Predator refuges for conservation biological control in an intermediately disturbed system: the rise and fall of a simple solution

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Summary

1. Managed systems harvested at intermediate time-scales have advantages over annual short-cycled systems in maintaining top-down control of insect herbivores, and the flexible harvest regimes in these systems provide opportunities for habitat management that can stabilize predator–prey population dynamics across harvests – resulting in reduced risk of pest outbreaks.

2. In a large-scale field experiment, we explored whether retaining refuges, that is preserving parts of the stand to reduce predator mortality, could reduce the risk of pest insect outbreaks in willow short-rotation coppice. Population densities of three omnivorous predator species and three outbreaking herbivorous leaf beetle species were monitored over four years after coppice (stem harvest) in eight stands with refuges (treatment) and eight stands without refuges (control). Predation pressure was estimated in years three and four.

3. Contrary to our predictions, leaf beetle densities were higher in stands with refuges and predator densities were higher in stands without refuges. Leaf beetle egg mortality increased with total predator density, but did not differ between stands with and without refuges.

4. These unexpected results can be attributed to interactions between dispersal and patch age. The altered phenology of coppiced stems may have triggered leaf beetle aggregation in refuges and migration from stands without refuges. A behavioural response to resource concentration in retained old patches likely transformed the predator refuge from a 'source' to a 'sink'.

5. *Synthesis and applications.* This study shows that retaining refuges in willow short-rotation coppice to facilitate predator population recovery after harvest can come at the cost of more attractive herbivore habitats – and thus increased pest problems. We conclude that crop refuges in systems with intermediate disturbance regimes pose new challenges for conservation biological control, in particular the need to consider how patch age affects dispersal and recolonization of both pest and predators.

Key-words: conservation biological control, harvest, insect outbreak, omnivore, patch age, perennial crop, recolonization, refuge, short-rotation coppice

Introduction

Habitat stability is a well-recognized prerequisite for top-down control of herbivorous insect pests (Southwood 1977). Periodical disturbance such as harvest and tillage in agricultural systems displaces the resident insect community and leads to cyclic recolonization from refuge habitats (Letourneau & Altieri 1999; Hossain *et al.* 2002; Thorbek & Bilde 2004). Predators and parasitoids often follow in response to prey aggregations – which limit their ability to establish in frequently disturbed cropping systems (Wissinger 1997). Generalist and omnivorous predators exhibit weaker aggregative and numerical responses to abundance of specific prey species and tend to recolonize disturbed habitats relatively late (Symondson, Sunderland & Grennstone 2002). The so-called background or early-season control of insect pests provided by polyphagous predators could thus be especially sensitive to frequent and intense disturbances and especially favoured

by management for habitat stability (Symondson, Sunderland & Grennstone 2002; Welch, Pfannenstiel & Harwood 2012).

Complementary refuge habitats external to or inside annual crops can enhance the impact of arthropod generalist predators. An accumulation of studies in annual systems shows that hedgerows and ditches or temporary structures such as field margins, grass covered earth banks or strips with herbaceous ground flora can act as refuges to reduce winter mortality and improve predator reproduction (Thomas, Wratten & Sotherton 1991; Dennis, Thomas & Sotherton 1994; Collins *et al.* 2002; Olson & Wäckers 2007; Griffiths *et al.* 2008; Ramsden *et al.* 2015). Conservation tillage provides refuges of previous years' crop residues on the soil surface, which by similar mechanisms act to increase generalist predator density in annual systems (Stinner & House 1990; Symondson, Sunderland & Grennstone 2002; Tamburini *et al.* 2016).

The intermediate disturbance regimes in many perennial cropping systems make them potentially even more amenable to habitat management than annual crops (Landis, Wratten & Gurr 2000). Perennial arboreal systems, for example orchards and short-rotation forestry, provide structurally complex, heterogeneous semi-permanent habitats that favour insect community diversity, stability and resilience (Simon *et al.* 2009). Orchards have a long history of habitat management for conservation biological control, utilizing the low soil disturbance and multi-strata design (tree canopy with herbaceous understorey ground cover) inherent to these systems and management of adjacent hedgerows and grasslands to provide refuges for generalist predators (Altieri & Letourneau 1982; Simon *et al.* 2009; Silva *et al.* 2010; Paredes *et al.* 2015). There are also recent examples illustrating that preserving the understorey cover of weeds in short-rotation forestry can improve generalist predator density in the tree canopy (Stephan *et al.* 2015).

