UNIVERSITÀ DEGLI STUDI DI PADOVA

Department of Agronomy, Food, Natural Resources, Animals and Environment

(DAFNAE)

DOCTORAL COURSE IN CROP SCIENCE

XXX CYCLE

Spatio-temporal dynamics of Drosophila suzukii: A landscape perspective

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Academic Year 2016/2017

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Legnaro, 30 October 2017 Giacomo Santoiemma

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Summary

Landscape processes play a fundamental role in pest population dynamics. In particular, natural and semi-natural habitats, despite delivering important ecosystem services, can also support insect pest populations by providing refuge during pesticide applications, suitable overwintering sites and availability of alternative host plants. Against this background, my PhD thesis aimed at investigating the relationship between the distribution and damage of *Drosophila suzukii*, an invasive polyphagous pest, and landscape processes at multiple spatial scales. *D. suzukii* recently invaded Europe causing considerable economic damage on several thin-skinned fruits. The management of this pest is particularly complex due to its high dispersal potential, mobility and polyphagy.

In Chapter 2 and 3 we studied the influence of landscape complexity on *D. suzukii* distribution and crop damage. During the growing season, semi-natural habitats enhanced population density and damage in cherry orchards. In particular, orchards within forested-dominated landscape appeared to be more susceptible to *D. suzukii* attacks.

In Chapter 4 we examined at large geographical scale the temporal dynamics and synchronization of *D. suzukii* activity along steep elevational gradients in Alpine environments. Due to the high dispersal potential and mobility, the insect revealed an extremely high synchronization of population fluctuations across different locations and elevations.

In Chapter 5 we introduced a preliminary meta-analysis work to evaluate how a large number of insect pests respond to landscape composition. Consistently with previous findings on *D. suzukii*, we found a positive relationship between pest density and landscape complexity.

Considering the emerging problems linked to the invasion of *D. suzukii* and other invasive generalist pests across several temperate countries, our work emphasized the need to incorporate landscape processes to understand the spatio-temporal dynamics of pest populations across complex landscapes.

Riassunto

La composizione del paesaggio svolge un ruolo fondamentale nel controllo delle dinamiche degli insetti. Gli habitat naturali e semi-naturali, nonostante siano fonte di importanti servizi ecosistemici, forniscono siti di svernamento ottimali nonché un'ampia gamma di piante ospiti per numerose specie dannose alle colture. In tal modo possono potenzialmente favorire un aumento delle densità di popolazione di queste specie, promuovendo la loro diffusione nel territorio. A questo proposito, il presente lavoro di tesi si propone di approfondire la relazione tra la distribuzione e il danno di una specie invasiva polifaga, *Drosophila suzukii*, e l'ambiente fisico circostante. *D. suzukii* è un insetto approdato di recente in Europa, provocando ingenti danni economici su diversi piccoli frutti di interesse commerciale. La gestione di questo carpofago è particolarmente complessa a causa del suo elevato potenziale dispersivo e della sua polifagia.

Nei capitoli 2 e 3 si è studiato l'effetto della composizione del paesaggio sulla distribuzione di *D. suzukii* e sul danno provocato alle coltivazioni. Nel corso della stagione vegetativa, la marcata presenza di habitat semi-naturali ha fortemente influenzato la risposta del carpofago, con conseguente incremento della densità di popolazione. In particolare, i ceraseti situati in zone boschive sono risultati essere i più attaccati dall'insetto.

Nel capitolo 4 è stato attuato un monitoraggio a grande scala geografica al fine di determinare le dinamiche temporali e la sincronizzazione dell'attività di *D. suzukii* lungo gradienti altitudinali in ambiente alpino. A causa dell'elevato potenziale di dispersione, la sincronizzazione dell’attività delle popolazioni dell'insetto è risultata essere estremamente elevata sia a grandi distanze che a quote molto diverse.

Nel capitolo 5 è stato svolto un lavoro preliminare di meta-analisi atto a valutare la relazione tra gli insetti dannosi alle colture e la composizione del paesaggio. Coerentemente con quanto ottenuto dai precedenti studi su *D. suzukii*, si può osservare come un'alta presenza di habitat naturali e semi-naturali nel paesaggio comporti un aumento delle densità di popolazione di queste specie.

Considerando i problemi emergenti legati al recente arrivo di *D. suzukii* ed altre specie invasive in zone temperate, questo lavoro sottolinea la necessità di approfondire lo studio dei potenziali effetti che la composizione paesaggistica può avere sulle dinamiche spazio-temporali delle popolazioni di insetti invasivi.

Chapter 1

Introduction

Landscape effects on insect pests

Increasing landscape complexity is a key intervention to achieve sustainable pest control (Bianchi et al., 2006; Rusch et al., 2016). The available evidence indicates that landscape complexity in agro-ecosystems matters more to natural enemies than to pests (Chaplin-Kramer et al., 2011). Landscape complexity could be defined either as the amount of natural, semi-natural or non-crop habitats in the landscape surrounding a crop habitat (Thies and Tscharntke, 1999), or the diversity/heterogeneity of habitats around the crop (Östman et al., 2001). In particular, landscape composition could directly impact pest dynamics through bottom-up processes, or indirectly by affecting its natural enemies (Veres et al., 2013). Concerning the direct effects on pests, the expectations are that landscape complexity should reduce pest abundance mainly by improved biocontrol (Bianchi et al., 2006), and/or by increasing the cover of unsuitable habitat and dispersal barriers (Bhar and Fahrig, 1998). Despite these expectations, there is no clear empirical evidence about the negative effect of increasing landscape complexity on pest abundance and crop damage (Veres et al., 2013). Theoretical and empirical studies demonstrate that pest density should decline as the area or connectivity of host habitat is reduced (Rand et al., 2014). However, these expectations are largely based on the response of pests with high host specialization, while the response of pests feeding on multiple crops and using multiple habitats can be more complex (Chaplin-Kramer et al., 2011; Tscharntke et al., 2016).

Among generalist pests, invasive species usually arrive to a new area without their coevolved predators, parasites, and pathogens and, by escaping from these mortality agents, often increase and spread rapidly in the new environment (Tscharntke et al., 2016). In some cases, natural and semi-natural habitats proved to be a suitable environment, in terms of both abiotic and biotic factors, for a large number of pest species at several key stages of their life-cycle (Blitzer et al., 2012; Carrière et al., 2012; Midega et al., 2014; Parry et al., 2015; Power and Mitchell, 2004; Rusch et al., 2013; Wisler and Norris, 2005).

Among invasive generalist species, *Drosophila suzukii* is a polyphagous crop pest that originated in South-East Asia. In recent years, the insect rapidly invaded USA and Europe causing severe yield losses (Lee et al., 2011b; Walsh et al., 2011). A large body of research on *D. suzukii* is now available, primarily focusing on crop damage, control measures and potential for biocontrol. However, little is known on how the landscape composition surrounding the crop can affect the distribution and damage of the pest.

Model species

Origin, distribution and dispersal potential

Drosophila suzukii (Matsumura, 1931), also known as Spotted Wing Drosophila (SWD), is a polyphagous invasive crop pest native of South-East Asia. The pest has been introduced in Spain, Italy and North America in 2008 (Calabria et al., 2012; Cini et al., 2012; Hauser, 2011) and it is now widely distribute in large part of Europe and Unites States (Dos Santos et al., 2017). The insect reveals a high dispersal potential both active, moving up to 1400 km/year, and passive through the trade of infested fruits and plants (Calabria et al., 2012; Hauser, 2011; Westphal et al., 2008). The high adaptability to different climates and wide host range are key factors of the successful establishment. SWD invasion is partly due to a series of adaptations to temperate climates (Rota-Stabelli et al., 2013). For instance, the species is freeze-intolerant and chill-susceptible (Enriquez and Colinet, 2017) but has a large thermal tolerance plasticity which likely favors its overwintering (Jakobs et al., 2015). The pest is highly mobile and opportunistic moving rapidly from one habitat to another when resources are not accessible or in decline (Mitsui et al., 2010) and exploiting a wide number of host plants, either wild or cultivated (Kenis et al., 2016). Along with its high fertility, these traits increase the likelihood of a rapid spread of the insect globally (Walsh et al., 2011), resulting in a great economic concern for the world fruit production.

Morphological traits and biological cycle

The adult fly (Diptera: Drosophilidae) has a length of 2-3 mm and a wingspan of 6-8 mm. It has red eyes and exhibits a yellowish brown thorax, darker in winter morphs (Shearer et al., 2016), with unbroken black stripes on the abdomen (characteristic of the subgenus *Sophophora*). The species shows a clear sexual dimorphism (Fig. 1). Males display a dark spot on the leading top edge of each wing and one pair of sex combs on the foretarsi. Females are on average larger than males and possess a sclerotized, hard, shiny and dark ovipositor with strong serrations of teeth, saw-like edge when fully exposed (Fig. 2) (Kanzawa, 1939; Vlach, 2010; Walsh et al., 2011). The particular ovipositor, peculiarity of this drosophilid species, allows flies to pierce through ripening skin fruit and lay their eggs into a very large host range (Enriquez and Colinet, 2017; Kenis et al., 2016). Females lay between 7 and 16 eggs each day, for a total of 350-400 eggs during their lifecycle (Tonina, 2016). Eggs are provided with two filamentous spiracles, which leak from fruit skin ensuring the oxygen supply (Kanzawa, 1939; Walsh et al., 2011). Larvae have three instars, large from 0.5 to 4 mm, and feed on decaying tissues of fruits. The pupation can take place directly in the fruit or externally in close proximity (Walsh et al., 2011). The duration of the cycle is dependent on temperature (Tochen et al., 2014). At constant temperature of 15°C SWD completes the cycle in 21-25 days; at 25°C in 9-11 days (Kanzawa, 1939; Walsh et al., 2011). In one year, the species completes up to 13 generations, according to the climatic zones (Tonina, 2016).

Effect of climate on life history

Adults are particularly tolerant to cold temperatures than other drosophilid species (Kimura, 1988). Ideal temperature range for reproduction lies between 10 and 30°C, with the highest fertility rate at around 20-25°C. Above 30°C, males become sterile and cease reproducing (Tonina, 2016; Walsh et al., 2011). The overwintering phase of the adult stage begins when winter temperatures drop below 5°C. During this phase, adults can live 200-300 days due to reduced metabolism (Dreves et al., 2009). To avoid freezing damage, the species usually finds shelters within habitats with ideal microclimatic conditions (i.e. buffered temperatures) as natural and semi-natural habitats (Pelton et al., 2016; Zerulla et al., 2015).

Impact on crop and wild plants and control strategies

In recent years, various studies documented the presence of this polyphagous species on several host plants, which fruits are characterized mainly by soft skin (Grassi et al., 2011; Kenis et al., 2016; Lee et al., 2011b; Seljak, 2011; Walsh et al., 2011). Among cultivated plants, SWD can cause considerable economic damage on sweet cherry, strawberry, blueberry, raspberry and, to a lesser extent, grape (Ioriatti et al., 2015; Lee et al., 2011a; Tochen et al., 2014). Laying eggs, females cause small skin lacerations and, within a couple of days, the affected fruits collapse up to a complete disintegration of internal tissues (Tonina, 2016). A consistent infestation leads to a total depreciation of the commercial value of the damaged fruits (Bolda et al., 2010). While it is difficult to estimate economic damage because of significant gaps in scientific knowledge about SWD biology and control (but see Goodhue et al., 2011; Hauser, 2011), in USA yield loss (estimates from 2009 observations) range from negligible to 80% (Walsh et al., 2011). In Trentino and Verona regions (Italy), SWD attack can lead to crop losses of 30-40% (up to

90% in sweet cherry), with annual costs estimated at € 3-5 million on an average revenue of € 30 million per year (De Ros et al., 2013; Grassi et al., 2011; Ioriatti et al., 2015).

The main measures adopted to control the insect damage to crops are specific chemical control, mass trapping and insect-proof nets (Ioriatti et al., 2015; Kawase et al., 2007; Van Timmeren and Isaacs, 2013). These measures often entail high environmental and economic costs. Moreover, the pest may find refuge and sustain populations in semi-natural habitats, due to the high mobility and dispersal (Calabria et al., 2012; Hauser, 2011). Several wild host plants, among which the genera *Cornus*, *Prunus*, *Rubus* and *Sambucus*, proved to be the highest sources of infestation (Kenis et al., 2016). In view of this, biological control may prove to be the best strategy for a long-term containment of the species. Numerous studies have investigated the effectiveness of natural enemies as parasitoids and predators, which can help to reduce large reservoir populations of SWD from semi-natural areas surrounding crop fields. (Chabert et al., 2012; Cini et al., 2012; Knoll et al., 2017; Rossi Stacconi et al., 2017; Woltz and Lee, 2017). Two different approaches have been taken into consideration so far. The first relies on the introduction and permanent establishment of natural enemies hailing from the SWD native range, among which *Asobara japonica* Belokobylskij (Hymenoptera: Braconidae) *Ganaspis brasiliensis* Ihering and *Leptopilina japonica japonica* Novković and Kimura (Hymenoptera: Figitidae) (Cini et al., 2012; Daane et al., 2016). However, this approach is complicated by very strict laws regulating the importation of alien species, even as biocontrol agents. The second approach is based on the enhancement of parasitoid species already present in newly invaded areas, e.g. *Pachycrepoideus vindemiae* Rondani (Hymenoptera; Pteromalidae), *Trichopria drosophilae* Perkins (Hymenoptera; Diapriidae) and *Leptopilina heterotoma* Thomson (Hymenoptera; Figitidae). These populations, according to the Enemy Release Hypothesis (Keane and Crawley, 2002), may gradually adapt to the new host, establishing and strengthening new associations with the pest, thus contributing to its demographic control. However, the adaptation process of local natural enemies requires a variable amount of time, depending on the parasitoid plasticity level (Chabert et al., 2012; Rossi Stacconi et al., 2017).

Aims

My PhD thesis focused mainly on SWD spatio-temporal dynamics across different habitats, investigating the key factors that promote the spread and damage of the pest at different spatial scales.

Chapter 2 investigates the seasonal distribution of SWD across forest, grassland and vineyard habitats along a gradient of semi-natural habitats characterized by different proportions and edge lengths in the landscape.

Chapter 3 focuses on SWD population dynamics and damage on cherry orchards surrounded by different proportions of semi-natural and crop habitats in the landscape.

Chapter 4 studies the temporal dynamics and synchronization of the activity of SWD populations along steep elevational gradients in Alpine environments, describing the distribution of SWD outside crop-dominated landscapes.

Chapter 5 aims, with a meta-analysis, to evaluate how insect pests respond to landscape composition, so extending my work on SWD to a large number of species.

Chapter 6 provides a summarizing discussion on the research findings.

FIGURES

Fig. 1. Female (on the left) and male (on the right) of SWD.

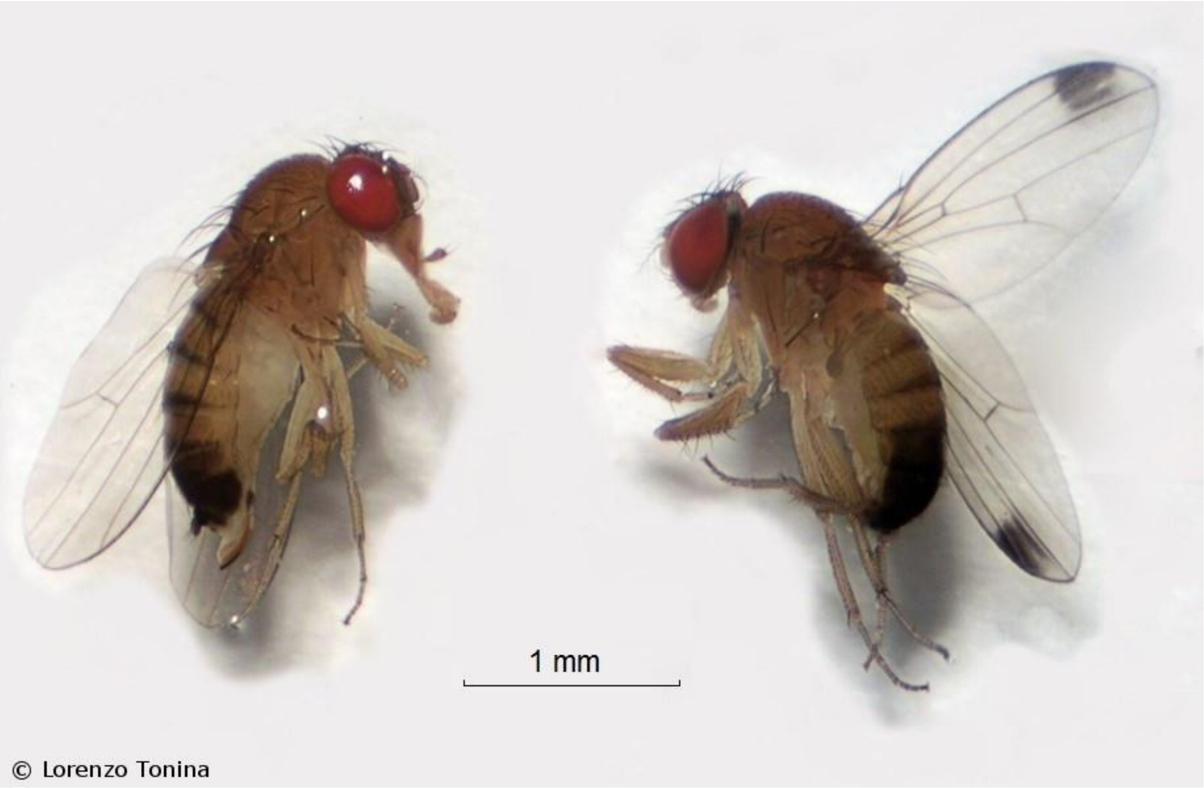

Fig. 2. Ovipositor of an adult SWD female (Hirox Digital Microscope RH-2000, Simitecno S.r.l.).

