similar both years, although stronger in 2006, with maximal correlations at 100 m (Fig. 3a1). This pattern was

Table 1 Correlation coefficients between raster maps of landscape variables using values in each 100 × 100 m cell

Variables	PP	PA	PC	PO	HL
PA	0.228 ***				
PC	0.949 ***	0.02 NS			
PO	0.141 ***	0.046 ***	0.004 NS		
HL	0.260 ***	0.095 ***	0.246 ***	0.051 ***	
HO	0.266 ***	0.087 ***	0.253 ***	0.037 ***	0.462 ***

PP, Proportion of pomefruit orchards; PA, Proportion of abandoned orchards; PC, Proportion of conventional orchards; PO, Proportion of organic orchards; HL, Hedgerow network length index; HO, Hedgerow network orientation index. Level of significance: NS, not significant

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 2 Mean number of codling moths in different categories of focus orchards (mean number of overwintering larvae trapped per tree)

Type of focus orchards	Number of orchards	2006 Mean ± SD	2007 Mean ± SD
All orchards	76	1.29 ± 2.54	0.73 ± 1.48
Organic	10	2.39 ± 3.66	1.02 ± 2.12
Conventional	66	1.12 ± 2.32	0.68 ± 1.38
Apple	50	1.88 ± 2.96	1.07 ± 1.74
Pear	26	0.14 ± 0.27	0.07 ± 0.15

maintained when considering only apple focus orchards (Fig. 3a2). For pear focus orchards (Fig. 3a3), correlations were weaker and the only significant correlation was for the 50 m wide buffer.

Connectivity

The number of codling moths was not correlated to d, the distance to the nearest orchard (2006: $r = -0.14$, $P = 0.22$; 2007: $r = -0.12$, $P = 0.31$). Conversely, there was a significant negative correlation (2006: $r = -0.28$, $P = 0.016$; 2007: $r = -0.23$, $P = 0.047$) with C, that estimates the pomefruit orchard area within reach of codling moth. Moreover, C was also highly correlated with the proportion of pomefruit orchards (r from 0.77 to 0.92, depending on buffer width; $P < 0.001$ both years).

Densities of the three orchard categories

Proportion of conventional orchards The number of codling moths was negatively correlated to the proportion of conventional orchards (Fig. 3b1), indicating that there were less codling moths in orchards surrounded by a large area of conventional orchards. The maximal correlation was at a distance of 250 m for both years. Correlations were all significant in 2006 and higher than correlations to the proportion of pomefruit orchards (Fig. 3a1). In 2007, correlations were weaker and mostly marginally significant. Correlations were still negative and mostly significant for all but the largest buffers when the apple (Fig. 3b2) and the pear (Fig. 3b3) focus orchards were considered separately.

Proportion of abandoned orchards Correlations between the number of codling moths and the proportion of abandoned orchards were positive both years but never significant (2006: r from 0.07, $P = 0.56$, to 0.19, $P = 0.09$; 2007: r from 0.004, $P = 0.97$, to 0.11, $P = 0.38$, depending on buffer width).

Proportion of organic orchards Correlations between the number of codling moths and the proportion of organic orchards were also not significant (2006: r from -0.007, $P = 0.95$, to 0.14, $P = 0.23$; 2007: r from 0.02, $P = 0.87$, to 0.05, $P = 0.66$ depending on buffer width).

Correlations between characteristics of hedgerows and the number of codling moths

Hedgerow length

Correlations between the number of codling moths and the hedgerow network length index were weak and not significant considering either all orchards or pear and apple orchards separately (Fig. 3c). Unexpectedly, correlations were all positive in 2006 and negative in 2007 for apple focus orchards (Fig. 3c2).