Preservation of omnivorous predators with strong association to specific host plants (e.g. for overwintering, reproduction and alternative food resources) can only be achieved by crop refuges, that is retention of parts of the field (Björkman *et al.* 2004). The role of crop refuges in perennial agricultural systems has rarely been explored, with a few exceptions (Summers 1976; Hossain *et al.* 2002). Harvest regimes, such as strip harvest or dispersed retention, create a spatial mosaic of differently aged crop patches that may reduce omnivore mortality and act as a source pool for recolonization. Crop refuges may, however, also directly affect abundance of the target insect pest – a problem not necessarily associated with non-crop refuges.

Willow short-rotation coppice (SRC) is an intense form of short-rotation forestry, mainly dedicated to producing biomass for energy with the use of management that is more similar to annual agricultural systems than to traditional forest management (Dimitriou *et al.* 2009). Three willow leaf beetle species frequently reach outbreak levels

above the threshold for economic loss (population densities >1 ind.* shoot^{-1} or 10 000 ind.*ha^{-1}) and defoliation result in substantial reductions in biomass production in willow SRC and in natural willow stands in northern Europe (Sage & Tucker 1997, 1998; Björkman *et al.* 2000, 2004; Bell, Clawson & Watson 2006; Dalin 2006). Predation by several species of omnivorous heteropteran bugs contributes to the control of leaf beetle populations in both natural and managed willow stands (Björkman, Dalin & Eklund 2003; Björkman *et al.* 2004; Dalin 2006). Leaf beetle population densities and thus outbreak risks are lower in willow stands in agriculture-dominated landscapes – partly due to the high density of omnivorous predators in these landscapes (Liman, Dalin & Björkman 2015).

In willow SRC, the stems are repeatedly cut back (coppiced) and harvested at regular intervals of three to five years, through the crops life span of 15–25 years (Ledin & Willebrand 1995). Winter coppicing causes high mortality in the omnivorous predatory bugs that hibernate in the willow stand and disrupts the predator–prey interaction the first years after harvest (Björkman *et al.* 2004). The herbivorous leaf beetles are not as sensitive to the direct effect of coppicing, since they hibernate off-site and recolonize the willow stands in spring (Kendall & Wiltshire 1998; Sage *et al.* 1999; Peacock & Herrick 2000; Björkman & Eklund 2006). Reduced predator populations after harvest allow for fast population growth rates in willow leaf beetle populations on resprouting willows the following spring (Björkman *et al.* 2004). Predator–prey modelling suggests that reducing average predator coppice mortality from the current 80% down to 40% would stabilize predator–prey dynamics and reduce the risk of willow leaf beetle outbreaks (Dalin *et al.* 2011). One option to prevent severe reductions in local predator abundance and facilitate predator population recovery in willow SRC would be to retain refuges of unharvested stems.

The aim of this large-scale, four-year field experiment was to empirically test the theoretical predictions that leaving willow refuges would (i) prevent severe reductions in local predator population density and (ii) facilitate predator population recovery and, thereby, (iii) increase predation pressure on willow leaf beetles. More specifically, we expected resprouting SRC willow stands with refuges to have higher densities of predators and lower densities of herbivores, than stands without refuges. Leaf beetle egg mortality was expected to increase with predator population density and, as a consequence, be higher in stands with refuges as compared to the control stands. In stands with refuges, we expected predator densities and predation rate to be higher in the refuges compared to the resprouting part of the stand during the first year after coppicing. We did not expect this within-stand difference for leaf beetle densities since these species overwinter off-site and thus do not depend on the willow stems for hibernation (Sage *et al.* 1999).

The results show the complexity of utilizing crop refuges in intermediately disturbed systems and illustrate how interactions between patch age and dispersal can create predator 'sink effects' that increase rather than decrease the risk of pest outbreaks.

Materials and methods

STUDY SYSTEM

The SRC stands were all planted with varieties of *Salix viminalis* L. according to the current standard, that is to plant cuttings in a double-row system, with 0·75–1·5 m distances between rows and a spacing of 0·6 m within the rows (Mola-Yudego 2010). With a coppicing cycle of 3–5 years, scrubs grow up to 3–5 m tall before stems are harvested (Ledin & Willebrand 1995). Normally all stems in a stand are cut back the same winter.