Chapter 2

Habitat use and movement of *Drosophila suzukii* across heterogeneous landscapes

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Abstract

In temperate regions, generalist insect pests are expected to use multiple habitats and host species over the different seasons. In particular, landscape composition and configuration can provide a diversity of thermal resources and host plants that can modify insect activity and movement. Here, we tested the seasonal response of a destructive invasive pest, Spotted Wing Drosophila (SWD), to landscape composition (i.e. proportion of forest habitat) and configuration (i.e. length of forest edge). We selected a triplet of habitat patches (forest, vineyard and grassland) in 17 landscapes in North-eastern Italy characterized by different proportions of forest and forest edge length and monitored pest activity for one year in the three habitats. We found that SWD moved from open to forest habitats during the cold season while SWD occurred equally in the three habitats during plant growing season. In summer, when high temperatures can be limiting, landscapes with large forest edge length presented an increase in activity density suggesting a large spill-over between crop and non-crop areas. In light of these results, one can assume that pest control in crop fields located in landscapes with complex configurations can be particularly challenging. The high density in non-crop areas suggests that this invasive species can have pervasive impact also on wild plant species occurring in semi-natural and natural habitats.

Keywords

Drosophila suzukii; Forest; Invasive pest; Landscape configuration; Spill-over; Vineyard.

Introduction

Seasonal variation in climatic variables such as temperature, rainfall and moisture are known to affect individual physiology, behaviour, and population dynamics of ectothermic organisms (Hodkinson, 2005). As small, poikilothermic organisms, insect pests are especially sensitive to temperature fluctuations (Block et al., 1990). Extreme weather events, such as unusually hot or dry conditions, can cause mortality by exceeding physiological limits or reduced fitness. Survival and fitness will also depend on whether or not susceptible organisms can find thermal resources to buffer extreme conditions (Scheffers et al., 2014). Behavioural adaptations such as habitat selection, dispersal or thermoregulatory movements can be crucial individual responses to cope with a thermal changing environment (Deutsch et al., 2008). In this context, heterogeneous landscapes provide a diversity of thermal resources that can modify the environmental temperature effect on the reproductive success and distribution of mobile organisms (Sears et al., 2011). For instance, the presence of semi-natural habitats such forest or hedgerows in open agricultural landscapes can modify the local microclimate buffering extreme temperatures compared to homogenous crop-dominated landscapes.

In this context, generalist insect pests that use multiple habitats and host plants can experience different operative temperatures, depending on the physical environment such as the composition (i.e. proportion of habitat types) and configuration (i.e. edge length of habitat types) of the landscape mosaic or topographic relief (i.e. elevation). Furthermore, this variation in abiotic factors can be modulated by potential thermoregulatory behaviours that many animals use to balance heat loads (Sears et al., 2011). Although the increase of natural and semi-natural habitats in the landscape is often advocated as a key mitigation strategy to improve biodiversity and ecosystem services (Schellhorn et al., 2014), they can also provide suitable habitats for pest populations (Chaplin-Kramer et al., 2011). For instance, natural habitats can represent ideal overwintering habitats for several insect pests, providing buffered microclimatic conditions in winter, or shelter areas from extreme high temperatures in summer (Sivakoff et al., 2013; Tscharntke et al., 2016). Investigating the spatio-temporal distribution of generalist pests across the whole landscape and their response to climate seasonal variation is essential to improve our understanding of pest dynamics.

To test how seasonal pest population dynamics is affected by the proportion and edge length of forest habitat in the landscape, we used the Spotted Wing Drosophila (SWD) (*Drosophila suzukii* Matsumura, 1931) as a model species. Among generalist pests, SWD is a destructive invasive pest attacking on a wide range of thin-skinned fruits causing severe yield losses in Europe and North America (Walsh et al., 2011). The species presents multiple generations and is active most of the year. Temperature is a key factor affecting population dynamics of SWD (Wiman et al., 2014). First, winter cold temperatures represent a limiting factor in the geographic range of several *Drosophila* spp. (Andersen et al., 2015; Kimura, 1988). Overwintering individuals can more likely survive cold in temperate climes if they find a refuge to escape the cold, such as under snow or in sheltered forest habitat. Second, SWD is strongly limited by high temperatures, particularly in dry conditions (Enriquez and Colinet, 2017). The limiting temperatures for oviposition are below 10 and above 32°C and above 30°C for male fertility (Sakai, 2005). The impact of such effects assume that an insect can experience the same temperatures irrespective of landscape heterogeneity. These predictions ignore how the spatial distribution of thermal resources constrains species performance and fitness over space and time (Sears and Angilletta, 2015).

Here, we aim at describing SWD activity within three different habitat types dominant in the study region (forest, grassland, and vineyard) along a landscape gradient of semi-natural habitats (increasing cover of forest and increasing forest edge length). The three habitats provide very different host plants and thermal resources to SWD. First, we hypothesized a directional movement from crops to woodlands during the non-growing season, while the pest should move to the crop when the host plants are available. Forests should sustain pest density by providing microclimatic refuges during winter (Briem et al., 2017). Second, we expected that increasing forest edge in the landscape should reduce the negative effect of summer temperatures on SWD (Enriquez and Colinet, 2017; Mitsui et al., 2010). High amount of edges between forest and other habitats is expected to facilitate the spill-over from forests to crop favouring the species activity (Duflot et al., 2014; González et al., 2016; Tscharntke et al., 2005).

Materials and Methods

Study area

We carried out the study within an area of c. 100 km^2 in the Valpolicella hills (province of Verona, N 45°31’, E 11°58’). The area is a wine grape-growing region. The climate is mostly continental. The maximum temperatures in the growing season are usually between 25 and 30°C, while the minimum temperatures ranges between 18 and 20°C, with average rainfall around 860 mm. The elevation of the study area ranges from 190 to 570 m a.s.l. The landscape of the sampling area was characterized mainly by six habitat types: forest (average cover about 40%), grassland (20%), vineyard (15%), urban (10%), olive (5%) and cherry orchard (5%). The forests were mainly composed of broad-leaf species among which the most common are *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Quercus pubescens* Willd., *Acer campestre* L., *Robinia pseudoacacia* L., and *Prunus mahaleb* L. The forests are coppiced every 25-30 years with small clear-cut (<0.5 ha). Red grape varieties (Corvina, Corvinone, Rondinella) are dominant in this region.

Sampling design

Seventeen landscapes (0.5 km radius) were selected after a preliminary screening realized by using Google Earth Pro (© 2015, Google Inc.). Within each landscape, three sites representing forest, vineyard and grassland habitats were selected. The three sites were separated by no more than 100 m and were located around the centre of each landscape (Fig. 1). The landscape composition within a 0.5 km radius around the three selected habitats was quantified. The scale was selected according to a study where multiple scales were evaluated (Chapter 3 in this thesis). Forest, grassland and vineyard patches were manually digitized in Google Earth Pro (Google Inc. ©, 2015) from a visual inspection of high-resolution satellite images. In Quantum GIS 2.14 (QGIS Development Team, 2014), we quantified percentage cover of the habitats. Forest cover ranged from 10 to 70%, grassland cover from 3 to 50%, vineyard cover from 4 to 55%. In each landscape, we quantified total edge length of forest patches, i.e. total length of forest edge bordering non-forest habitats, using FRAGSTATS 4.2 (McGarigal et al., 2012). Edge length ranged from c. 4,400 to 15,000 m. The landscapes were chosen ensuring that the mean elevation, forest cover and forest edge were not correlated (Pearson correlation indexes: elevation-forest cover = -0.02, elevation-forest edge = 0.36, forest cover-forest edge = -0.21), in order to avoid collinearity between elevation and our landscape metrics. The difference in elevation among landscapes results in a temperature variation among landscapes (Rolland, 2003). As temperature can control insect activity and density, our design allowed separating the effect of forest from the effect of temperature. The presence of urban patches and waterways across the landscapes was negligible. Therefore, we did not consider them as covariates in the study.

Insect sampling

Biobest red traps (Droso-Trap® by Biobest) were placed in the 51 sites across the 17 landscapes, at least 20 m from the habitat border and at c. 1.5 m above the ground. The traps were lured with Suzukii Trap® (Bioibérica S.A.) attractant, highly selective for SWD (Tonina et al., 2017). The lure was replaced once per month. The sampling started in March 2015 and ended in February 2016. Every two weeks the content of the traps was collected, preserved in ethanol (70% v/v), and the number of individuals was determined in the laboratory. In three cases the sampling interval was of four weeks.

Climate data

For each sampling period, we quantified the mean regional air temperature by averaging the mean regional daily values. Data were collected from the closest meteorological station (Grezzana, 156 m a.s.l.), managed by ARPAV (Regional Agency for Environmental Protection). Due to the focus on the seasonal variation in SWD activity, we did not correct the mean regional temperature for the elevation. We instead included explicitly elevation in the model to describe the seasonal fluctuations at different elevations.

Statistical analyses

To test the effects of landscape metrics and environmental variables we used general linear mixed models (GLMM) because residuals approximated a normal distribution and exhibited homoscedasticity. We adopted a multi-model inference approach (Burnham and Anderson, 2002) to evaluate the role of the selected variables in explaining patterns of SWD abundance. The response variable was the number of SWD individuals per trap obtained for each sampling event, divided by the effective number of days of each sampling and ln-transformed to improve linearity. The explanatory variables were habitat type (grassland, forest and vineyard), temperature, elevation, forest cover, forest edge and the interactions between habitat and temperature, forest cover and temperature, forest cover and elevation, forest edge and temperature, forest edge and elevation, elevation and temperature (as we also hypothesized an elevational shift over the season). We included only interactions that were linked to clear ecological hypotheses. The explanatory variables were standardized by subtracting their mean and dividing by two standard deviations to make regression coefficients interpretable. Indeed subtracting the mean typically improves the interpretation of main effects in the presence of interactions, while dividing by two standard deviations puts all predictors on a common scale and allows the coefficients to be interpreted in the same way as with binary inputs (Gelman, 2008). We accounted for the nested design of our study by including landscape identity (n = 17) and site identity within each landscape (n = 51) as random factors. The GLMM model included a temporal autoregressive structure of order 1 (corAR1) to account for the temporal auto-correlation in the time-series. The corAR1 considers correlations to be highest for adjacent time points, and a systematically decreasing correlation with increasing distance between time points. From an ecological point of view, the corAR1 resulted to be the most appropriate covariance structure to fit our data. After the inclusion of the autoregressive structure, the model residuals presented very little temporal autocorrelation. Temporal auto-correlation was evaluated using the "acf" function implemented in R (R Core Team, 2017). Models were selected basing on Akaike Information Criterion (AICc), which is a measure of relative model fit, proportional to the likelihood of the model and the number of parameters used to generate it. The best fitting model is the one with the lowest AICc. In a set of *n* models, each model *i* can be ranked using its difference in AICc score with the best-fitting model ($\Delta AICc_i = AICc_i – AICc$ minimum). The difference in AICc values indicates the relative support for the different models. A model is usually considered plausible when its ΔAICc is below 2 (Burnham and Anderson, 2002). For each model *i* we also calculated an Akaike's weight, which is the probability that model *i* would be selected as the best fitting model if the data were collected again under identical circumstances (Burnham and Anderson, 2002). Akaike's weight should be interpreted as a measure of model selection uncertainty. For each variable, we also provided model-averaged coefficients and intervals of confidence (CI 95%) (Burnham and Anderson, 2004; Lukacs et al., 2010). The multi-model inference analyses were performed using the 'MuMIn' package (Barton, 2016) implemented in R (R Core Team, 2017).

Results

General results

We counted ca. 131,000 SWD individuals during the sampling. We observed a greater abundance of SWD in forest habitat from March to late April 2015, with a subsequent increase in the other habitats from June 2015 (Fig. A1 in Appendix Chapter 2). The population peak occurred in September-October 2015 in all of the three habitats, period that coincided with the harvest in vineyards. Since December 2015, a new increase of the species in forests was observed, along with a decline in grasslands and vineyards, up to a return of the initial level of abundance in February 2016.

Multi-model inference

We found relatively large model selection uncertainty, with four models included in the set with ΔAICc<2. The best models often included the main effects of habitat, temperature, forest edge, forest cover and two interactions: habitat x temperature and forest edge x temperature (Table 1). Here, temperature represented the seasonal variation signal while elevation incorporated the temperature spatial component. Habitat, temperature and the two interactions presented CI (95%) that did not overlap with 0 (Table 2). The strongest interaction, was the one between habitat type and temperature, i.e. SWD at lower temperatures (i.e. winter) showed a greater density in forest than in grassland and vineyard habitats, while at intermediate temperatures this difference decreased. The overall density was more evenly distributed at high summer temperatures, although lower than in the other seasons (Fig. 2). Second, a strong interaction was found between forest edge and temperature. The pest was not affected by forest edge length during winter, whereas during summer its density increased with increasing edge length in the landscape (Fig. 3). We found no support of the effects of forest cover in the landscape and elevation.

Discussion

We showed that SWD moved from open to forest habitats according to the season, i.e. forest was used for overwintering while during plant growing season SWD explored equally forest and open habitats. The movement of the pest is likely to be the dominant mechanism that can explain the changes in abundance among habitats, due to its high mobility and dispersal potential (Calabria et al., 2012; Cini et al., 2012; Mitsui et al., 2010). We found no effect of forest cover in the landscape on SWD spatio-temporal dynamics. During summer, there was an increased activity density across all habitats in landscapes with large forest edge length, irrespective of the total cover of forest.

Temperature seasonal fluctuation is a key driver of pest distribution and dispersal. SWD activity is considerably reduced when temperatures drop below zero or when they exceed 28-30°C (Enriquez and Colinet, 2017; Shearer et al., 2016; Tochen et al., 2014). To avoid exposure to these limiting conditions, the insect might move across the landscapes and use different thermal habitats. In its native range, SWD is highly mobile and opportunistic moving rapidly from one habitat to another when resources are not accessible or in decline (Mitsui et al., 2010). In our case study, forest habitats resulted as the most suitable one for SWD during the cold season, probably due to ideal microclimatic conditions as overwintering sites (Briem et al., 2017; Pelton et al., 2016; Zerulla et al., 2015). The difference in activity density between habitats decreased with increasing temperatures during the plant growing season. This could be attributable to both a reduction of pest activity in forests and a movement towards open areas, i.e. vineyards and grasslands (Calabria et al., 2012; Cini et al., 2012; Hauser, 2011). In late summer and autumn, we observed the highest density in all habitats. This was due to optimal mean temperatures, between 15 and 20°C (Tochen et al., 2014), and the presence of host plants both in vineyards and forests (among which the genera *Cornus*, *Prunus*, *Rubus* and *Sambucus*) (Kenis et al., 2016; Lee et al., 2011b).

Forest edge affected species activity over the seasons more than forest cover in the landscape. We observed an increase of pest density along with increasing edge length between forest and the other habitats, but only during summer. Edge effects can have pervasive impacts on small organisms such as insects (Blitzer et al., 2012; Ewers and Didham, 2008; Fahrig, 2003). The flow of organisms across these boundaries is known to occur between different semi-natural habitats as well as across the crop-non crop interface (González et al., 2016; Tscharntke et al., 2005). Several studies proved the importance of semi-natural edge on natural enemies (e.g. Marino and Landis 1996; Bianchi et al. 2008; Duflot et al. 2014). However, evidence suggests that hedgerows and other natural areas adjacent to crops can also be suitable habitats for a large variety of pests (Burgess, 1981; Gravesen and Toft, 1987). On the one hand, large edge length indicated landscapes with high contact zones between forest and open habitats, probably favouring spill-over of individuals (Calabria et al., 2012; Mitsui et al., 2010). On the other hand, in landscapes with large, consolidated forest patches SWD probably remained more often within the core area of forest patches.