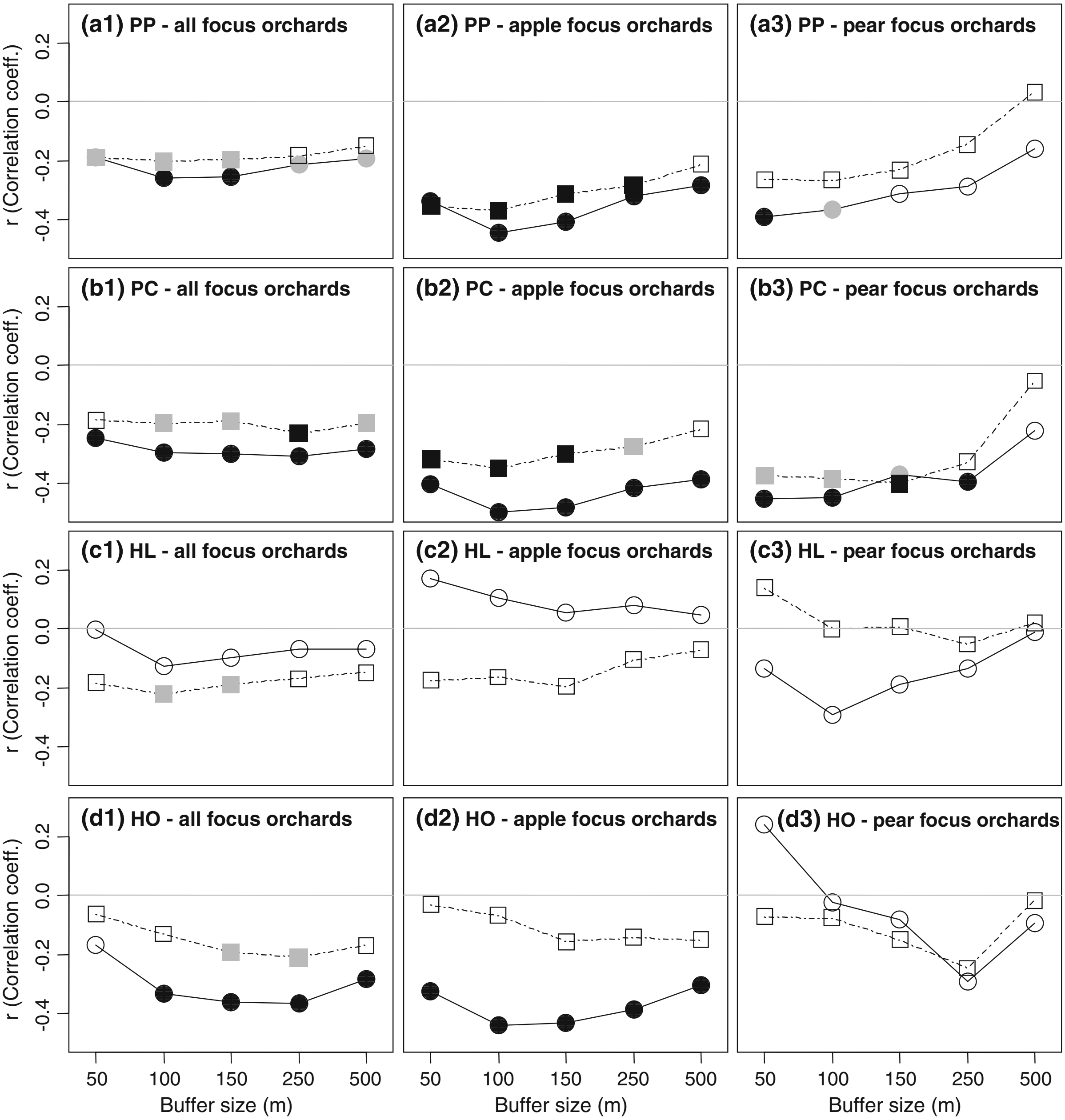


Fig 3 Correlations between the number of codling moths and landscape variables in 2006 (*circles* and *solid lines*) and 2007 (*squares* and *dotted lines*). Correlations to proportion of pomefruit orchards (PP) considering (*a1*) all focus orchards ($N = 76$), (*a2*) apple focus orchards ($N = 50$) and (*a3*) pear focus orchards ($N = 26$); correlations to proportion of conventional orchards (PC) considering (*b1*) all focus orchards ($N = 76$), (*b2*) apple focus orchards ($N = 50$) and (*b3*) pear focus orchards ($N = 26$); correlations to the hedgerow network length index (HL) considering (*c1*) all focus orchards ($N = 76$), (*c2*) apple focus orchards ($N = 50$) and (*c3*) pear focus orchards ($N = 26$); correlations to the hedgerow network orientation index (HO) considering (*d1*) all focus orchards (N = 76), (*d2*) apple focus orchards ($N = 50$) and (*d3*) pear focus orchards ($N = 26$). Symbol shade indicates the level of statistical significance: *black* for $P < 0.05$, *grey* for $0.05 < P < 0.10$, and *white* for $P > 0.10$

Hedgerow orientation

The correlations between the number of codling moths and the hedgerow network orientation index were negative for all distances for both years and significant for buffers of 100–500 m widths in 2006 (Fig. 3d1). These correlations were mainly due to the apple focus orchards (Fig. 3d2). For pear focus orchards, the correlations were never significant (Fig. 3d3).