Three species of herbivorous willow leaf beetles occur at high densities in willow SRC and in natural willow systems: *Phratora vulgatissima* L., *Galerucella lineola* F. and *Lochmea caprea* L. (Coleoptera: Chrysomelidae) (Björkman *et al.* 2004). Adult *P. vulgatissima* and *G. lineola* hibernate in large aggregations under loose bark, in cracks in wooden fence posts or similar narrow sheltering structures usually within a few hundred metres from the willow SRC, while *L. caprea* overwinters in the soil (Sage *et al.* 1999). The adult beetles emerge from their hibernation sites in mid-May, congregate at the stand edge and then disperse into the stand to lay their eggs on the underside of willow leaves (Sage *et al.* 1999; Björkman & Eklund 2006). The larvae feed gregariously (*P. vulgatissima*) or alone (*G. lineola* and *L. caprea*). In July, the larvae drop to the ground to pupate in the soil and a new generation of adults emerges a month later. Both adults and larvae are *Salix* generalists, even though leaf beetle performance varies among host plants and among *S. viminalis* clones with different content of phenolic compounds (Tahvanainen, Julkunen-Tiitto & Kettunen 1985; Lehrman *et al.* 2012).

Three species of omnivorous bugs, *Orthotylus marginalis* Reut., *Closterotomus fulvomaculatus* De Geer (Heteroptera: Miridae) and *Anthocoris nemorum* L. (Heteroptera: Anthocoridae), are the main predators of willow leaf beetles (Björkman *et al.* 2004). All three heteropterans are trophic omnivores, that is they alternate between plant feeding and predation. They feed by means of extra-oral digestion, an adaptation that allows for a very broad diet (i.e. access to plant tissue of various quality and prey of various size) (Kullenberg 1944; Wheeler 2001). All species frequently consume eggs of *P. vulgatissima* and young larvae of all the leaf beetle species (Björkman, Dalin & Eklund 2003). The two mirid species hibernate as eggs in the bark of the willow stems (Kullenberg 1944), while the anthocorids hibernate as adults in crevices in the bark of willow stems or in dead leaves and litter and insert their eggs into leaf tissue (Sigsgaard 2004). The mirids are winged adults for approximately a week in late summer, providing a short period for active dispersal (Kullenberg 1944). Maximum dispersal distances up to 200 m have been recorded for mirid species with similar life histories (Waloff & Bakker 1963). The two mirid species occur on a couple of *Salix* species, whereas the anthocorids are host plant generalists. Natural grey willow (*Salix cinerea* L.) is common in the landscapes where SRC willow is grown and probably the main source of predators and leaf beetles recolonizing harvested stands.

EXPERIMENTAL SET-UP

A full management-scale field experiment was set up during 2002–2005 in 16 geographically paired SRC willow stands in south-central Sweden (58·120–60·273°N, 15·572–18·416°E). The selected stands were established in 1990 or 1992, and coppicing cycles were synchronized in all stands at four-year intervals from 1994 to 2002 – which suggests that past disturbance frequencies were similar among stands.

All 16 willow stands were coppiced within a 2-week period in February 2002. In eight stands, approximately 50% of the stand was coppiced, while the rest of the stand was retained as a refuge (treatment). The stand was thus divided into two parts, where the retained four-year-old stems formed one single coherent refuge which was harvested with a two or three-year lag from the rest of the stand. In the remaining eight stands, 100% of the stems were harvested, that is no predator refuges were left (control). The stands were haphazardly assigned to the two different treatments.

Stand area ranged from 1·2 to 11·3 ha (mean = 3·8, SE = 1·2) for the refuge stands and from 0·8 to 11·0 ha (mean = 4·4, SE = 1·1) for the control stands. Refuge area thus ranged from 0·6 to 5·7 ha. The average distance between pairs of stands with different treatments (refuge and control) was 61 km and the shortest distance 7·4 km. Stands in the different treatments were distributed along a similar gradient with regard to the relative proportion of open agricultural and forest land cover. The relative proportion open habitat in 1000-m buffer zones from the refuge stands ranged from 0·21 to 0·97 (mean = 0·58, SE = 0·11) and in the control stands from 0·18 to 0·98 (mean = 0·56, SE = 0·08).