Current SWD control in crops relies heavily on the use of insecticides with several well-known negative environmental impacts (Walsh et al., 2011). The high dispersal and mobility of the pest (Calabria et al., 2012; Hauser, 2011; Mitsui et al., 2010), together with the presence of refuge-habitats such as forests, can reduce the effectiveness of the insecticide treatments. It is therefore necessary to develop integrated pest management strategies that incorporated a landscape perspective (Chabert et al., 2012; Cini et al., 2012; Knoll et al., 2017; Rossi Stacconi et al., 2017; Woltz and Lee, 2017). Moreover, in the future changes in landscape composition and configuration can play a fundamental role in enhancing natural enemy populations (Bianchi et al., 2006; Steingröver et al., 2010). Our results indicated that pest control in crop fields located in landscape with complex configurations can be particularly challenging. Finally, the very high density in non-crop areas suggest that this invasive species might have pervasive impact on semi-natural and natural habitats.

Acknowledgments

We are grateful to the farmers who allowed us to carry out the experiments on their land. We thank Bioibérica S.A. Company and Michele Brardinelli for providing Suzukii Trap® attractant.

Funding: This work was supported by the European Union’s Seventh Framework Programme for Research, Technological Development and Demonstration, DROPSA [grant number 613678]. GS received a grant from Aldo Gini Foundation (Padova).

TABLES

Table 1. Best candidate models from the multi-model procedure explaining SWD density. Models are ranked according to their second-order Akaike's information criterion (AICc). Only models with ΔAICc<2 are shown. Pseudo-R^2, Log-likelihood (logLik) and model weights are also reported. *df* indicated the number of estimated parameters calculated as the number of fixed effect coefficients + number of variance parameters.

Rank	**Daily captures of SWD**	**Pseudo-R^2**	**df**	**logLik**	**ΔAICc**	**weight**
1	*Hab* + *Temp* + *For Edge* + *For Cover* + *Hab* x *Temp* + *For Edge* x *Temp* + *For Cover* x *Temp*	0.14	14	-1400.0	0.00	0.113
2	*Hab* + *Temp* + *For Edge* + *Hab* x *Temp* + *For Edge* x *Temp*	0.13	12	-1402.3	0.54	0.087
3	*Hab* + *Temp* + *For Edge* + *For Cover* + *Hab* x *Temp* + *For Edge* x *Temp*	0.13	13	-1401.4	0.76	0.077
4	*Hab* + *Temp* + *For Edge* + *For Cover* + *Elev* + *Hab x Temp* + *For Edge* x *Temp* + *For Cover* x *Temp*	0.14	15	-1399.9	1.90	0.044

Table 2. Model-averaged estimates and conditional confidence intervals (CI 95%) from the multi-model procedure (F = Forest, G = Grassland, V = Vineyard). Habitat F was used as baseline for the other two habitats and their interactions with temperature.

Variables	**Estimates**	**Confidence intervals**	
		2.5%	**97.5%**
Intercept	1.6983	1.4820	1.9145
Habitat G	**-0.7538**	**-1.0784**	**-0.4293**
Habitat V	**-0.6546**	**-0.9695**	**-0.3396**
Temperature	**-0.5227**	**-0.8692**	**-0.1762**
Elevation	-0.0457	-0.3308	0.2394
Forest Cover	0.1866	-0.0795	0.4528
Forest Edge	0.1847	-0.1308	0.5002
Hab G* x *Temp	**0.7882**	**0.2840**	**1.2923**
Hab V* x *Temp	**0.9946**	**0.5081**	**1.4811**
For Edge* x *Temp	**0.4813**	**0.0533**	**0.9093**
For Cover x *Temp*	0.3279	-0.1025	0.7582
Elev x *Temp*	0.3109	-0.1253	0.7471
Elev x *For Edge*	0.3012	-0.3939	0.9961
Elev x *For Cover*	-0.1834	-0.7719	0.4052

FIGURES

Fig. 1. Sampling design of the study. We sampled SWD for one year in 17 triplets of habitats (vineyard, forest and grassland) along a gradient of forest cover and forest edge length.

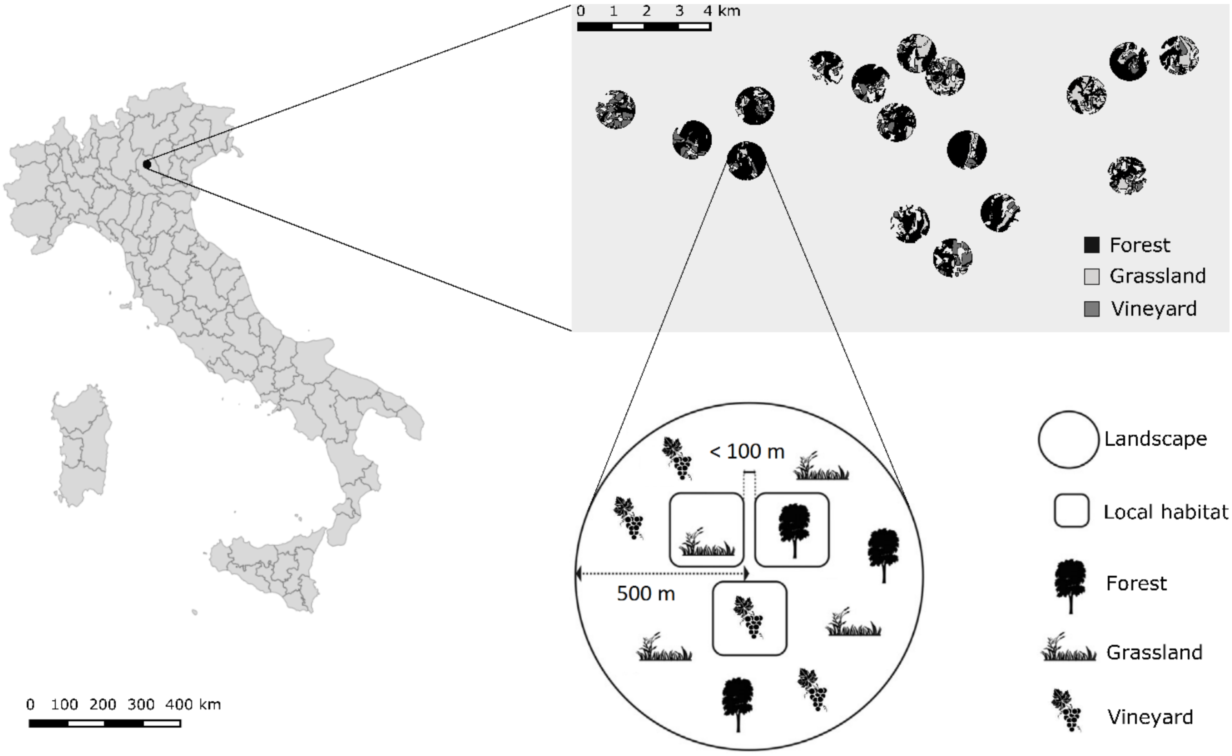


Fig. 2. Distribution of SWD (ln-normalized daily capture) in the three habitats (F = Forest, G = Grassland, V = Vineyard) at different seasonal temperatures (Low: winter, Medium: spring and fall, High: summer).

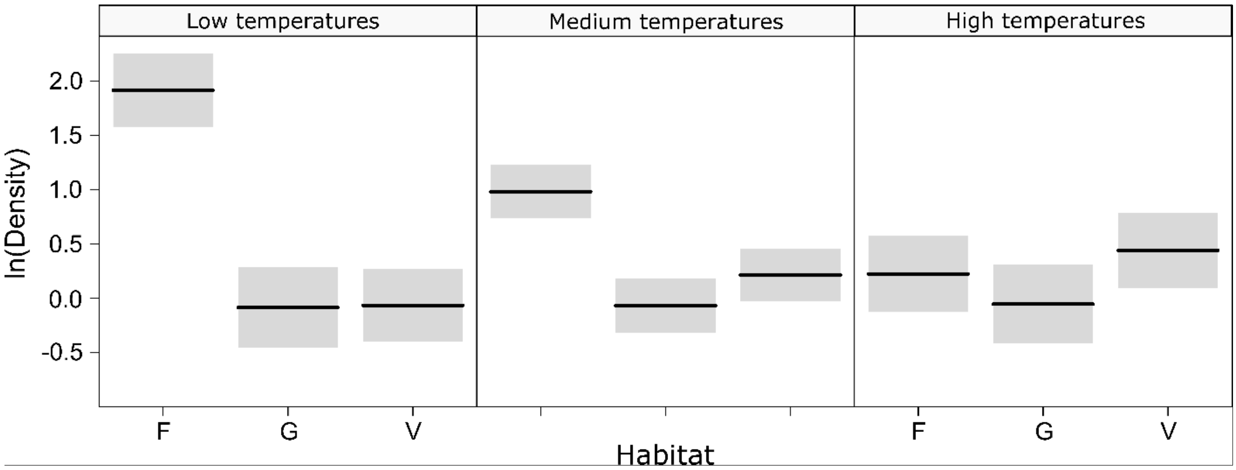
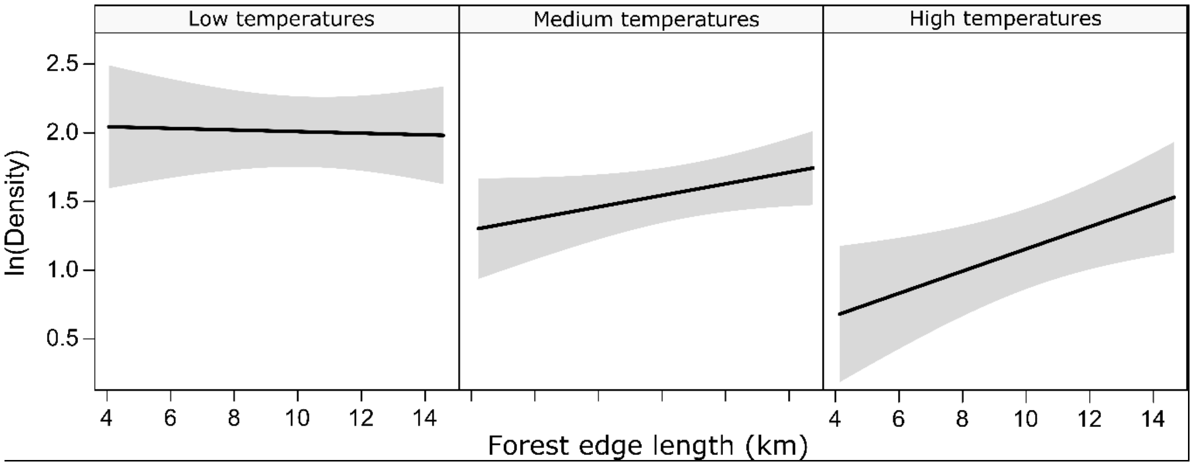
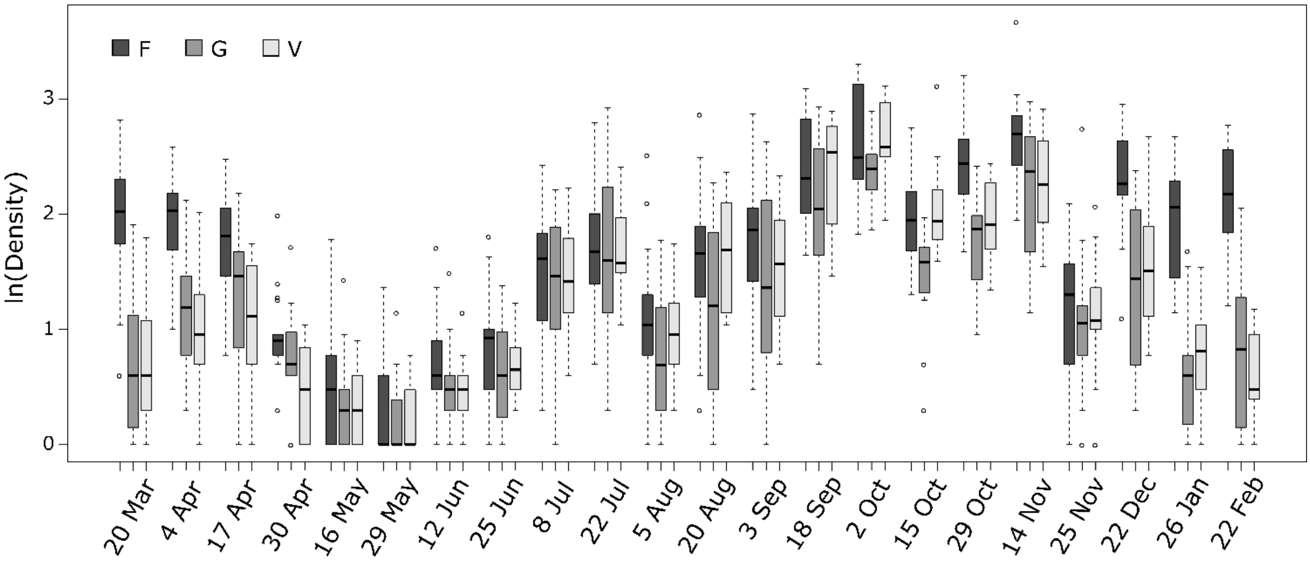


Fig. 3. Relationship between SWD density (ln-normalized daily capture) and forest edge length at different temperatures (Low: winter, Medium: spring and fall, High: summer).



Appendix Chapter 2

Fig. A1. Seasonal population dynamics of SWD in the three habitats (F = Forest, G = Grassland, V = Vineyard).



Chapter 3

Semi-natural habitats boost *Drosophila suzukii* populations and crop damage in sweet cherry*

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*Manuscript under review for Agriculture, Ecosystems & Environment

Abstract

Although increasing landscape complexity is often advocated as a key intervention to sustain pest biocontrol, little is known on how increasing semi-natural habitats surrounding the crop can directly affect the density and damage of generalist pests. Our aim was to test how semi-natural habitats in the landscape influences the density and the impact of *Drosophila suzukii* (Matsumura, 1931) (SWD) on sweet cherry. SWD is an invasive pest native of South-East Asia that causes severe yield losses in several crops worldwide. We selected 32 conventional cherry orchards in NE Italy surrounded by landscapes with different proportions of semi-natural habitats and we quantified both pest density and crop damage using sentinel fruits. We observed a larger attack density in orchards surrounded by higher forest cover. The same trend was observed for female adult density. Forest habitats can provide ideal microclimatic conditions and alternative host plants that can promote population growth. The effect size of forest cover on both adult density and crop damage, despite the very large tested forest gradient (0-60%), suggests that a reduction of forest cover is not a viable option for controlling SWD. However, current integrated pest management should take into account landscape composition and interventions should be timely in forested landscapes where SWD can quickly attack the crop at higher density.

Keywords

Cherry; *Drosophila suzukii*; Forest; Generalist pest; Invasive pest; Landscape.

Introduction

Increasing landscape complexity is often advocated as a key intervention to achieve sustainable pest control (Bianchi et al., 2006). The available evidence indicates that landscape complexity in agro-ecosystems matters more to natural enemies than to pests (Chaplin-Kramer et al., 2011). Landscape composition, in particular, could either directly impact pest dynamics through bottom-up processes or indirectly by affecting its natural enemies (Veres et al., 2013). Concerning the direct effects on pests, the expectations are that landscape complexity should reduce pest abundance mainly by improved biocontrol (Bianchi et al., 2006), and/or by increasing the cover of unsuitable habitat and dispersal barriers (Bhar and Fahrig, 1998). Despite these expectations, there is no clear empirical evidence about the negative effect of increasing landscape complexity on pest abundance and crop damage (Veres et al., 2013), but see (Rusch et al., 2016). Theoretical and empirical studies demonstrate that pest density should decline as the area or connectivity of host habitat is reduced (Rand et al., 2014). However, these expectations are largely based on the response of pests with high host specialization, while the response of pests feeding on multiple crops and using multiple habitats can be more complex (Chaplin-Kramer et al., 2011).

Among generalist pests, invasive species usually arrive to a new area without their coevolved natural enemies. By escaping from these mortality agents, invasive species often spread rapidly in the new environment (Gariepy et al., 2014; Tscharntke et al., 2016; Wolfe, 2002). As generalist pests can use multiple host plants and use multiple habitats, increasing landscape complexity can provide more suitable conditions compared to landscapes dominated by a single crop (Tscharntke et al., 2016). Among invasive generalist pests, the Spotted Wing Drosophila (SWD) (*Drosophila suzukii* Matsumura,

1931) is a polyphagous invasive crop pest that originated in South East Asia. In recent years, SWD rapidly invaded large areas of the USA (Lee et al., 2011b) and Canada, as well as most of European countries causing severe yield losses (Walsh et al., 2011). The species is one of the most serious pests of commercial fruits such as cherry, blueberry, raspberry and strawberry (Ioriatti et al., 2015; Lee et al., 2011a; Tochen et al., 2014). A large body of research on SWD is now available, primarily focusing on population dynamics, crop damage (Harris et al., 2014; Lee et al., 2011b), control measures (Cuthbertson et al., 2014; Van Timmeren and Isaacs, 2013) and potential for biocontrol (Chabert et al., 2012; Rossi Stacconi et al., 2013). However, little is known on how landscape composition surrounding the crop can affect the distribution and damage of pests (Papadopoulos et al., 2003; Sciarretta and Trematerra, 2014, 2011). To fill this gap, we aimed to test whether the landscape composition surrounding the cherry orchards influences the density of SWD and the associated crop damage. In particular, we wanted to investigate the link between pest abundance, crop damage and the presence of semi-natural habitats.