To take the correlation between hedgerow network orientation index and the proportion of pomefruit orchards into account (Table 1), we calculated a partial correlation between the number of codling moths and hedgerow network orientation index in the 250 m wide buffer, controlling for the effect of the proportion of pomefruit orchards (see supplementary material S3). The correlation was still negative and significant in 2006 ($r = -0.33$, $P = 0.003$), which indicates an independent correlation with hedgerow orientation. The correlation remained not significant in 2007 ($r = -0.17$, $P = 0.15$).

Explaining the number of codling moths with local and landscape variables

The study year, the plant species and their interactions were all significant in the model including all local variables (Table 3). There was also a marginally significant difference between organic and conventional orchards ($P = 0.052$). We therefore kept the year, the plant species, the type of orchards and the interaction between the year and the plant species in all subsequent models including landscape variables. The model including only this selected set of significant local variables (subsequently referred to as the "local model") had an AIC equal to 234.2.

Adding one landscape variable at one distance (and the interaction between this variable and year) to the local model provided an AIC lower than 234.2

Table 3 Effect of local variables and interactions on the number of codling moths. For each factor effect, a reference level is set to zero (indicated in brackets)

Effect	*df*	*F*	*P*	Estimate ± Standard error
Orchard area	1	1.42	0.2380	$-1 \times 10^{-5} \pm 8.57 \times 10^{-6}$
Year (2006 or 2007)	1	4.65	0.0344	2006: 0.71 ± 0.25 (2007: 0)
Plant species (apple or pear)	1	20.28	<0.0001	Pear: −0.45 ± 0.28 (apple: 0)
Type of orchard (organic or conventional)	1	3.91	0.0518	Conventional: −0.16 ± 0.21 (organic: 0)
Plant species × year	1	4.47	0.0381	Pear × 2006: −0.78 ± 0.35 (others: 0)
Type of orchard × year	1	1.39	0.2415	Conventional × 2006: −0.60 ± 0.27 (others: 0)
Plant species × type of orchard	1	1.10	0.2971	Pear × conventional: −0.049 ± 0.30 (others: 0)
Plant species × type of orchard × year	1	3.65	0.0601	Pear × conventional × 2006: 0.74 ± 0.39 (others: 0)

Table 4 AIC values of models including the selected local variables, one landscape variable at one distance and the interaction between this landscape variable and the year

Distance	Local + PP	Local + PC	Local + PO	Local + PA	Local + HL	Local + HO
50 m	**229.3**	**228.8**	**233.0**	237.7	**230.9**	234.5
100 m	**224.6**	**224.5**	234.4	237.6	**233.8**	**232.4**
150 m	**224.8**	**224.2**	234.6	237.2	235.6	**230.4**
250 m	**228.1**	**226.2**	234.5	237.9	236.7	**231.4**
500 m	**226.9**	**225.1**	236.5	238.1	237.6	**234.1**

PP, Proportion of pomefruit orchards; PC, Proportion of conventional orchards; PO, Proportion of organic orchards; PA, Proportion of abandoned orchards; HL, Hedgerow network length index; HO, Hedgerow network orientation index. Bold values indicate models that are better than the model including only the selected local variables (AIC lower than 234.2). Underlined values indicate the distance that result in the lowest AIC for a given landscape variable

Table 5 Best model including all selected local variables and the best combination of the selected landscape variables