COMPARISONS BETWEEN STANDS WITH AND WITHOUT REFUGES

Population densities of the three willow leaf beetle species (*P. vulgatissima*, *G. lineola* and *L. caprea*) and the three predator species (*O. marginalis*, *C. fulvomaculatus* and *A. nemorum*) were monitored in late spring (mid-May–early June) in all 16 stands during the four years following harvest (2002–2005). Densities were estimated using a 'knockdown' sampling technique; all insects on current year's shoot were dislodged into a white plastic container and the focal species were counted (Björkman *et al.* 2004). Samples were taken every 10–15 m along six transects in the coppiced part of the stand. The number of observations per transect in the refuge stands ranged from 6 to 26 (mean = 12) and in the control stands from 5 to 23 (mean = 13). The timing, distribution and spatial extent of this sampling methodology capture the population dynamics of all species at stand level, even though individuals may redistribute within stands during a season (Björkman *et al.* 2004).

Predation rate on *P. vulgatissima* eggs in all 16 stands was compared during the third and fourth years after coppicing (2004–2005). Predation rate was estimated by attaching a leaf with an egg clutch of 10–20 eggs to the underside of ten leaves on randomly assigned willow stems in the centre of each stand. Egg clutches were collected after 8 days, and the number of predated eggs was recorded. This method for estimating egg predation is well developed within this system, and gives trustworthy estimates on egg mortality caused by predation as well as an indication of overall predation rate (Björkman, Dalin & Eklund 2003; Björkman *et al.* 2004)

COMPARISONS WITHIN STANDS WITH REFUGES

We undertook more detailed monitoring in the eight refuge stands the first year after coppicing (2002). Densities of predators and leaf beetles and *P. vulgatissima* egg mortality were estimated in the refuge (distance = 0 m, 45 samples equally distributed across the refuge) and at three distances from the refuge into the coppiced part of the stand (distance = 2, 8 and 30 m; 15 samples per distance). Egg mortality was estimated following the same procedure as previously described, but using six leaves with eggs at each of the four distances from the refuge.

METHODOLOGICAL LIMITATIONS

The original intention was to monitor predator and herbivore population densities from the year before coppicing until the fourth year after coppicing (a full cycle), in stands with different refuge treatments. However, we were for logistic reasons not able to collect a complete control stand data set until year two after coppicing and could therefore not study the effect of refuges on harvest mortality or recolonization during the first year. The more detailed first year monitoring of the local refuge effect partly compensates for the first years missing control data, for example by allowing for a comparison between predator and leaf beetle abundances in refuges vs. the coppiced part of the stands.

STATISTICAL ANALYSES

Two generalized linear mixed models (GLMMs) were used to describe the relationship between population densities of predators and leaf beetles in the coppiced part of the stand and treatment (presence or absence of refuge). The models were fitted using transect counts summed by stand (Poisson distribution, log link) with an offset for the total number of samples in each stand. The fixed effects were refuge treatment, species and year since harvest (all were treated as factor variables). Including interactions between these factors allowed for different effects of treatment between years and between species. Non-significant interaction terms (i.e. in the predator model, refuge treatment*predator species; and in the herbivore model, refuge treatment*herbivore species and refuge treatment* year) were removed from the final models. Over-dispersion was handled by incorporating a random effect at the individual sample level (Hinde 1982). A random effect for site nested in species was incorporated to allow for potential spatial autocorrelation between sites. The temporal autocorrelation was accounted for by using a first-order autoregressive structure, with observation year nested within stand.

A GLMM was also used to model the relationship between proportion egg mortality (binomial distribution and a logit link) in the coppiced part of the stand and treatment (presence/absence of refuge). Fixed effects were refuge treatment and total predator density (sum of all predator species), with stand as a random effect and a first-order autoregressive correlation structure to account for repeated measures within stands.

A zero-inflated generalized linear model (GLM) was used to model the association between predator and leaf beetle population densities, within the refuge and in the adjacent coppiced part of the stand. This is a so-called mixture model, where the count process, that is the probability of counts vs. true zeros (Poisson distribution, log link with an offset for the number of samples), and the logistic process, that is the probability of false zeros vs. counts and true zeros (binomial distribution and logit link), are modelled separately (Zuur *et al.* 2009). Zero-inflated Poisson models are appropriate when over-dispersion in count data is caused by an excessive number of zeroes. To reduce part of the zero inflation, we summed population densities by treatment, that is associated with the refuge (distance 0 m) or the adjacent coppiced part of the stand (distance 2–30 m from the refuge). Since species patterns were consistent within trophic levels, we also summed predator and leaf beetle densities, respectively. A similar residual spread in the two species groups suggested putting all data into a single model. Thus, the fixed effects in the model were treatment (refuge or coppiced) and trophic level (i.e. predator or herbivore). An interaction term was included to allow the effect of treatment to vary between trophic levels. A GLM (binomial distribution, logit link) was used to test the difference in egg mortality between the refuge (distance 0 m) and the adjacent coppiced part of the stand (distance 2–30 m from the refuge).