Here, we tested the effect of forest and crop cover in the landscape on the SWD population and attack dynamics in sweet cherry (*Prunus avium* L.). We expected a positive effect of forest cover in the landscape on pest population and crop damage. We expected that forest areas should sustain higher pest density for four main reasons. First, forests represent overwintering habitats for the pest (Zerulla et al., 2015). Second, they provide suitable micro-climatic conditions during summer, e.g. high humidity levels (Tochen et al., 2016). Third, they supply multiple suitable hosts for the development of SWD (Kenis et al., 2016; Lee et al., 2015; Ramsden et al., 2014). Last, they can act as habitat refuges when crops are sprayed with insecticides (Kenis et al., 2016). Due to these potential roles of semi-natural habitats in driving pest population, it is crucial to investigate the influence on surrounding non-crop vegetation on pest population and associated damage in multiple crops and regions. We do not expect any positive effect of forest areas in sustaining species that can counteract the spread of the pest, due to the current lack of specialist and effective natural enemies in our territory (Chabert et al., 2012). Considering the crop cover in the landscape, we hypothesize a reduction of SWD abundance and damage with increasing orchard cover, despite being an host resource, due to the high pesticide pressure over crop-dominated landscapes (Vreysen et al., 2007).

Materials and Methods

Study area

The study was conducted in a hilly area of c. 200 km^2 (Valpolicella, Valpantena and Val di Mezzane). The region is a grape and cherry-growing zone of the province of Verona (NE Italy). During the growing season, maximum temperatures are usually between 25 and 30°C, while the minimum temperatures range between 18 and 20°C. Annual average annual rainfall is around 860 mm. The elevation of the study area ranges from 190 to 570 m a.s.l. The landscape of the sampling area was characterized mainly by the dominance of six habitat types: forest (average cover about 40%), grassland (20%), vineyard (15%), urban (10%), olive (5%) and cherry orchards (5%). The forests are mainly composed of broadleaf species among which the most common are *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Quercus pubescens* Willd., *Acer campestre* L., *Robinia pseudoacacia* L., and *Prunus mahaleb* L. The forests are coppiced every 25-30 years with small clear-cut (<0.5 ha).

Sampling design

Thirty-two cherry orchards surrounded by different forest and cherry cover were selected after a preliminary screening realized by using Google Earth Pro (Google Inc. ©, 2015). The quantification of landscape composition was made within a 250, 500 and 1000 m radius buffer around each cherry orchard (Fig. 1). For each buffer, forest, vineyard and cherry orchard patches were manually digitized from a visual inspection of high-resolution satellite images (Google Earth Pro). In QGIS 2.14 (QGIS Development Team, 2014), we quantified the area of each patch and then we calculated the cover percentage of habitats at the three landscape scales (see Table A1 in Appendix Chapter 3). The landscapes were chosen ensuring that the mean elevation and the forest cover were uncorrelated (Table A2 in Appendix Chapter 3). As temperature can control insect activity and density, our design allowed separating the effect of forest cover from the effect of temperature (due to differences in elevation). However, mean elevation resulted, respectively, slightly negatively and positively correlated with vineyard and cherry orchard cover (Table A2 in Appendix Chapter 3). The 32 cherry orchards had mixed cherry varieties, among which the main ones were Adriana, Giorgia (early maturation), Mora Di Cazzano, Van, Black Star (medium maturation), Regina and Ferrovia (late maturation). The orchards were conventionally managed and were sprayed with commercial ovicide-larvicides against SWD during the experiment. All the farmers were contacted and interviewed about the management of their orchard.

Adult insect sampling

In the centre of the cherry orchard, a Biobest red trap (Droso-Trap® by Biobest) was placed and hung at about 1.5 m from the ground. The red traps were lured with Droskidrink attractant (75% apple cider vinegar, 25% red wine, 20 g l^{-1} sugar), specific for SWD (Grassi et al., 2014). The attractant was replaced every week. The sampling started on the 16th of May 2016 and ended on the 10th of June 2016. Each sampling round lasted either three or four days (constant duration within each round), with a total of seven consecutive monitoring rounds. The first round (16th-19th May) occurred at the beginning of fruit colouring phase. The last one (7th-10th June) occurred after cherry harvest (no fruits left on trees). At each round, the content of the traps was collected, preserved in ethanol (70% v/v), and the number of individuals (males and females) was determined in the laboratory. During the sampling period the minimum daily temperature recorded was 14°C and the maximum was c. 20°C. The cumulative rainfall was 176.5 mm (data collected from the local weather stations of Grezzana, 156 m a.s.l.).

Crop damage quantification

In each site (n = 32), to quantify crop damage 20 pesticide-free and un-infested cherries were exposed into an anti-bird cage (mesh 5 x 5 mm, hung at about 1.5 m from the ground). The cages were located within the cherry orchard at least 10 m from the closest edge. To avoid interference with the trap attractant, the cages were at least 20 m away from the adult traps. The sentinel fruits were collected from an experimental cherry orchard (San Floriano, Verona province). The experimental orchard was not sprayed with pesticides and included several early-flowering varieties (Early Magyar, Sweet Early, Isabella, Adriana, Giorgia). Several trees were covered with fine anti-SWD net before the fruit colouring phase of the fruits (at the end of April) and treated with a fungicide to prevent *Monilia* fungi development. The sentinel fruit exposure was simultaneous with the adult monitoring (see above) for a total of seven sampling rounds. When the adult traps were collected also the sentinel fruits were collected and replaced with new non-infested fruits. The fruits were inspected in the laboratory for the presence of SWD by counting the number of eggs laid. For each sampling round, the same cherry variety was exposed in all sites, while between rounds the variety changed. As the orchards were conventionally managed and we exposed the sentinel fruits continuously, in some occasions the exposed fruits were placed just before the insecticide spraying. In these cases the sentinel fruits were protected by the insecticide treatment and therefore these data points were excluded from the analyses. We omitted these points based on the farmers' interviews. All the samples excluded had no egg laid.

Statistical analyses

To test the effect of landscape variables at different spatial scales (250, 500 and 1000 m radius) on SWD populations and crop damage, we used a general linear mixed model (GLMM) because residuals approximated a normal distribution and exhibited homoscedasticity. The response variables were the number of eggs found in each fruit sample and the number of female individuals per trap. We considered adult female individuals, since they are responsible for crop damage. Data were first standardized by dividing the abundance by the days of exposure and log-transformed to improve linearity. Forest cover, cherry orchard cover, monitoring round and the interactions between the two landscape variables and monitoring round were included in the model as fixed effects while orchard identity was included as a random factor. Vineyard cover was not included in the model as it strongly negatively correlated with forest cover (Table A2 in Appendix Chapter 3). Moreover, this variable had no strong biological significance during the sampling period since grapes ripen in late summer in the region.

We fitted the models described above for each spatial scale, adopting a multi-model inference approach (Burnham and Anderson, 2002). Models were selected basing on Akaike Information Criterion (AICc), which is a measure of relative model fit, proportional to the likelihood of the model and the number of parameters used to generate it. The best fitting model is the one with the lowest AICc. In a set of *n* models, each model *i* can be ranked using its difference in AICc score with the best-fitting model ($\Delta AICc_i = AICc_i - AICc$ minimum). The difference in AICc values indicates the relative support for the different models. A model is usually considered plausible when its ΔAICc is below 2 (Burnham and Anderson, 2002). For each model *i* we also calculated an Akaike's weight, which is the probability that model *i* would be selected as the best fitting model if the data were collected again under identical circumstances (Burnham and Anderson, 2002). Akaike's weight should be interpreted as a measure of model selection uncertainty. The multi-model inference analyses were performed using the 'MuMIn' package (Barton, 2016) implemented in R version 3.3.2, R Development Core Team 2016. There were no evidence of spatial autocorrelation of model residuals (analysis performed using the 'ncf' package (Bjørnstad, 2016) implemented in R (R Core Team, 2017).

Results

General results

We counted ca. 17,000 SWD females (mean per trap = 76, min. = 0, max. = 704, SD= ± 108.4). We checked 4480 cherries finding 675 eggs (mean per cage = 3, min. = 0, max. = 36, SD= ± 5.8). The average attack rate, i.e. the mean proportion of damaged sentinel fruits, was 16%.

Female density

The multi-model inference analysis indicated that 500 m was the scale that yielded the lowest AICc. At this scale, we found relatively low model selection uncertainty with only one model within the ΔAICc<2. This model had high weight and included the main effects of monitoring round, cherry orchard cover, forest cover and two interactions: cherry orchard cover x monitoring round and forest cover x monitoring round (Table 1). Female density was negatively correlated with cherry orchard cover (Fig. 2). The relation between forest and female population density also changed over time: the relation between forest cover and density remained positive from the second to the sixth round, while this trend was not detectable in the first and the last sampling round (Fig. 3), when the cherry trees did not have ripe fruits.

Crop damage

The multi-model inference analysis indicated that the 250 m and 500 m scales yielded very similar results (Table 2). At both scales the best model included only the main effects of forest cover and monitoring round, with no significant interaction. The amount of forest cover in the landscape had a positive effect on crop damage (Fig. 4). No effect of cherry cover was detected.

Discussion

We found that SWD responded positively to increasing cover of semi-natural habitats in the landscape. Cherry orchards characterized by a greater amount of semi-natural habitat in the close surrounding (250-500 m), appeared to be more susceptible to SWD attack. However, we found that even in the orchards located in crop-dominated landscapes with no forest the SWD density and the damage were substantial, considering that even a reduced harvest loss may have considerable economic effects (Mazzi et al., 2017). The large cover of cherry orchards in the landscape seemed to negatively affect SWD density but not the damage.

Effects of landscape on pest density and crop damage

SWD adults can benefit from forest-dominated landscapes for various reasons. First, this habitat represents preferential overwintering sites due to its microclimatic conditions (Pelton et al., 2016). In fact, population density and dynamics is dependent on winter survival and winter temperatures. To effectively overwinter, SWD requires the presence of protected microclimates, and forest leaf litter can create suitable conditions (Zerulla et al., 2015). Therefore, a higher presence of semi-natural habitats in the landscape can facilitate the winter survival of the pest. On the other hand, crop-dominated landscapes (mainly vineyards, in the study region) do not provide the same amount of shelter (Pfiffner and

Luka, 2000). Second, during the growing season SWD population growth and activity is linked to high atmospheric humidity conditions (Calabria et al., 2012; Tochen et al., 2016). In forest habitats, relative humidity maintains higher levels compared to open habitats, thereby creating suitable conditions for improved SWD survival and fitness. In addition to the abiotic factors described above, forests can also provide alternative wild host plants that can sustain the population when the crop is not available (Pelton et al., 2016). For instance, in Europe Kenis et al. (2016) observed eighty-four different host plant species, among which the genera *Cornus*, *Prunus*, *Rubus* and *Sambucus* proved to be the highest sources of infestation. Most of these species are widespread in our broad-leaf forests and the late-fruiting period of some of these (e.g. *Sambucus nigra* L.) probably sustain and boost SWD population before winter. The large availability of wild host plants justifies the higher pest densities found in cherry orchards located in high forested landscape rather than a possible resource concentration effect due to the orchards (Otway et al., 2005). Furthermore, alternative non-crop habitats can serve as a physical refuge for SWD while crop fields are sprayed with insecticides. Insecticide applications occur repeatedly throughout the entire harvest season, given their low persistence (Bruck et al., 2011) and low effectiveness in case of rain (Gautam et al., 2016; Van Timmeren and Isaacs, 2013). To support this hypothesis we found that a high proportion of cherry orchards in the landscape reduced the density of SWD. The most plausible explanation is linked to the repeated insecticide treatments over the orchards. As the pressure of the insecticide treatments on SWD populations is expected to be proportional to the cover of conventional orchard. In landscapes with large covers of orchards, the almost synchronous pesticide applications over large areas probably reduced population refugia from which the pest could recolonize the crop fields.

Implications for pest management

The effect size of forest cover on both adult density and crop damage, despite the very wide tested gradient, suggests that a reduction of forest cover is not a viable option for controlling SWD. Therefore, any removal or management of semi-natural habitats should be carefully considered as these habitats deliver multiple fundamental ecosystem services to several crops (Chaplin-Kramer and Kremen, 2012; Kennedy et al., 2013; Nayak et al., 2015; Rusch et al., 2013; Rusch et al., 2011; Taki et al., 2007; Veres et al., 2013) and have been demonstrated to increase farmland biodiversity (e.g. Dainese et al., 2015). However, our results also indicate that the high availability of natural habitats in the landscape can complicate the current integrated pest management options. Our data revealed that, even if the whole orchards were conventionally sprayed, the pest could colonize the orchards and attack effectively the sentinel fruits. SWD is highly mobile and opportunistic moving rapidly from one habitat to another when resources are not accessible or in decline (Mitsui et al., 2010). Hence, the large dispersal ability of the species does not allow placing the natural habitats at distances to the crop larger than the dispersal range of the pest (e.g. Baur, 2014). Current SWD control relies heavily on the use of insecticides with several negative environmental impacts (Walsh et al., 2011). To be effective, pesticide applications should be timely in orchards close to forests due to the higher and quicker colonization of SWD. Few among the indigenous parasitoids proved to be sufficiently effective to control the species population (Chabert et al., 2012) and the current lack of specialist natural enemies in the recently invaded territories is probably a key determinant of the observed negative effect of semi-natural habitats.

Perspectives

Although at the moment the presence of forest habitats appears to be a greater source of pest than of natural enemies, one should consider the potential of semi-natural habitats to provide biocontrol in the future by providing suitable conditions for the populations of both native natural enemies and of eventual released biocontrol agents. Shifts of native natural enemies to a new invasive pest are common but they usually occur in the long-term (Novković and Kimura, 2015) and, therefore, cannot be expected to regulate the invasive species population at the beginning of its spread. Considering the emerging problems linked to the invasion of invasive generalist pests across several temperate countries across Europe and North America, our study emphasizes the need to explore the potential effects of landscape processes on the spatio-temporal dynamics of pest populations.

Acknowledgments

We are grateful to the directors of cherry markets for their help in field selection and to the farmers who allowed us to carry out the experiments on their land. We thank Flavia Venturelli and Michele Spinello for their help in sorting the insect material. We thank two anonymous reviewers for providing insightful comments that improved the manuscript.

Funding: This work was supported by the European Union’s Seventh Framework Programme for Research, Technological Development and Demonstration, DROPSA [grant number 613678]. GS received a further grant from Aldo Gini Foundation (Padova).

TABLES

Table 1. Best candidate models from the multi-model procedure explaining adult density. Models are ranked according to their second-order Akaike's information criterion (AICc). Only models with ΔAICc<7 are shown. Log-likelihood (logLik), and model weights are also reported. *df* indicated the number of estimated parameters calculated as the number of fixed effect coefficients + number of variance parameters.

Rank	**Female density**	**Pseudo-R^2**	**df**	**logLik**	**AICc**	**delta**	**weight**
	Landscape scale - 250 m radius						
1	*Round + Cher + For + Cher x Round + For x Round*	0.46	23	-229.1	510.0	0.00	0.313
2	*Round + Cher + For + Cher x Round*	0.45	17	-236.6	510.3	0.29	0.271
3	*Round + Cher + For + For x Round*	0.44	17	-237.3	511.8	1.76	0.130
4	*Round + Cher + Cher x Round*	0.41	16	-238.5	511.8	1.81	0.126
5	*Round + Cher + For*	0.43	11	-244.6	512.5	2.51	0.089
6	*Round + Cher*	0.39	10	-246.5	514.1	4.07	0.041
7	*Round + For + For x Round*	0.36	16	-240.7	516.1	6.06	0.015
	Landscape scale - 500 m radius						
1	*Round + Cher + Cher x Round + For + For x Round*	0.51	23	-222.8	497.5	0.00	0.635
2	*Round + Cher + Cher x Round*	0.48	16	-232.4	499.6	2.15	0.217
3	*Round + Cher + Cher x Round + For*	0.49	17	-231.7	500.6	3.06	0.138
	Landscape scale - 1000 m radius						
1	*Round + Cher + Cher x Round*	0.38	16	-239.6	513.9	0.00	0.463
2	*Round + Cher*	0.36	10	-247.5	516.2	2.22	0.152
3	*Round + Cher + Cher x Round + For*	0.38	17	-239.5	516.2	2.25	0.150
4	*Round*	0.31	9	-249.5	517.9	3.94	0.065
5	*Round + Cher + Cher x Round + For + For x Round*	0.40	23	-233.1	518.1	4.14	0.059
6	*Round + Cher + For*	0.36	11	-247.5	518.3	4.35	0.053
7	*Round + Cher + For + For x Round*	0.38	17	-241.4	519.9	5.91	0.024
8	*Round + For*	0.30	10	-249.4	519.9	5.99	0.023

Table 2. Best candidate models from the multi-model procedure explaining crop damage. Models are ranked according to their second-order Akaike's information criterion (AICc). Only models with ΔAICc<7 are shown. Log-likelihood (logLik), and model weights are also reported. *df* indicated the number of estimated parameters calculated as the number of fixed effect coefficients + number of variance parameters.