Effect	*df*	*F*	*P*	Estimate ± Standard error
Year (2006 or 2007)	1	1.98	0.1641	2006: 0.71 ± 0.45 (2007: 0)
Plant species (pear or apple)	1	33.59	<0.0001	Pear: −0.52 ± 0.10 (apple: 0)
Type of orchard (conventional or organic)	1	2.62	0.1100	Conventional: −0.23 ± 0.14 (organic: 0)
Plant species × year	1	1.13	0.2908	Pear × 2006: −0.14 ± 0.13 (others: 0)
$\text{PP}_{0\text{–}100}$	1	8.96	0.0038	$-7.77 \times 10^{-3} \pm 2.60 \times 10^{-3}$
$\text{HL}_{0\text{–}50}$	1	0.03	0.8592	$-0.12 \pm 7.44 \times 10^{-2}$
$\text{HO}_{0\text{–}150}$	1	3.09	0.0832	−0.19 ± 0.48
$\text{HL}_{0\text{–}50}$ × year	1	8.42	0.0050	HL × 2006: $0.27 \pm 9.15 \times 10^{-2}$ (HL × 2007: 0)
$\text{HO}_{0\text{–}150}$ × year	1	4.80	0.0317	HO × 2006: −1.26 ± 0.58 (HO × 2007: 0)

For each factor effect, a reference level is set to zero (indicated in brackets). PP, Proportion of pomefruit orchards; HL, Hedgerow network length index; HO, Hedgerow network orientation index

(i.e. better than that of the local model) in 16 cases out of 30 (Table 4). Only models including the proportion of abandoned orchards were worse than the local model, regardless of the distance. Models with the lowest AIC were for a distance of 100 m for the proportion of pomefruit orchards, a distance of 150 m for the proportion of conventional orchards, a distance of 50 m for the hedgerow network length index and the proportion of organic orchards, and a distance of 150 m for the hedgerow network orientation index.

All possible models including (1) all selected local variables, (2) any combination of these landscape variables at these selected buffer widths and (3) their interactions with the year were better than the local model. Among these 152 models, 58 were better than the full model including all these variables (AIC = 224.7). The best model provided an AIC of 220.1 and twelve models did not significantly differ from this model (AIC ≤ 222.1, see supplementary material S4). The landscape variables retained in the best model were the proportion of pomefruit orchards at 100 m, the hedgerow network length index at 50 m and its interaction with the year, the hedgerow network orientation index at 150 m and its interaction with the year (Table 5). There were significantly less codling moths in orchards with a high proportion of pomefruit orchards density at 100 m ($F_{1,70} = 8.96$; $P = 0.0038$). The interaction between the hedgerow network length index and the year and between the hedgerow network orientation index and the year were also significant. In order to understand the meaning of these interactions, we performed the best model again for each year separately. There was a negative effect of the hedgerow network orientation index, but it was only significant in 2007. The effect of the hedgerow network length index was positive in 2006 and negative in 2007 but never significant.

Discussion

We found in this study that the number of codling moths depended not only on local orchard characteristics but also on characteristics of the surrounding landscape despite intense control of local populations by insecticides. This result was true for both study years although the intensity of infestation was much lower in 2007 than in 2006.

Landscape characteristics were shown to have an impact on numerous insect species populations (e.g. Wiegand 1999; Jeanneret et al. 2003; Taki et al. 2007), and particularly Lepidoptera species for which both abundance and species richness were positively correlated with habitat density (e.g. Öckinger and Smith 2006). A somewhat unexpected result is that the correlation with the proportion of orchards was negative although orchards are the habitat of the codling moth. There are two possible non-exclusive explanations for this result. Either this could be the result of a dilution effect whereby a given number of individuals is distributed at a lower density over a larger area (e.g. Veddeler et al. 2006; Zaller et al. 2008), or it could result from a metapopulation dynamics where only a few orchards hosted high codling moth populations, while most of them were unfavourable habitats due to insecticide control that maintained populations at very low densities. Interpreting the impact of the proportion of orchards on population dynamics is difficult here since the quantity of habitat and its connectivity are highly correlated, as is often the case (Haynes et al. 2007).

One possible clue is provided by the correlations of the number of codling moths with the proportion of conventional orchards that were generally better than correlations with the proportion of all pomefruit orchards (Fig. 3). This may be evidence of the impact of insecticide treatments in surrounding orchards on the codling moth populations inside focus orchards. In the study region, conventional growers have a very low tolerance level for fruit damage compared to organic growers, and conventional orchards receive an average of 10.7 insecticide treatments per growing season. It should be observed, however, that the best linear model retained the proportion of pomefruit orchards but not that of conventional orchards as the main explanatory landscape variable, possibly calling for a better description of insecticide treatments within each orchard in the landscape.