Analyses were performed in R 3.1.0 (R Development Core Team. 2014) using the MASS package (Venables & Ripley 2002) glmmPQL function for both Poisson and logistic GLMMs. The pscl package (Jackman 2015) zeroinfl function was used for modelling zero-inflated data.

Results

COMPARISONS BETWEEN STANDS WITH AND WITHOUT REFUGES

Predator refuges had an effect on both predators and willow leaf beetles (Fig. 1, Table 1). Predator population densities were lower and leaf beetle densities were higher in stands with refuges compared to the control stands (Fig. 1, Table 1). The effects of treatment were consistent among species, within both trophic levels (Fig. 1, Table 1). Recorded average densities of the leaf beetles *P. vulgatissima*, *L. caprea* and *G. lineola* in the fourth year after coppicing were 85, 98 and 77% higher in the stands with refuges compared to the control stands.

Average predator population growth rates were positive in stands with refuges from year two to three and year three to four (Fig. 1). Population growth rates in the control stands were positive from year two to three and negative from year three to four (Fig. 1). Leaf beetle population growth rates were, on average, positive in both stands with refuges and control stands the second to third and third to fourth years after coppicing, with only one exception: *Phratora vulgatissima* growth rates were negative in the second to third year after coppicing in stands with refuges (Fig. 1).

The proportion of leaf beetle eggs that were predated in the third and fourth years after coppicing was positively related to total predator densities ($F_{1,13} = 11\cdot913$, $P = 0\cdot004$, Fig. 2). We observed no difference in egg mortality between stands with and without refuges ($F_{1,14} = 0\cdot144$, $P = 0\cdot710$, Fig. 2).

COMPARISONS WITHIN STANDS WITH REFUGES

Local population densities of both predators and leaf beetles in the first year after coppicing were higher in the

Table 1. Analysis of variance for GLMMs (Poisson distribution and log link function) describing population density (ind.*shoot^{-1}) of predators and herbivores as a function of treatment (presence or absence of predator refuge), species and year since coppicing. Non-significant fixed effects were removed from the final models

| Response variable	Model	Fixed effect	d.f.	*F*-value	*P*-value
Population density (ind.*shoot^{-1})	Predators	Refuge	1, 14	14·501	0·002**
		Year	2, 89	7·648	<0·001***
		Species	2, 30	7·434	0·002**
		Refuge*year	2, 89	5·343	0·006**
		Refuge*species	–	–	–
	Herbivores	Refuge	1, 14	13·348	0·003**
		Year	2, 89	14·749	<0·001***
		Species	2, 30	15·777	<0·001***
		Refuge*year	–	–	–
		Refuge*species	–	–	–

**$P \leq 0.01$, ***$P \leq 0.001$.

refuge than in the adjacent coppiced part of the same stand ($t_{1,6} = 6.433$, $P < 0.001$). This difference was more pronounced for the leaf beetles than for the predators ($t_{1,6} = 3.404$, $P = 0.002$). The probability of obtaining 'false' zero observations did not differ between the refuge and the coppiced part of the stand ($t_{1,6} = 0.863$, $P = 0.396$). There was no difference in the proportion egg mortality in the refuges compared to the adjacent coppiced part of the willow stands ($F_{1,6} = 0.455$, $P = 0.511$).

Discussion

Contrary to our theoretical prediction, refuges increased, rather than decreased, the risk of willow leaf beetle outbreaks. Leaf beetles reached higher densities in stands with refuges and predator densities were higher in stands without refuges (Fig. 1). The results were consistent across all predator and all leaf beetle species. Predation pressure on leaf beetle eggs was associated with predator density and therefore mirrored the predator density patterns between years. Local population densities of species at both trophic levels the first year after coppicing were higher in the refuges compared to the adjacent coppiced part of the stand. The difference in abundance, between refuges and coppiced parts, was greater for leaf beetles than for predators. We found no effect on predation pressure associated with the refuge, probably because of the uneven 'background' density of leaf beetle eggs (higher in the refuge than in the coppiced part of the stands).