Rank	**Crop damage**	**Pseudo-R^2**	**df**	**logLik**	**AICc**	**delta**	**weight**
	Landscape scale - 250 m radius						
1	*For + Round*	0.19	10	-94.1	210.1	0.00	0.315
2	*For + Round + Cher + For x Round*	0.28	11	-93.3	211.0	0.91	0.200
3	*For + Round + For x Round*	0.27	16	-86.9	211.0	0.92	0.198
4	*For + Round + Cher + For x Round + Cher x Round*	0.29	17	-86.4	212.6	2.50	0.090
5	*For + Cher*	0.10	5	-101.1	212.6	2.54	0.088
6	*For*	0.08	4	-102.2	212.8	2.73	0.081
7	*Round*	0.10	9	-98.5	216.6	6.46	0.012
	Landscape scale - 500 m radius						
1	*For + Round*	0.18	10	-94.3	210.5	0.00	0.531
2	*For + Round + Cher*	0.18	11	-94.1	212.6	2.06	0.190
3	*For*	0.07	4	-102.5	213.4	2.86	0.127
4	*For + Cher*	0.08	5	-102.2	214.9	4.39	0.059
5	*For + Round + For x Round*	0.24	16	-89.4	216.0	5.48	0.034
6	*Round*	0.11	9	-98.5	216.6	6.05	0.026
	Landscape scale - 1000 m radius						
1	*Round + For*	0.13	10	-97.2	216.3	0.00	0.275
2	*Round*	0.10	9	-98.5	216.6	0.26	0.241
3	*For*	0.03	4	-104.8	218.0	1..71	0.117
4	*Round + For + Cher*	0.13	11	-97.0	218.4	2.07	0.098
5	*Round + Cher*	0.11	10	-98.3	218.5	2.19	0.092
6		0.00	3	-106.3	218.8	2.48	0.080
7	*For + Cher*	0.03	5	-104.5	219.5	3.20	0.056
8	*Cher*	0.01	4	-105.9	220.1	3.80	0.041

FIGURES

Fig. 1. Location of the a) study area, b) spatial distribution of the 32 cherry orchards and c) example of a landscape buffer (500 m radius) where we measured forest, vineyard and cherry orchard cover.

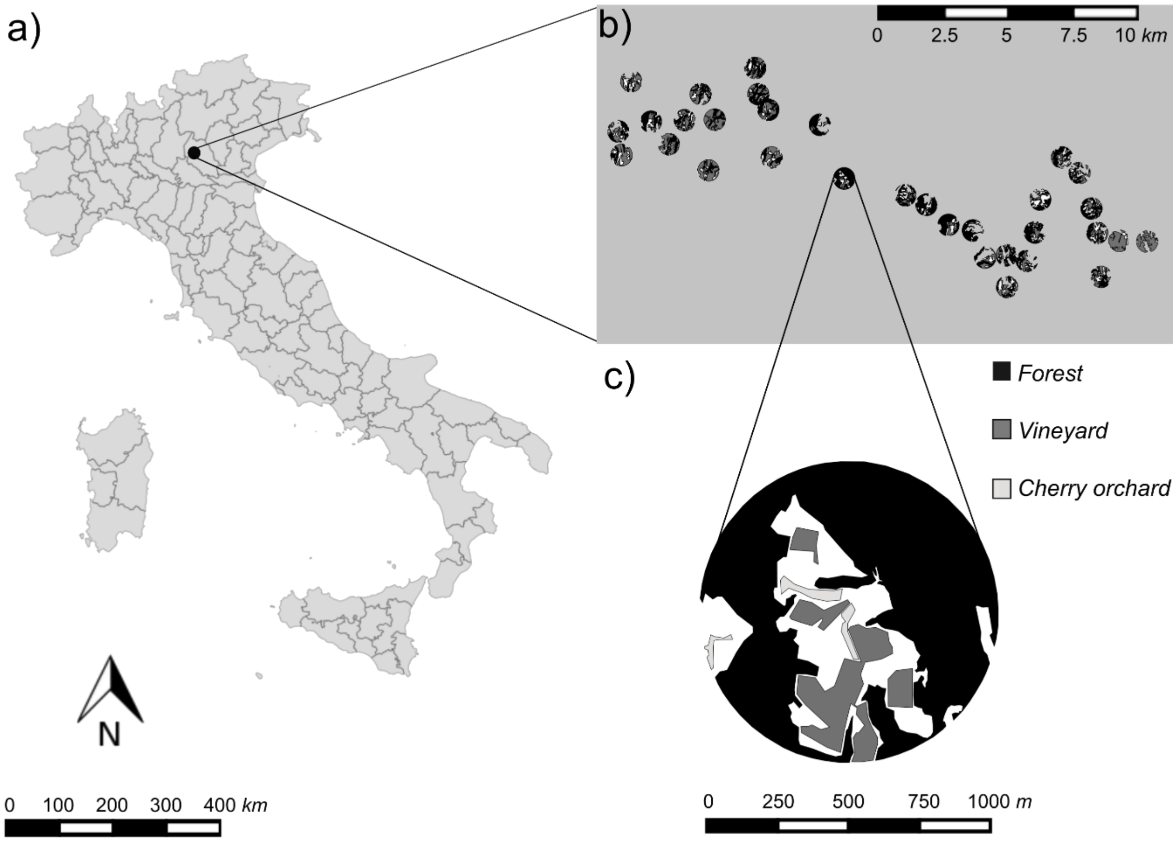


Fig. 2. Relationship between cherry orchard cover in the landscape (500 m radius scale) and female density in the seven sampling rounds in the 32 cherry orchards. The response variable was standardized per exposure day and log-transformed.

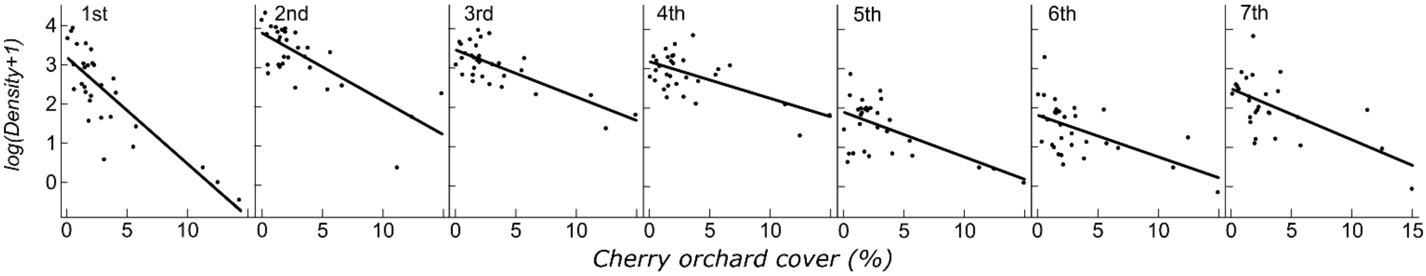


Fig. 3. Relationship between forest cover in the landscape (500 m radius scale) and female density in the seven sampling rounds in the 32 cherry orchards. The response variable was standardized per exposure day and log-transformed.

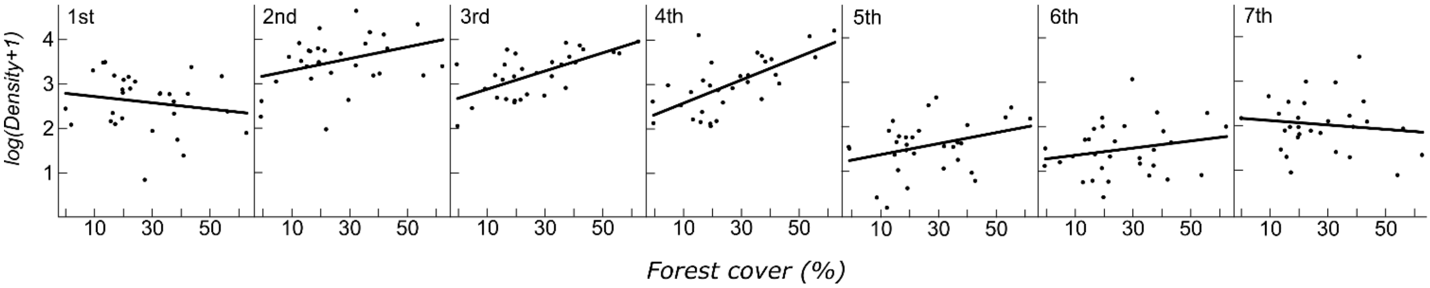
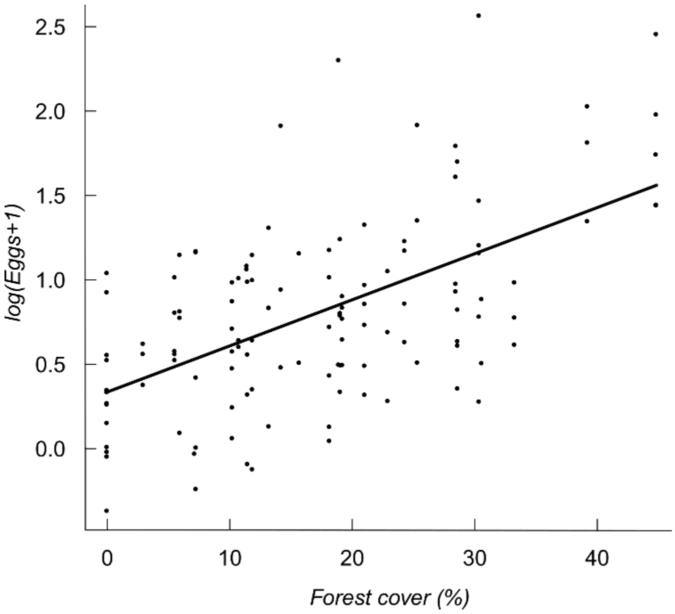


Fig. 4. Relationship between forest cover in the landscape (250 m radius scale) and crop damage found in the exposed cherries. The response variable was standardized per exposure day and log-transformed.



Appendix Chapter 3

Table A1. Minimum, maximum, mean and standard deviation values of cover percentage of forests, vineyards and cherry orchards at different landscape scales.

Site	**Forest (%)**			**Vineyard (%)**			**Cherry (%)**		
	Landscape scale (radius)								
	250 m	***500 m***	***1000 m***	***250 m***	***500 m***	***1000 m***	***250 m***	***500 m***	***1000 m***
Min.	0.00	0.00	6.42	0.00	1.24	0.37	0.40	0.12	0.27
Max.	44.84	62.85	69.52	97.66	69.86	65.14	18.82	15.00	18.09
Mean	18.35	26.55	31.19	33.95	29.96	26.10	5.06	3.36	3.08
St. Dev.	12.09	15.59	15.67	20.99	18.57	19.69	4.94	3.54	4.22

Table A2. Pearson's correlation indexes between elevation and cover percentage of forests, vineyards and cherry orchards at different landscape scales.

	Elevation (m)	**Forest (%)**	**Vineyard (%)**	**Cherry (%)**
		Landscape scale - 250 radius		
Elevation (m)	1.00	0.12	-0.40	0.50
Forest (%)	0.12	1.00	-0.54	0.01
Vineyard (%)	-0.40	-0.54	1.00	-0.29
Cherry (%)	0.50	0.01	-0.29	1.00
		Landscape scale - 500 radius		
Elevation (m)	1.00	0.18	-0.42	0.48
Forest (%)	0.18	1.00	-0.75	-0.05
Vineyard (%)	-0.42	-0.75	1.00	-0.26
Cherry (%)	0.48	-0.05	-0.26	1.00
		Landscape scale - 1000 radius		
Elevation (m)	1.00	0.30	-0.56	0.44
Forest (%)	0.30	1.00	-0.83	0.05
Vineyard (%)	-0.56	-0.83	1.00	-0.37
Cherry (%)	0.44	0.05	-0.37	1.00

Chapter 4

High synchronization of *Drosophila suzukii* activity along steep elevational gradients

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Abstract

Drosophila suzukii (Matsumura 1931) (SWD), is a polyphagous invasive crop pest native of South-East Asia characterized by high mobility. However, it is still unclear how SWD can move to different elevations over the seasons, depending on environmental conditions and food resources. We studied the temporal dynamics of several SWD populations along steep elevational gradients using a synchronization analysis. We selected 12 transects in Alpine environment, covering an overall elevational gradient of 2100 m where we monitored SWD density every two weeks during the growing season (from June to November 2015) when cultivated and wild hosts are potentially susceptible (i.e. fruits are ripe). SWD was widely distributed along all the tested elevations, revealing an extremely high synchronization of population activity even at large differences in elevation and geographical distance. We observed highly synchronized populations up to 100 km among sites with similar climatic conditions. The high dispersal potential of the pest is likely to be the dominant mechanism causing this strong spatial synchronization. This response demonstrated that SWD is able to potentially attack all the available host plants at all elevations irrespective of large local temperature differences.

Keywords

Altitude; Dispersal; Mountain; Population dynamics; Synchronicity; Temperature.

Introduction

Spotted Wing Drosophila (SWD) (*Drosophila suzukii* Matsumura, 1931) is a generalist invasive crop pest endemic of South East Asia. The species is one of the most serious pests of a wide range of crops such as cherry, blueberry, raspberry, grape and strawberry (Walsh et al., 2011). The wide host range (Kenis et al., 2016) together with its large fecundity (Cini et al., 2012) allowed SWD to become established over most of Asia, Europe and Americas, from mid subtropical production regions to cold continental climates (Isaacs and Hahn, 2010). Its activity, however, is not only limited to crop areas as the species can probably attack wild host plants across different natural and semi-natural habitats (Kenis et al., 2016). In particular, understanding species distribution and activity outside crop areas is still largely unknown in the newly invaded regions.

Due to its economic importance for crops, a large body of literature is now available, mainly focusing on population dynamics in agricultural landscapes, pest damage (Harris et al., 2014; Lee et al., 2011b), control measures (Chabert et al., 2012; Cuthbertson et al., 2014; Rossi Stacconi et al., 2013; Van Timmeren and Isaacs, 2013) and potential range expansion (Choi et al., 2017; Walsh et al., 2011). Despite its high cold tolerance and adaptation to mountain climate, few studies focused on pest activity at high elevations and in natural environments (but see De Ros et al. 2013). However, high-elevation ecosystems offer ideal temperatures during summer as well as large variety of suitable wild host plants (Kenis et al., 2016) to promote the development and reproduction of the pest. In particular, it is still unclear how SWD is able to move to different elevations depending on seasonal variation in environmental conditions and food resources (Hodkinson, 2005).

Among the abiotic factors, temperature is a major driver of SWD population dynamics (Wiman et al., 2014). The suitable temperatures for oviposition are between 10 and 32°C and up to 30°C for male fertility (Sakai, 2005). Hence, SWD is limited by high temperatures, particularly in dry conditions (Enriquez and Colinet, 2017). It has been suggested that the pest might progressively migrate to higher elevations over the summer to avoid high temperatures and to follow host plant phenology (Mitsui et al., 2010; Tonina et al., 2016). However, no studies have been specifically designed to describe the distribution of SWD and its activity dynamics along wide elevational gradients. Analyses of spatial synchrony, i.e. coincident changes in the abundance of geographically disjoint populations (Liebhold et al., 2004a), can be used to elucidate how SWD activity respond to temporal and spatial variation in temperature along elevational gradients.

Here, we studied the temporal dynamics of the activity of several SWD population along steep elevational gradients in Alpine environments. Specifically, we aimed at 1) describing the distribution, fertility and activity of SWD along steep elevational gradients when potential host plants are available; 2) testing the synchronization of SWD activity along steep elevational gradients and across different geographical locations. We hypothesized a high synchronization of the pest activity due to its high dispersal potential (Calabria et al., 2012; Hauser, 2011) and to similar climatic trends at large spatial scale (Post and Forchhammer, 2002).