In addition, we found no evidence of a specific influence of organic or abandoned orchards on the number of codling moths. Abandoned orchards are often suspected to be good habitats for codling moths because they are not sprayed. However, we did not trap large populations during both study years in abandoned orchards (data not shown), possibly because they were not irrigated, which limited their fruit production. The quality of these habitats probably depends on the amount of time after abandonment and is undoubtedly highly heterogeneous among orchards. Backyard trees and walnut or quince trees in hedgerows may also have an influence on codling moth dynamics. They would represent very small areas compared to orchards but might be sufficient to host relatively large populations, given the fecundity of codling moth females that can lay over 50 eggs. Wooden boxes for fruit harvesting are possible additional sources. It should be noted, however, that habitation densities were not correlated with the density of codling moth larvae (data not shown). A difficulty in investigating potential effects of these types of habitats is their small size that makes them inconspicuous.

Hedgerows are important landscape features for many species (Baudry et al. 2000; Le Coeur et al. 2002). The number of codling moths decreased with the increasing presence of windbreaks offering protection from the prevalent northern wind in 2006 and, to a lesser extent, in 2007. During the codling moth flight period, the number of days with a maximal wind higher than 10 ms^{-1} was 73 in 2006 and 55 in 2007 in the study area. The lower impact of the orientation of hedgerows in 2007 compared to 2006 may be consistent with these wind speed differences between years. In the study area, windbreaks are mainly monospecific, composed either of poplar or cypress trees. Their presence modifies nearby climatic conditions, thus potentially influencing codling moth phenology (Kührt et al. 2006) and movements within the orchard. Hedgerows may reduce the number of codling moths because they limit migration (Sciarretta and Trematerra 2006) and the diffusion of pheromones (Reardon et al. 2006). This may reduce the possibility of finding mates at low population densities and of colonising orchards again after insecticide applications. Windbreaks may also increase the efficiency of insecticide applications. Numerous experiments have shown a significant reduction of pesticide drift by natural windbreaks (Ucar and Hall 2001). In addition, hedgerows may be potential habitats for codling moths enemies such as parasitoids or predators (Landis et al. 2000). However, the present study did not provide evidence for such hedge impacts. The effect of the hedgerow network length index was not significant and of opposite direction each year. This might be partly due to insecticide treatments that also affect pest enemies (Suckling et al. 1999), or to the limited effect of natural enemies on this species.

In empirical approaches, conclusions obviously do not only depend just on biological processes (such as fecundity in good quality habitat, for example) but on the distributions of samples and of landscape characteristics as well. This study was conducted in a landscape where the proportion of pomefruit orchards is high but variable (see supplementary material S1). Since the codling moth is a specialist of these orchards, conditions were favourable for detecting a correlation between population densities and landscape characteristics (Wiegand 1999). We indeed found such a correlation. The spatial distribution of organic orchards that were few and grouped together in the area, thus creating possible confusion between local and landscape effects of organic production, may explain why we did not find any effect of their distribution on the number of codling moths. Similarly, abandoned orchards may have been too few for small effects to be detected. Unfortunately, these characteristics of the spatial distribution of organic and abandoned orchards are likely to be frequent, at least in European agricultural landscapes. Furthermore, studying landscape effects on pest populations is not easy because detection of landscape impacts on pests may be hindered by local management that largely controls population levels.

The need for management of dispersing pests over larger areas than that of the orchard is now well established (Calkins and Faust 2003). In this study, we investigated distances from 50 to 500 m in order to approximate the best scale for managing codling moth populations. Some landscape characteristics such as the proportion of pomefruit orchards had an impact on the number of codling moths for all these distances. However, both correlations and linear models suggest that landscape variables mainly influence the number of codling moths for distances up to 150 m. This is consistent with the order of magnitude of codling moth dispersal that we had chosen beforehand for the calculation of the connectivity based on a literature review.

In conclusion, our findings indicate that coordination of management (e.g. synchronisation of treatments) should be considered for areas of at least 16 ha (focus orchard of 1 ha and a 150 m buffer). This surface area is larger than that recommended by local technical advisers who advocate a minimum area of about 4 ha for mating disruption. They confirm that managing the spatial distributions of orchards and of the hedgerow network over such areas may help fight against codling moth. However, a better understanding of the underlying mechanisms is still necessary to make recommendations within a context of reduction of pesticide use.

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