This study is, as far as we know, the first to use repeated annual measures to evaluate a large-scale field experiment using crop refuges for conservation biological control in an intermediately disturbed system. The results show that time-series data (in this case a full coppice cycle) are valuable for understanding how different management alternatives influence the dynamics of pests and predators. Snapshots during the cycle could have underestimated the accumulated positive effect of refuges on leaf beetle densities and the potential consequences for willow biomass production.
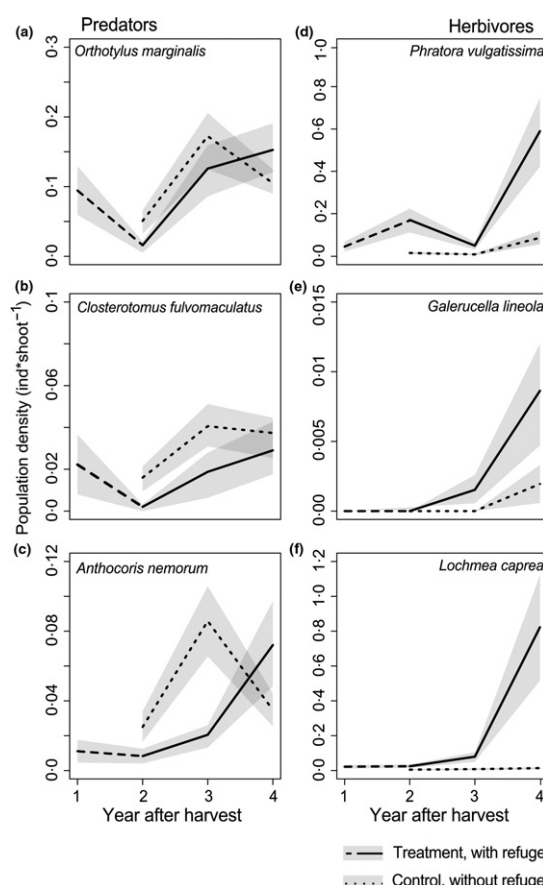
Fig. 1. Population densities of (a–c) omnivorous predatory bugs and (d–f) leaf beetle herbivores in four consecutive years after coppicing in SRC willow with refuges (treatment, $N = 8$) and without refuges (control, $N = 8$). The first year's population density data was not included in the model and thus shown as a raw data mean value. Error surfaces show standard errors calculated from the raw data. Note the different scales on the y-axes.

Crop refuges in perennial systems introduce a spatial mosaic of patches with different age, providing habitats with different structural complexity and microclimate. Here, we found that mainly herbivores but also predators tend to aggregate in patches of older stems. Leaf beetle
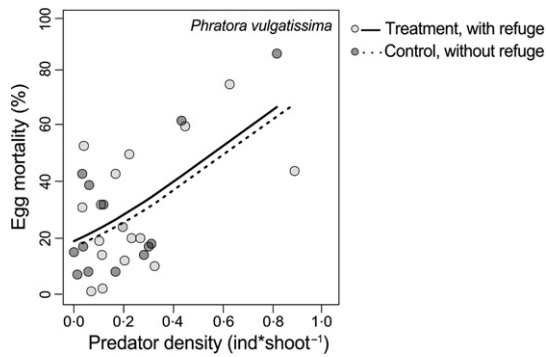
Fig. 2. Per cent leaf beetle egg mortality related to total predator density in SRC willow with refuges (treatment, $N = 8$) and without refuges (control, $N = 8$) year three and four after coppicing. Lines are model-predicted mean effects.

egg and larvae represent a major component of total prey available in willow stands, and concentration of this resource can have delayed predator dispersal from the old patch into the cut part of the stand. This predator 'sink effect' is predictable based on the concepts of optimal foraging, that is organisms should exhibit longer residence times in patches that provide higher abundance of resources (Schoener 1971; Corbett 1998). Omnivorous generalist predators may, however, disperse or aggregate in response to prey as well as plant resources (e.g. plant nutrient status and stem structures available for oviposition). Previous studies show that intraspecific variation in plant resources can override the importance of prey as the main driver for dispersal of omnivorous predators (Eubanks & Denno 1999, 2000). Omnivore aggregation in willow refuges can thus be a result of the integrated effect of prey distribution and plant resource variation. Future studies in this system should focus on relating dispersal and population dynamics to patch age, to reveal whether leaf beetles and predators discriminate between and perform differently on willow stems of different age.