Materials and Methods

Study area and sampling design

We considered three Alpine regions of Northern Italy (Fig. 1a): 1) Lessini (Verona and Trento province), 2) Grappa-Asiago (Treviso and Vicenza province), and 3) Dolomites (surrounding Cortina D’Ampezzo, Belluno province). After a preliminary screening on Google Earth Pro (Google Inc. ©, 2015), we selected twelve transects: four in Lessini and four in Grappa-Asiago, ranging between 120 and 1300 a.s.l. m and four in Dolomites, ranging between 1030 and 2200 m a.s.l. (Fig. 1b,c). They covered an overall elevational gradient of 2080 m. Every 100 m ca. elevation gain we identified a sampling site (N = 115, of which 37 in Lessini, 42 in Grappa-Asiago and 36 in Dolomites). We chose the elevational transects providing a representative and homogeneous sample of the habitat types (mainly semi-natural as forests and grasslands) in the regions. We quantified landscape composition within a 500 m radius buffer around each sampling site (Fig. 1c). We selected the scale according to a previous study where multiple scales were evaluated up to 1000 m (Chapter 3 in this thesis). For each buffer, we manually digitized forest patches from a visual inspection of high-resolution satellite images (Google Earth Pro, Google Inc. ©, 2015). In GIS (QGIS Development Team, 2014), we quantified the area of each patch and then we calculated the percentage of habitats cover. Half of the transects were covered mainly by forests (> 68%) and the other half consisted of mixed habitat of forests and open grasslands (forest cover between 30 and 60%). The presence of urban centers in the landscapes was negligible and discontinuous. Lessini transects had the highest percentage of crops (potential host), with a mean of 7% (mainly vineyards and cherry orchards). This proportion was higher in locations situated at low elevations (between 120 and 500 m a.s.l. where it reached 57% within some landscapes) and decreased to 0% with increasing elevation. The mean proportion of crop habitats in Grappa-Asiago transects was only 1% of crop habitats, higher at low elevations (up to 20%). In Dolomites, transects did not include crop habitats. In Fig. A1 (Appendix Chapter 4) for each region we reported the relative change in proportion of forest, grassland and crop (host) cover along the elevational gradient.

Insects sampling

In each site, we placed a Biobest red trap (Droso-Trap® by Biobest) at c. 1.5 m above the ground and lured with Bioiberica® attractant, specific for SWD (Tonina et al., 2017). The attractant was replaced once per month. We placed the traps at the edge between forest and grassland, far from potential host plants. The sampling season in Lessini and Grappa-Asiago regions started in early June 2015 and ended in the last days of November 2015. In Dolomites, due to colder weather, it lasted from early July 2015 to mid-November 2015. We chose the period when the host plants were available and subjected to potential damage by SWD. We checked and emptied the traps every two weeks. In the laboratory, we counted the number of individuals (adult males and females) and determined female fertility dissecting 20 females per sample. We categorized development of the ovaries into two stages: mature and absent. Potential fertility was estimated using the proportion of females with mature ovaries.

Climate data

For each geographical region, mean annual temperature ($T_{station}$, sampling season 2015) was obtained by the nearest meteorological stations (Lessini: Bosco Chiesanuova, 1050 m a.s.l, lat. 45°37', long. 11°02'; Grappa-Asiago: Pove del Grappa - Costalunga, 675 m a.s.l, lat. 45°48' long. 11°44'; Dolomites: Cortina d'Ampezzo - Gilardon, 1270 m a.s.l, lat. 46°32', long. 12°07'). In each transect, we placed a data-logger (HOBO® Data Loggers) at the lowest and highest sampling site to record air temperature and measure lapse rate (LR). LR is the difference between mean air temperature at the top and base divided by the difference in elevation of the transect. It ranged from -0.73 to -0.26 per 100 m. We estimated mean annual temperature for each sampling site (T_{site}) by the following formula:

$$T_{site} = T_{station} + \Delta E \times LR$$

where ΔE is the difference between the elevation of the station and elevation of each site ($\Delta E = E_{station} - E_{site}$). T_{site} is highly negatively correlated to E_{site} (Pearson correlation index = -0.98). T_{site} ranged from 4 to 16°C.

Statistical analyses

Temporal dynamics of species distribution

To describe the seasonal dynamics of SWD, we used general linear mixed models (GLMM) because residuals approximated a normal distribution and exhibited homoscedasticity. The response variables were 1) the number of individuals per trap and 2) the fraction of mature ovaries found every two weeks. The number of individuals was normalized by dividing the values by the days of trap exposure. All response variables were first ln-transformed to improve linearity. In the three models we included as continuous explanatory variables elevation (E_{site}), sampling date expressed in Julian date (*JD*) and interaction between the two variables. We added also a quadratic term of E_{site} and quadratic and cubic terms of *JD* variable, as we expected a non-linear dynamics of insect activity along the elevational gradient and over time.

The explanatory variables were standardized by subtracting their mean and dividing by two standard deviations to make regression coefficients interpretable. Indeed subtracting the mean typically improves the interpretation of main effects in the presence of interactions, while dividing by two standard deviations puts all predictors on a common scale and allows the coefficients to be interpreted in the same way as with binary inputs (Gelman, 2008). We accounted for the nested design of our study by including region identity (N = 3), transect identity within each region (N = 12) and site identity within each transect (N = 115) as random factors. The GLMM models included an autoregressive structure of order 1 (corAR1) to account for temporal auto-correlation in the time-series. After the inclusion of the autoregressive structure, the model residuals presented very little temporal autocorrelation. Temporal autocorrelation was evaluated using the “acf” function in “nmle” package (Pinheiro et al., 2017) implemented in R (R Core Team, 2017).

Synchronization analysis

To test the synchronization of the time series in function of temperature and geographical distance, we performed a spatial nonparametric covariance (NCF) (Bjørnstad et al., 1999; Bjørnstad and Falck, 2001) using the “ncf” package (Bjørnstad, 2016) implemented in R (R Core Team, 2017). The NCF uses a smoothing spline to produce direct estimates of the spatial covariance of various sets of time series as a function of lag distance (Liebhold et al., 2004b). First, within each study region we quantified the correlation between the time series of SWD density (i.e. the ln-transformed daily number of individuals) at each site in relation to T_{site}, regardless of its geographical location. This first analysis tested the synchronization of the SWD activity between sites located within short geographical distances but with very large temperature differences. Second, we split the entire dataset into three subsets, grouping the sites according to similar temperature (T_{site}). We performed this analysis since population dynamics can be synchronized by climate at large spatial scale (Moran, 1953; Post and Forchhammer, 2002) and SWD activity depends on temperature (Wiman et al., 2014). The selected T_{site} intervals were $4℃ \leq T_{site} < 8℃$ ($T_{med} = 6℃$, N = 31), $8℃ \leq T_{site} < 12℃$ ($T_{med} = 10℃$, N = 43) and $12℃ \leq T_{site} \leq 16℃$ ($T_{med} = 14℃$, N = 41). For each data subset, we related time series to geographical locations of each site, regardless of elevation. We expressed geographical distances in meters basing on Universal Transverse Mercator coordinate system (zones 32N and 33N). This analysis tested the synchronization of the SWD activity between sites located at relatively large geographical distances but with the same annual temperature. Before running NCF analyses, the degree of freedom, which determines the degree of smoothing, was set to the square root of the number of spatial observations (Bjørnstad and Falck, 2001). Confidence intervals for the estimated functions were calculated using bootstrap resampling (1000 iterations; Økland and Bjørnstad 2003).

Results

General results

We counted c. 541,000 individuals (mean per trap = 438, min. = 0, max. = 14,528, SD = ± 876.3). We observed the species at all sites up to 2200 m a.s.l. even during the fall when temperature dropped below 5°C. We found a highly significant effect of JD cubic term ($p < 0.0001$), E_{site} quadratic term ($p < 0.01$) and interaction between JD and E_{site} ($p < 0.0001$) on both SWD density (Fig. 2a) and female fertility (Fig. 2b). During the last period of the survey, we observed a decrease in abundance together with an increase in female fertility at high elevations.

Synchronization of SWD time series

NCF analyses revealed a high synchronization of SWD along the whole elevational gradient (Fig. 3) with the only exception of the Lessini region, whose covariance function decreased with increasing difference in T_{site} (Fig. 3a), i.e. the sites at the lowest elevations were not strongly synchronized with those at highest elevations. We observed the highest synchronization in Dolomites region (Fig. 3c), also when comparing sites located at 1000 and at 2200 m. When we considered sites with similar annual temperature ($T_{med} \approx 10$°C), we found that SWD density was highly synchronized up to 100 km, while for longer distances the synchronization tended to disappear (Fig. 4). Analyses performed across locations with $T_{med} \approx 6$ and $T_{med} \approx 14$°C included smaller distance ranges (respectively of 35 and 70 km) and showed similar, i.e. high synchronization of pest activity (Appendix A Chapter 4, Fig. A2).

Discussion

We found that SWD was widely distributed along all the tested elevations, revealing an extremely high synchronization of time series even when comparing sites at widely different elevations and located at long geographical distances. SWD was active throughout the entire growing season, even at the highest altitudes (i.e. 2200 m a.s.l.), where apparently there was no availability of host plants for reproduction. In late summer, we recorded the highest SWD density, especially around 1000 m a.s.l., since wild host plants were available and climatic conditions were optimal (temperature never exceeded the upper threshold, Sakai 2005). In October and November we observed a decline in density at high elevations probably due to low temperature, which were far below the activity threshold (Sakai, 2005). This decline may be due to a decrease in activity, an increase in mortality rate and/or a shift towards lower elevations. These findings are consistent with observations made by Mitsui et al. 2010 in its native area, confirming the extreme mobility and adaptability of the fly in response to changing environmental conditions (Cini et al., 2012; Hauser, 2011). We did not observe a clear elevational pattern of fertility distribution along the elevational gradients from June to September. SWD in summer showed a higher rate of developed ovaries at all tested elevations, supporting again the hypothesis of high dispersal potential of the pest (Calabria et al., 2012). Surprisingly, at the end of the sampling season we found an increase in female fertility at high elevations, despite the limiting temperatures and relative low number of recorded individuals. This phenomenon could be associated to a lack of resources and/or high competition at lower locations.

Spatial synchronization has been documented in the dynamics of multiple species (Liebhold et al., 2004a) and usually decreases as the distance between populations increases (Bjørnstad et al., 1999; Ranta et al., 1995; Sutcliffe et al., 1996). Several studies on insect herbivores reported considerable variation in the geographical range of synchronization, which can range from 1 km up to 1000 km (Hanski and Woiwod, 1993; Liebhold et al., 1996; Økland and Bjørnstad, 2003; Peltonen et al., 2002; Raimondo et al., 2004; Rossi and Fowler, 2003; Sutcliffe et al., 1996; Williams and Liebhold, 2000, 1995; Zhang and Alfaro, 2003). Spatial synchronization can arise from two primary mechanisms (Liebhold et al., 2004a): 1) dependence of population dynamics on a synchronous exogenous factor such as temperature ("Moran effect", Moran 1953); 2) large dispersal among populations that can blur the effect of environmental differences between sites (Markow and Castrezana 2000).

We found a strong synchronization of SWD activity even at relatively large geographical distances and at large difference in temperature. The high synchronization along elevational gradients within the three regions could be explained by the large dispersal potential, both active and passive, so far hypothesized by Hauser 2011 and Calabria et al. 2012. In detail, SWD activity revealed a high synchronization level (average correlation of spatial covariance function = 0.75), within Dolomites region without any detectable decline at large difference in temperature. We observed high synchronization across a 5°C temperature gradient indicating that SWD population did not present any phenological shift along the gradient. This was a quite surprising result, considering that we tested a wide elevational gradient (ca. 1200 m). The particularly high synchrony showed by SWD populations is consistent with its dispersal capability (Liebhold et al., 2004a; Paradis et al., 1999). On the other hand, host plants are expected to present a strong temperature-induced phenological shift. Interestingly, in one region (Lessini) the synchronization of SWD abundances decreased with increasing difference in T_{site}. The most likely reason that could explain the decline is linked to the phenology of the host plants distributed along this specific region (Coulson et al., 1976; Lawton et al., 1987). Lessini region had large areas covered by host plants (cherry and vineyard), which diminished as elevation increases. SWD can therefore benefit from earlier maturation of low-elevation crops (especially cherry orchards, which begin to ripe from late spring) and boost its population density compared to sites at higher elevations. The lag in host plant phenology along the elevational gradient could cause a de-synchronization of SWD time series. Here, synchronization does not depend only on dispersal , but also on insect-host interaction, i.e. SWD populations increase progressively together with the availability of ripe fruits. Consistently with this hypothesis, we found a stable, strong synchronization along the elevation gradients where there was no large cover of host plants.

A large number of studies reported that synchronization by climate of animal population dynamics might also occur at large geographical scale, even across regions that are clearly separated by geographic barriers (Bommarco et al., 2007; Hallett et al., 2004; Hanski and Woiwod, 1993; Økland and Bjørnstad, 2003; Peltonen et al., 2002; Williams and Liebhold, 2000). Indeed, several animal populations might respond simultaneously to climatic trends if their dynamics are entrained by environmental correlation (Post and Forchhammer, 2002). We performed a second analysis to verify if synchronization of SWD population activity occurred also at larger scale, when controlling for climatic conditions. After considering only sites with similar temperature we found that synchronization of SWD activity was still high. However, the synchronization declined above 100 km disappearing at a 150 km distance. Interestingly, few of the synchronization analyses performed on insect herbivores found in literature reported correlation values as high as our model species within a 100 km distance (but see Raimondo et al. 2004). Hanski and Woiwod (1993) and Peltonen et al. (2002) tested the spatial synchronization of the activity of moth and aphid species up to 1000 km. They showed a marked decline from the first km, although disappearing around 800 km. Økland and Bjørnstad (2003) reported a good synchronization of a bark beetle over 400 km, despite the covariance function never exceeded 0.5.

In conclusion, our main results indicate that SWD is widely distributed up to 2100 m, invading semi-natural and natural landscapes, and that SWD activity is highly synchronized across geographical distance up to 100 km and at locations with large temperature differences (up to 5°C). The only factor that seems to reduce synchronization is the large availability of host plants (i.e. crop) in lowland agricultural landscapes. SWD large dispersal potential is likely to be the dominant mechanism causing this spatial synchronization within the regions. Seasonal variation in temperature is likely to be the main factor explaining the synchronization among insect populations at large geographic distances. The impact that the insect can have on the ecosystem is not negligible. The wide distribution and polyphagy of SWD together with the high synchrony of the pest activity during the growing seasons could have negative effects (e.g. reduction of biodiversity) on the large array of cultivated and wild host plants potentially attacked by SWD. Moreover, SWD spread in natural habitats can harm other native species and communities through more complex mechanisms such as competition for resources and/or apparent competition (Kenis et al., 2009). From a pest management point of view, a high synchronization of insect activity results in concurrent outbreaks across both crop and non-crop areas. This implies that the classical chemical control through a massive and localized use of insecticides (Van Timmeren and Isaacs, 2013) should be discouraged in favor of biocontrol strategies (Rossi Stacconi et al., 2017).

Acknowledgments

We thank Bioibérica S.A. Company and Michele Brardinelli for providing Suzukii Trap® attractant.

Funding: This work was supported by the European Union’s Seventh Framework Programme for Research, Technological Development and Demonstration, DROPSA [grant number 613678]. GS received a grant from Aldo Gini Foundation (Padova).

FIGURES

Fig. 1. Location of a) the study area, b) the 12 elevational transects and example of c) sampling sites within a transect (landscape scale = 500 m radius).

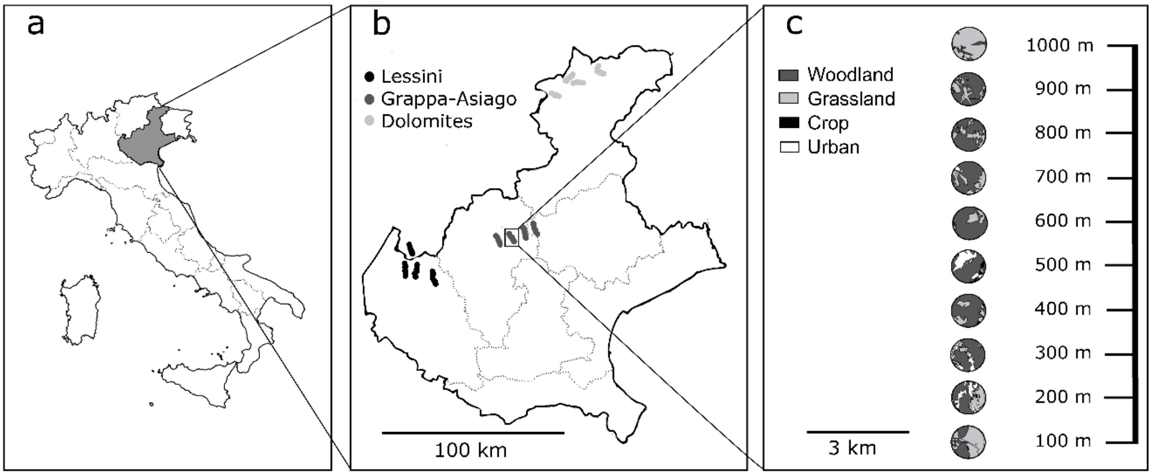


Fig. 2. Elevational distribution of a) SWD density and b) female fertility over the host plant growing season. Points are partial residuals.