Retention of willow stems can, in addition, create patches of host plants with different phenology. Coppicing during the dormant season removes the generative buds and can modify the phenology of the shoots, so that leaves on younger shoots unfold later and attain smaller sizes, than leaves on older shoots (Saska & Kuzovkina 2010). Older stems may provide a better phenological match for the leaf beetles, whereas coppicing may introduce phenological asynchrony. Further attention should therefore also be given to the direct effect of refuges on the dispersal of leaf beetles, within and between stands.

Habitat management utilizing crop refuges may to a different extent than non-crop refuges affect dispersal and recolonization of highly specialized target pests, whereas non-crop refuges, such as herbaceous ground cover, field margins and hedgerows, may similarly affect overwintering and dispersal of generalist pests. Both types of refuges can, in addition, provide more structurally complex habitats with complementary floral resources and alternative prey

that may trap generalist predators, omnivorous predators and parasitoids (Kemp & Barrett 1989; Corbett 1998; Symondson, Sunderland & Grennstone 2002; Langellotto & Denno 2004; Tylianakis, Didham & Wratten 2004). In other words, there are no simple solutions for refuge provisioning, and non-crop refuges are not necessarily better than crop refuges. Understanding how habitat management alters the behaviours of target pests and predators as they disperse from refuge habitats is one of the keys to success, in annual as well as perennial systems.

The detectable impact of refuges for overwintering predators often decreases rapidly with increasing distance to refuge (Corbett & Rosenheim 1996; Hossain *et al.* 2002; Griffiths *et al.* 2008). The setting used in this study (aggregated retention of 50 per cent of the stand) may partly explain the slow recolonization of predators and should be seen as a first step towards more functional provisioning of refuges in willow SRC. The next step would be to explore other alternatives for management of refuges, with the aim to identify spatial and temporal extents that better balance factors that facilitate (e.g. spatial configuration of stems) or delay (e.g. pest aggregation) dispersal of predators into the adjacent part of the stand. Dispersed retention would greatly reduce predator recolonization distances in willow SRC compared to aggregated retention – but would not be applicable under conventional coppicing. Permanent strips of willow stems or native willow within and at the edge of the stand would be an equivalent option for a less aggregated spatial design, with limited negative effects on management.

IMPLICATIONS FOR MANAGEMENT

Our results indicate that retaining crop refuges to facilitate predator population recovery after harvest may come at the cost of more attractive herbivore habitats – and thus increased pest problems. In addition, asynchronous coppicing of neighbouring SRC stands may increase the risk of pest outbreaks compared to the situation when resprouting stands are more geographically isolated. The result presented here does not imply any changes to current harvesting regimes. Future recommendations may, however, change in the light of a better mechanistic understanding and with a refuge design that better balances the trade-off between promoting predator densities and leaf beetle aggregation in refuges.

Current political targets of increased renewable energy, agricultural diversification and ecological intensification have led to an increased interest in a range of crops characterized by intermediate disturbance regimes, from multi-annual grains to short-rotation forestry (Wright 2006; Glover *et al.* 2010; Lin 2011; Bommarco, Kleijn & Potts 2013; Marquardt *et al.* 2016). An expansion of intermediately disturbed cropping systems will increase the opportunities for and importance of habitat management for conservation biological control (Landis & Werling 2010). A majority of the studies in this field of research have

explored non-crop refuges in annual and perennial orchard systems, whereas the consequences of altered harvest regimes and crop plant refuges in perennial agricultural systems remain almost unexplored. From the present study, we conclude that crop refuges in systems with intermediate harvest regimes may pose new and sometimes unexpected challenges for conservation biological control. Retention of crop refuges to increase predator survival across harvest resulted in pest aggregation in the refuge – eventually transforming the refuge from a predator 'source' to a 'sink'.

Acknowledgements

Data accessibility

All data used in this paper are available from Appendix S1–S4 in Supporting Information.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Population densities of predators and herbivores in SRC willow with/without refuges.

Appendix S2. Population densities of predators and herbivores and proportion of leaf beetle eggs predated, in relation to distance from refuge.

Appendix S3. Predation rates in SRC willow with/without refuges.

Appendix S4. Metadata Appendix S1–S3.