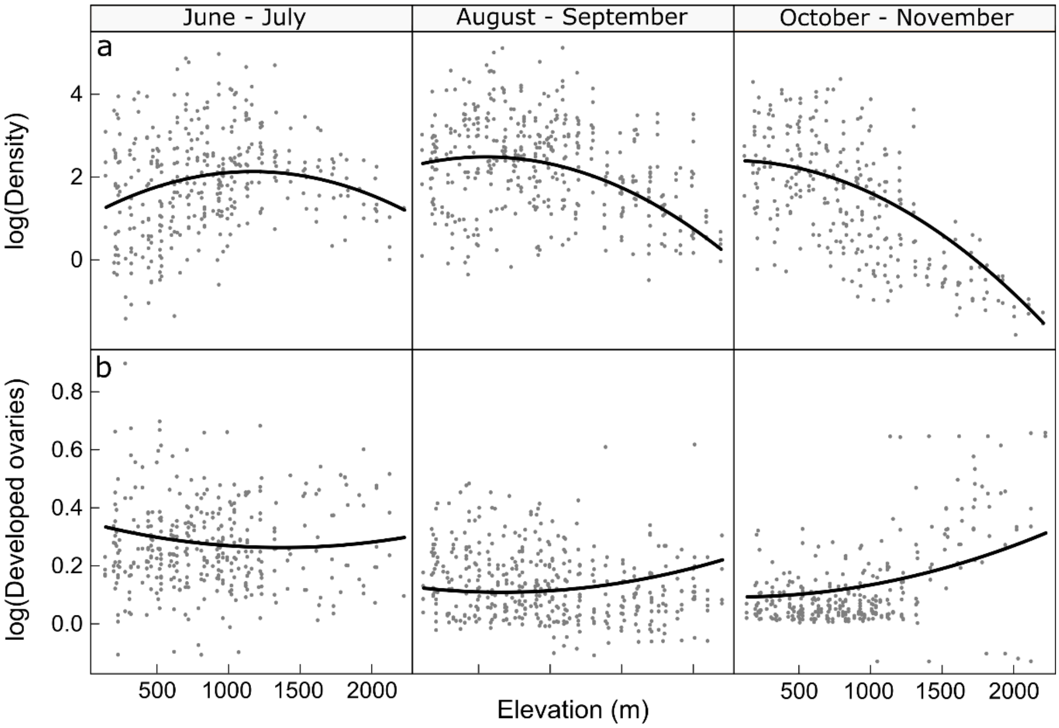


Fig. 3. Spatial covariance functions estimated from SWD density across sites with different mean annual temperatures, for each study region. Thin lines represent the 95% bootstrap confidence intervals. In each region, the sites are located within a 35 km distance. Dashed lines represent regional average correlations of spatial covariance functions: a) 0.58, b) 0.62 and c) 0.75.

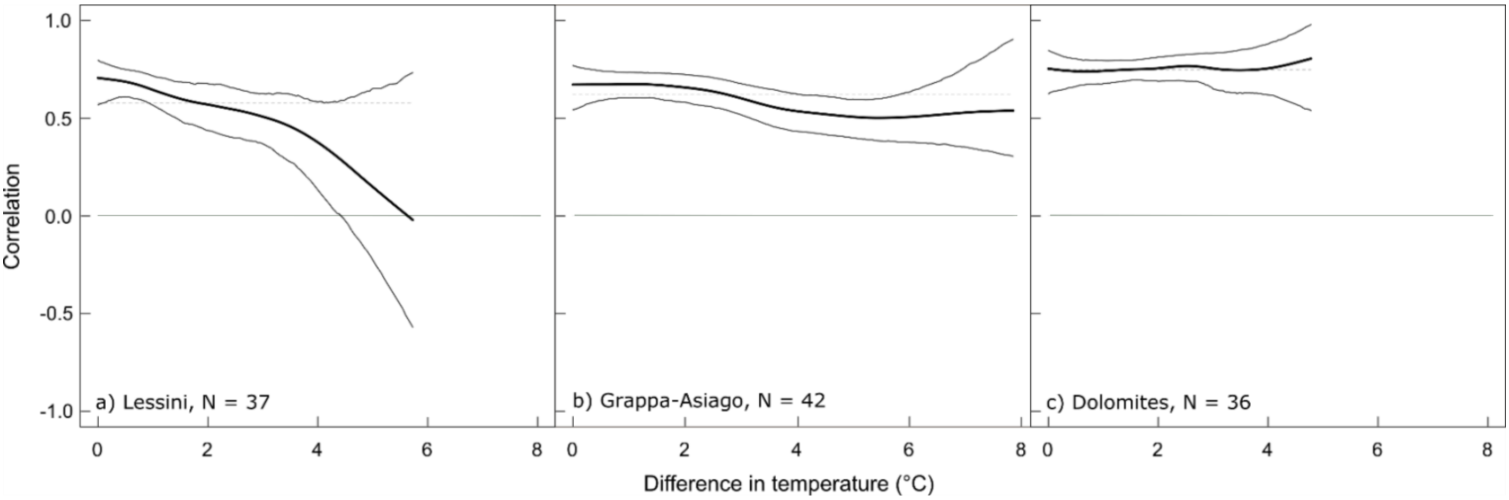
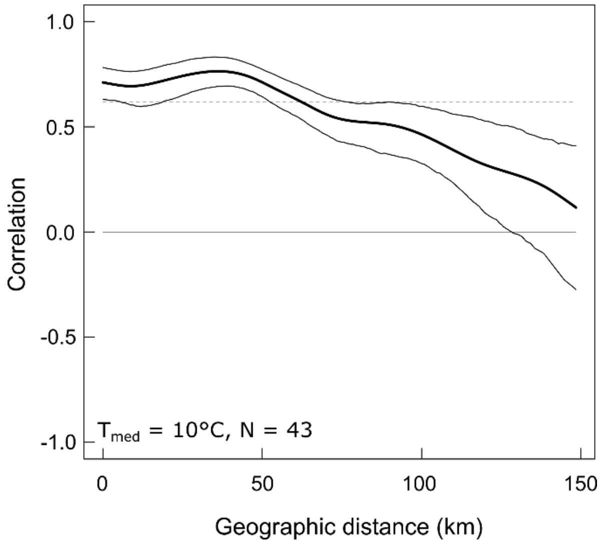


Fig. 4. Spatial covariance functions estimated from SWD density across different sites with similar mean annual temperature of 10°C ($8℃ \leq T_{site} < 12℃$). Thin lines represent the 95% bootstrap confidence intervals. Dashed line represents regional average correlation of spatial covariance function (0.62).



Appendix A Chapter 4

Fig. A1. Relative change in proportion of forest, grassland and crop (i.e. vineyard + cherry orchard) covers along the tested elevational gradient in a) Lessini, b) Grappa-Asiago and c) Dolomites regions. For each region, percentage values of habitat covers were averaged within landscapes located at the same elevation.

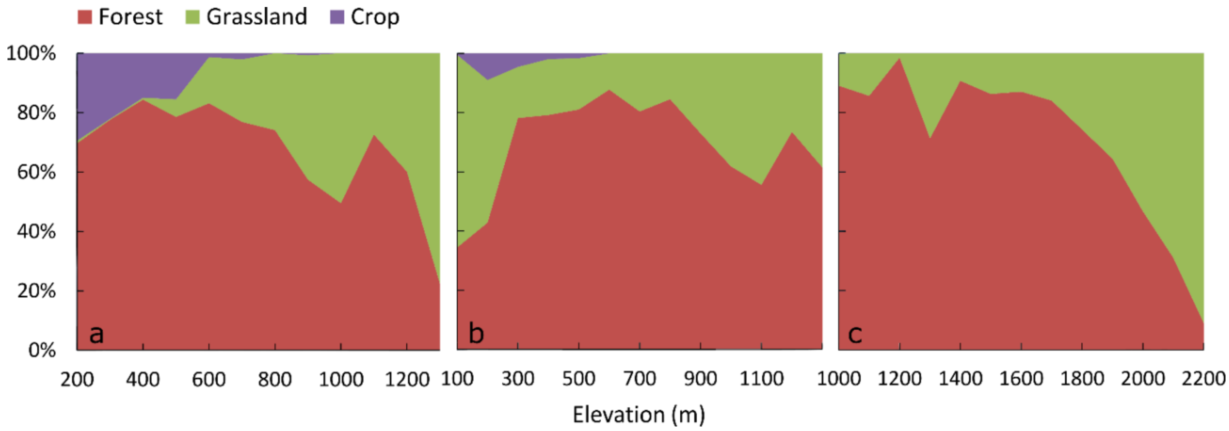
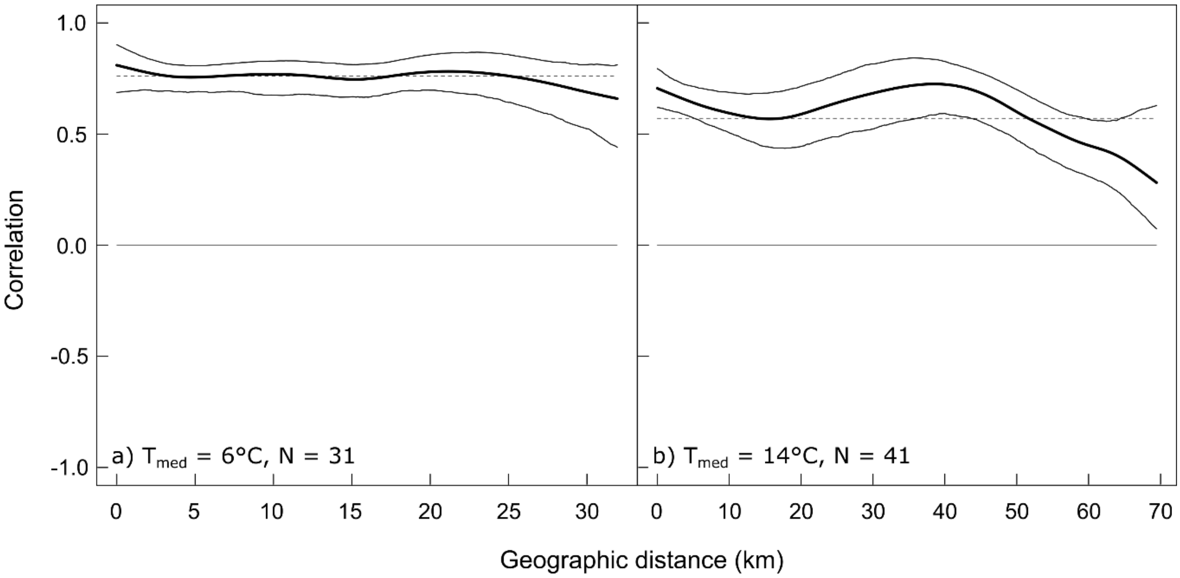


Fig. A2. Spatial covariance functions estimated from SWD density across different sites with similar mean annual temperature of a) 6°C ($4℃ \leq T_{site} < 8℃$) and b) 14°C ($12℃ \leq T_{site} \leq 16℃$). Thin lines represent the 95% bootstrap confidence intervals. Dashed lines represent regional average correlation of spatial covariance function: a) 0.76 and b) 0.57.



Chapter 5

Landscape complexity and crop pests: A meta-analysis

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Abstract

Complex landscapes are often associated with a more effective biological control on insect pests than simple landscapes. Indeed, evidence proved that natural and semi-natural habitats promote conservation of biodiversity in agricultural landscape and provide important ecosystem services. Nevertheless, in some cases natural habitats can fail to support biological pest control and become a greater source of crop pests than natural enemies. Despite the wide literature concerning biological control at the landscape scale, very few studies have investigated the effects of landscape composition on insect pests, and little is known about the driving factors that can favour the spread of a pest in a complex landscape. Here, we collected 36 studies that related response of various insect pests to landscape composition metrics. We performed a random-effects meta-analysis, which indicated a positive link between pest abundance and increasing in landscape complexity. Natural habitats can be a potential resource for pests, providing various host plants suitable for pest development. Invasive generalist insects could take advantage of a high amount of wild habitats in the landscape.

Keywords

Crop pests; Invasive species; Landscape complexity; Meta-analysis; Polyphagy.

Introduction

Natural and semi-natural habitats enhance conservation of biodiversity in agricultural landscape, providing important ecosystem services including pest control, crop pollination, soil conservation, nutrient retention and cultural services (Bianchi et al., 2006; Landis et al., 2000). They represent the major determinant of biodiversity in agriculture (Benton et al., 2003; Schellhorn et al., 2015). In recent years a large body of research investigated the relationship between landscape complexity (i.e. amount of natural or non-crop habitats in the landscape, e.g. Thies and Tscharntke, 1999) and natural enemies and pest control (Chaplin-Kramer et al., 2011). Natural enemy populations and pest pressure are on average higher and lower, respectively, in complex versus simple landscapes, leading to enhanced pest suppression and lower crop damage (Bianchi et al., 2006; Blitzer et al., 2012; Chaplin-Kramer et al., 2011; Rusch et al., 2016; Tscharntke et al., 2016). Despite the general evidence for the benefits that natural habitats produce in terms of biocontrol and reduction of crop pests in agricultural landscapes, variability is high and we can find also scattered evidence for the reverse (Veres et al., 2013).

Tscharntke et al. (2016) provided several hypotheses explaining the potential failure of natural habitats to support biological pest control. Among these, the authors reported that in some cases natural and semi-natural habitats were a greater source of crop pests than natural enemies (Blitzer et al., 2012; Carrière et al., 2012; Landis et al., 2000; Midega et al., 2014; Parry et al., 2015; Power and Mitchell, 2004; Rusch et al., 2013; Wisler and Norris, 2005). First, natural enemies can have large populations in natural habitats but will not disperse, whereas pests from natural habitat can spill over into crops (Blitzer et al., 2012; Fischer et al., 2013; Gaines and Gratton, 2010). In other cases, pests from natural habitats might colonize crops to a greater extent than natural enemies (Midega et al., 2014; Rusch et al., 2013; Rusch et al., 2011). Insect pests can benefit from complex landscapes especially when non-native plants invade natural habitats. Indeed, native habitats in agricultural landscapes can contain a high proportion of invasive plants (McIntyre and Hobbs, 1999), which act as hosts sustaining pest populations. Recent systematic reviews explored the impact of landscape composition on insect pests linked to the biological control by natural enemies (Chaplin-Kramer et al., 2011; Veres et al., 2013). Our meta-analysis intended to focus on the direct relationship between landscape complexity and insect pests, extending the study to a larger dataset than previous studies. In addition to this, we collected details on insect pest traits as degree of polyphagy and geographic origin. These traits could explain the response to landscape complexity. For instance polyphagous invasive pests are expected to be able to exploit multiple habitats, both wild and cultivated (Kenis et al., 2016, 2009; Pfiffner and Luka, 2000). Here we presented the results of meta-analysis, which related pest responses to different level of landscape complexity.

Materials and Methods

Study selection

We identified the studies through a comprehensive research on Google Scholar (2017) using the search string “landscape AND insect pests”. We reviewed over 100 papers, ultimately selecting 36 studies by the following criteria: 1) quantitative measurements of landscape metrics (defined below) at different scales around a farm or a crop habitat; 2) statistics reported as the univariate relationship between landscape metrics and response of insect pest, or the partial contribution of landscape traits among other factors. We selected the studies that quantified landscape composition metrics (see below). We considered as response of insect pests only density values.

Traits of insect pests

We accounted for degree of polyphagy by reporting the number of host plant families, genera and species (Table 1) suitable for insect development. Depending on geographic origin of the species and on location of the studies, we categorized the status of the pests as native (if indigenous of the study area) or invasive (if introduced in the study area in the near or distant past). Polyphagy and status data were collected from Commonwealth Agricultural Bureaux International website (www.cabi.org) and double-checked and/or corrected with proper bibliographic references found on Google Scholar (2017). In some studies, insect pests were considered as a guild and not as a single species. In those cases, when possible the degree of polyphagy was determined basing on the most abundant species within the guild.

Landscape metrics

The selected studies related pest abundance to 1) amount of non-crop habitats in the landscape (N = 41) and/or 2) amount of crop habitats in the landscape (N = 19) and/or 3) Shannon-diversity index (H) of landscape (N = 8). Non-crop habitats included natural and semi-natural habitats as forests, woodlands and unmanaged grasslands. In Table 1 we also reported the landscape scale tested in each study. In case of multiple scales were tested, we reported only the most predictive one, i.e. the best scale to which the pest showed the high response.

Meta-analysis

In order to make the studies comparable, we converted the test statistic from each response reported in a study (Mean values, F, χ^2, t, R^2 or standardized regression coefficients) to a standard statistic, the correlation coefficient r (Borenstein et al., 2009; Chaplin-Kramer et al., 2011; Nieminen et al., 2013). Thus, we computed the effect sizes as Fisher's Z, using the equation (Rosenthal and DiMatteo, 2001): $Z = 1/2 \ln[(1 + R)/(1 - R)]$. Fisher’s Z transformation is a variance stabilizing transformation for correlation coefficients with the added benefit of also being a rather effective normalizing transformation (Fisher, 1921). It estimates the magnitude of the relationship between a predictor variable and its response using any test statistic (Chaplin-Kramer et al., 2011). In our study case, predictor variables were non-crop cover, crop cover and H-index. For each Z value we computed the corresponding variance basing on the sample size of the studies (Borenstein et al., 2009). We generated 68 effect sizes (Z) from 36 studies. For each predictor, we performed a random-effects meta-analysis using “metafor” package (Viechtbauer, 2017, 2010) implemented in R (R Core Team, 2017). We decided to perform a random-effects model since the series of studies that we collected had been performed by researcher operating independently. Therefore, all the selected works were not functionally equivalent as required for a fixed-effect model (Borenstein et al., 2009). We used a restricted maximum-likelihood method (REML) to estimate the total amount of heterogeneity among the true effects. The REML estimator is approximately unbiased and quite efficient (Viechtbauer, 2005).

Results and perspectives

In Fig. 1 we reported the output of random-effects meta-analysis of insect pest responses to amount of non-crop cover in the landscape. We found an overall positive summary effect, which presents confidence intervals (95% CI) that did not overlap with 0 ($p = 0.03$). We did not find any significant relation between pest density and both crop cover in the landscape and H-index, since the summary effects of the meta-analyses were not significant (i.e. 95% CI overlapped with 0). Our findings support the overall trend of insect pests to increase with increasing landscape complexity around the crops, as previously observed by Chaplin-Kramer et al. (2011). Although it is often true that the presence of non-crop habitats enhances pest biocontrol through natural enemies (Bianchi et al., 2006;

Landis et al., 2000), one should be considered that natural habitats can be a potential resource for pests. These habitats provide various host plants suitable for pest development (Tscharntke et al., 2016). Thus, insects with a wide range of host plants can take advantage of a high amount of wild habitats in the landscape. Also the geographic origin could be a key factor to understand how pests behave depending on the surrounding physical environment. Invasive pests can probably benefit from natural resources when colonize new areas, due to the absence or low presence of specific natural enemies (Kenis et al., 2009). To test these hypotheses, we will deepen the meta-analysis taking into account the degree of polyphagy and geographic origin of the pests. Furthermore, we will better explore our dataset to evaluate if include one or more moderators (study-level variables) in the model that may account for at least part of the heterogeneity in the true effects (Viechtbauer, 2010), as well as we will evaluate the presence of publication bias through proper analyses (Nakagawa and Santos, 2012; Rothstein et al., 2005; Viechtbauer, 2005).

TABLES

Table 1. List of 36 papers included in the meta-analysis. Main traits of insect pests are reported.

Paper	**Pest (species or guild)**	**Status**	**Host plants**			**Landscape metrics**	**Landscape scale (radius, m)**
			Family	**Genus**	**Species**		
Bailey et al., 2010	*Phyllobius oblongus*	Native	7	16	22	Non-crop	500
Bergman et al., 2004	Nymphalidae					Non-crop	5000
	Pieris brassicae	Native	6	17	36	Non-crop	5000
	Pieris rapae	Native	3	20	39	Non-crop	5000
	Zyganeidae					Non-crop	5000
Blackshaw and Hicks, 2013	*Agriotes lineatus*	Native	13	22	27	Non-crop	700-1700 (linear transect)
	Agriotes obscurus	Native	3	4	4	Non-crop	700-1700 (linear transect)
	Agriotes sputator	Native	1	4	4	Non-crop	700-1700 (linear transect)
	Tipula paludosa	Native	10	20	22	Non-crop	700-1700 (linear transect)
Carrière et al., 2006	*Lygus hesperus*	Native	24	81	111	Crop	500-1000 (ring)
Den Belder et al., 2002	*Thrips tabaci*	Native	40		140	Non-crop	5000
						Crop	5000

Eilers and Klein, 2009	*Amyelois transitella*	Native	5	5	13	Non-crop	1000
	Beetles					Non-crop	1000
Grilli and Bruno, 2007	*Delphacodes kuscheli*	Native	1	2	12	Crop	2500
Holland and Fahrig, 2000	*Hypera postica*	Invasive	8	19	47	Non-crop	1000
Huseth et al., 2012	*Leptinotarsa decemlineata*	Native	1	3	5	Non-crop	1500
Jonsen and Fahrig, 1997	Leafhoppers, weevils					Diversity index	1000
Kruess, 2003	Stem-boring herbivores	Native	4	11		Non-crop	2000
Kuntz, 2014	*Halyomorpha halys*	Invasive	48	87	211	Non-crop	2000
	Popilia japonica	Invasive	79		300	Diversity index	2000
Letourneau and Goldstein, 2001	*Aphis fabae*	Native	22	53	100	Non-crop	1000
	Empoasca spp.	Native	26		200	Non-crop	1000
	Limothrips cerealium	Invasive	8	15	77	Non-crop	1000
	Myzus persicae	Native	40	94	116	Non-crop	1000
Liu et al., 2016	*Laodelphax striatellus*	Native	1	9	10	Diversity index	200
Lundin et al., 2016	*Protapion* spp.	Native	1	1	4	Crop	5000
Martin et al., 2015	Lepidoptera, cereal aphids	Invasive	23	68	96	Non-crop	300

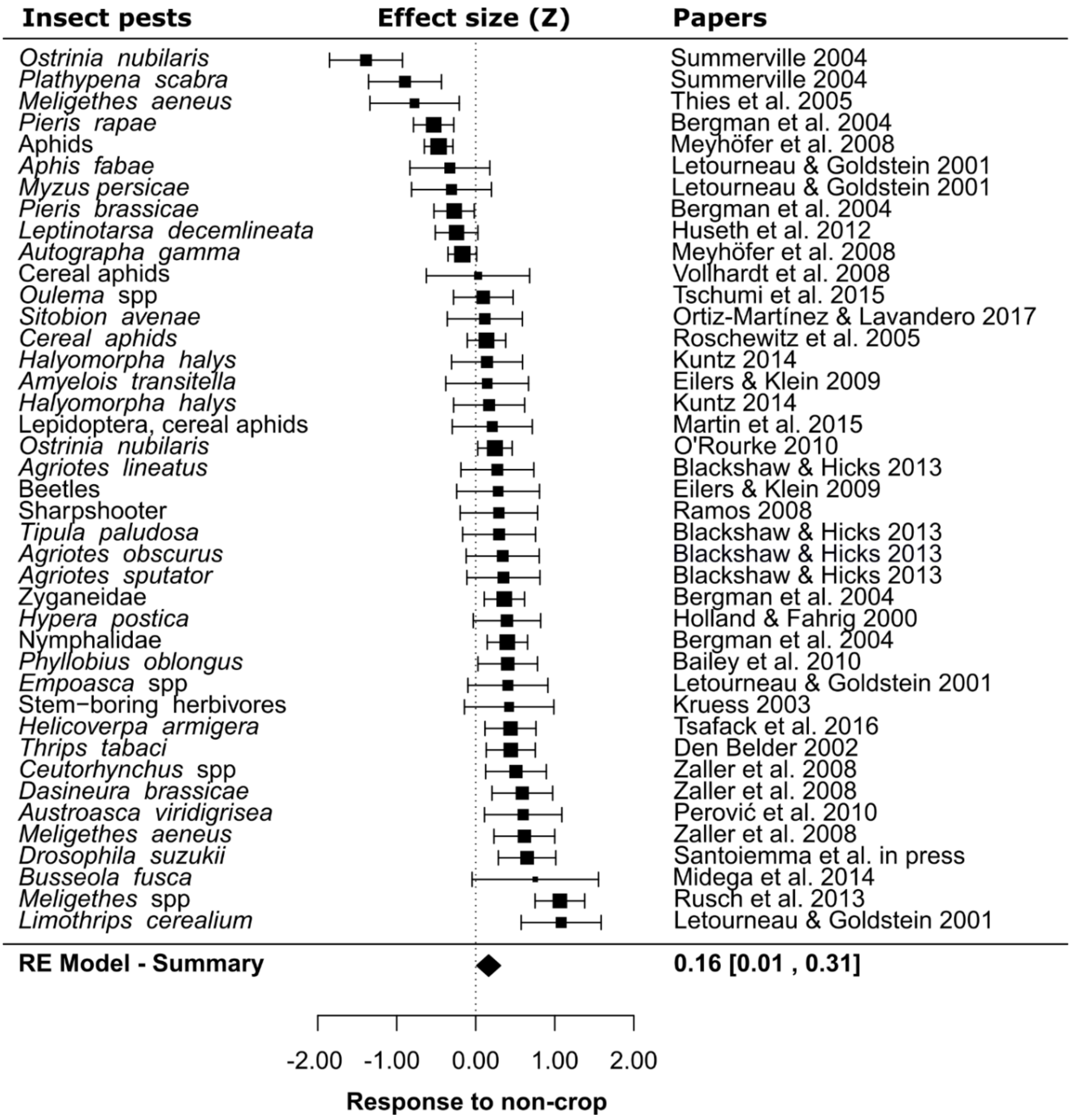
Meyhöfer et al., 2008	*Autographa gamma*	Native	14	27	200	Non-crop	600
						Crop	600
	Aphids					Non-crop	1200
						Crop	1200
Midega et al., 2014	*Busseola fusca*	Native	3	9	13	Non-crop	400
Noma et al., 2010	*Aphis glycines*	Invasive	3	4	6	Diversity index	2000
						Crop	2000
O’Rourke, 2010	*Diabrotica virgifera*	Invasive	4	9	10	Crop	20000
	Ostrinia nubilaris	Invasive	9	25	223	Non-crop	20000
						Crop	20000
Ortiz-Martínez and Lavandero, 2017	*Sitobion avenae*	Native	1	9	11	Non-crop	500
Perović et al., 2010	*Austroasca viridigrisea*	Native	4			Non-crop	3000
Poveda et al., 2012	*Tecia solanivora*	Native	1	1	1	Non-crop	3000
Ramos, 2008	Sharpshooters					Non-crop	100
Ricci et al., 2009	*Cydia pomonella*	Native	6	10	16	Crop	250
Roschewitz et al., 2005	Cereal aphids	Native	4	13	16	Non-crop	1500

Rusch et al., 2013	*Meligethes* spp.	Native	4	8	17	Non-crop	1750
Santoiemma et al., in press	*Drosophila suzukii*	Invasive	19	29	84	Non-crop	500
Schneider, 2015	*Meligethes aeneus*	Native	4	8	17	Crop	1000
Summerville, 2004	*Ostrinia nubilaris*	Invasive	9	25	223	Non-crop	80-890
	Plathypena scabra	Invasive	2	5	34	Non-crop	80-890
Thies et al., 2005	Cereal aphids	Native	4	13	16	Crop	1000
	Meligethes aeneus	Native	4	8	17	Non-crop	1500
Tsafack et al., 2016	*Helicoverpa armigera*	Native	40	51	172	Non-crop	500
						Diversity index	500
						Crop	500
Tschumi et al., 2015	*Oulema* spp.	Native	1	10	11	Non-crop	750
Van Helden et al., 2008	*Empoasca vitis*	Native	3	3	3	Crop	750
	Lobesia botrana	Native	19	24	34	Crop	750
Vollhardt et al., 2008	Cereal aphids		4	8	17	Non-crop	500
Zaller et al., 2008	*Ceutorhynchus* spp.	Native	2	2	4	Non-crop	750
						Diversity index	1750
						Crop	750

Dasineura brassicae	Native	1	1	5	Non-crop	250
					Diversity index	1000
					Crop	1000
Meligethes aeneus	Native	4	8	17	Non-crop	1000
					Diversity index	1500
					Crop	1000

FIGURES

Fig. 1. Random-effects forest plot of insect pest responses to amount of non-crop cover in the landscape, based on 26 studies and 41 responses. Lines demark 95% CI around mean effect size for each pest. Summary effect and its 95% CI values are reported at the bottom of the plot.



Chapter 6

Conclusions

In this thesis we explored the influence of landscape composition and configuration on the spatio-temporal dynamics of SWD activity in crop and non-crop habitats.

In Chapter 2 we investigated the temporal spillover of SWD in Valpolicella region between forest, grassland and vineyard habitats. Temperature and landscape resulted to be strong drivers of species activity. SWD moved from open to forest habitats for overwintering, while landscapes with high forest edge length seemed to enhance the insect density during the growing season.

In Chapter 3 we tested the effect of forest and crop cover in the landscape surrounding cherry orchards on SWD population and attack dynamics in sweet cherry. We observed a larger attack density in orchards surrounded by higher forest cover.

In Chapter 4 we described the temporal dynamics and synchronization of the activity of SWD populations along steep elevational gradients in Alpine environments. Due to the high dispersal potential and mobility, the insect revealed an extremely high synchronization of population fluctuations across both different locations and elevations.

In Chapter 5 we presented a meta-analysis aimed at evaluating in a quantitative way the link between insect pests and landscape composition. Preliminary results indicated an overall positive relationship between pest abundance and landscape complexity.

A large number of previous studies has focused on the role of natural and semi-natural habitats to promote biodiversity and ecosystem services beneficial to the crops such as pollination and biological control (Chaplin-Kramer and Kremen, 2012; Holland et al., 2017; Kennedy et al., 2013; Kleijn et al., 2015; Nayak et al., 2015; Taki et al., 2007). In this thesis we explored the potential effects of natural and semi-natural habitats on the spatio-temporal dynamics of pest populations. The main findings proved that forest habitats, providing suitable abiotic and biotic conditions, can boost pest density, increasing the likelihood of crop damage (Chapter 2, 3 and 5). Curiously in Chapter 2 we did not find significant effects of forest cover in the landscape on SWD density, whereas in Chapter 3 we observed a positive relation between the two variables. Even though these results may appear conflicting at first, one should be considered the different sampling time frames. While the sampling in Chapter 2 lasted one whole year, in Chapter 3 we performed a short-term experiment aimed at monitoring the pest activity during a period of high availability of both crop and wild host plants. This can shed light on the stronger forest effect size detected in the second case. Despite this short-term negative effect, this result must not lead to wrong management implications. Any removal of semi-natural habitats aimed at reducing pest density is not a viable option. Although at the moment semi-natural habitats appears to be a great source of SWD, one should consider the potential of forest habitats to enhance biocontrol in the near future (Knoll et al., 2017), providing suitable conditions for the development of natural enemy populations. In light of our results, further studies should be carried out to identify effective natural enemies and realize a viable biocontrol strategy, which might also consider the release of alien specific biocontrol agents (Daane et al., 2016). The introduction of alien biocontrol organisms to counteract invasive species proved to be effective in some cases (see Colombari and Battisti, 2016). However one should evaluate the eventual non-target effects of alien biocontrol agents on native predators and parasitoids (Ferracini et al., 2017). Shifts of native natural enemies to a new invasive pest are common but they usually occur in the long-term (Novković and Kimura, 2015) and cannot be expected to regulate the exotic species population at the beginning of its spread. At the beginning of the spread phase, farmers should consider that planting orchards in close proximity to complex forest landscapes is causing a consistent spill-over towards the crops during the growing season. However, the same orchards could be those that will benefit the most by the spill-over of potential natural enemies. The high synchronization of SWD activity discussed in Chapter 4 provides other interesting implications for pest management. The concurrent outbreaks of the pest across the wide tested area imply that the classical chemical control through a massive use of insecticides (Van Timmeren and Isaacs, 2013) should be discouraged in favor of biological control strategies. Indeed, the high dispersal potential and prolonged activity throughout the year can make ineffective localized insecticide treatments. Analyses of synchronization of population activity, as well as landscape processes, have been proved to greatly enhance our understanding of SWD population dynamics. This work suggests that the control of invasive generalist pests will probably constitute the greatest challenge for crop protection due to the pest interactions with multiple habitats and host plants across our agricultural landscapes.

Acknowledgments

The author thanks Prof Riccardo Bommarco and Dr. Mark Kenis for providing valuable corrections and suggestions to improve the manuscript.

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