

# Conserving carnivorous arthropods: an example from early-season cranberry (*Ericaceae*) flooding

J. van Zoeren, C. Guédot, S.A. Steffan<sup>1\*</sup>

**Abstract**—Biological control plays an important role in many integrated pest management programmes, but can be disrupted by other control strategies, including chemical and cultural controls. In commercial cranberry (*Vaccinium macrocarpon* Aiton; Ericaceae) production, a spring flood can replace an insecticide application, providing an opportunity to study the compatibility of the flood (a cultural control) with biological control. We suspect that chemical controls will tend to reduce the number of natural enemies, while the flood, through removal of detritus and detritivores, may cause generalist predators to prey-switch to consume proportionally more pest individuals. We measured the abundance of herbivores (Lepidoptera), detritivores, Arachnida, and parasitoids (Hymenoptera) every week for six weeks in Wisconsin (United States of America) cranberry beds following either an insecticide spray or a cultural control flood. We found that detritivore populations rapidly declined in both flood and spray treatments; conversely, carnivore populations (spiders and parasitoids) were more abundant in the flooded beds than in sprayed beds. Populations of key cranberry pests were similar between flooded and sprayed beds. Our results showed that early-season flooding preserved more natural enemies than an insecticide application. This increase in natural enemy abundance after the flood may allow for greater continuity in herbivore suppression, potentially providing a basis for long-term cranberry pest management.

**Résumé**—La lutte biologique est une branche importante de la lutte intégrée qui est parfois perturbée par d'autres stratégies de lutte, telles que les mesures culturales ou chimiques. Dans la production commerciale de canneberges (*Vaccinium macrocarpon* Aiton; Ericaceae) l'inondation des champs de canneberge au printemps peut remplacer une application d'insecticide, ce qui procure l'opportunité d'étudier la compatibilité entre l'inondation des champs (mesure culturale) et la lutte biologique. Nous suggérons que les mesures chimiques auront tendance à réduire le nombre d'ennemis naturels, alors que l'inondation des champs, de par l'élimination des débris et détritivores, entraînerait les prédateurs généralistes à consommer plus de ravageurs. Nous avons mesuré l'abondance d'herbivores (Lepidoptera), de détritivores, Arachnida, et de parasitoïdes (Hymenoptera) chaque semaine pendant six semaines dans des champs de canneberges soit après l'application d'un insecticide, soit après l'inondation des champs. Nous avons observé que les populations de détritivores diminuaient rapidement après l'application d'insecticide ainsi qu'après l'inondation des champs et les populations de carnivores (araignées et parasitoïdes) augmentaient dans les champs inondés comparé aux champs pulvérisés. L'abondance des populations de ravageurs étaient similaires entre les champs inondés et les champs pulvérisés. L'augmentation de l'abondance d'ennemis naturels après l'inondation pourrait permettre une meilleure continuité dans la suppression des herbivores, et ainsi procurer la base d'une gestion à long terme des ravageurs.

## Introduction

Biological control can be a highly effective and cost-efficient pest control method (Van den Bosch

and Telford 1964; DeBach and Rosen 1991). However, as living organisms, biological control agents are strongly influenced by farm management decisions. In an integrated pest management

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(IPM) programme, chemical and cultural controls are often used concurrently with biocontrol. Broad-spectrum insecticides may kill the natural enemies along with the targeted pests (DeBach 1947; Settle *et al.* 1996; Fagan *et al.* 1998; Bommarco *et al.* 2011), while cultural controls may either augment or diminish biocontrol potential (DeBach and Rosen 1991; Marc *et al.* 1999). Because integrated pest management has been a cornerstone of agricultural production since the concept was developed in the mid-1900s (Stern *et al.* 1959; Smith *et al.* 1976), a critical focus of recent agricultural research has been on predicting which control strategies will be most compatible with each other, and on reconciling the use of chemical and biological controls. Specifically, conservation biological control involves deliberate maintenance of natural enemy niche requisites, while reducing disruptive factors that inhibit natural enemy activity (DeBach 1964; DeBach and Rosen 1991; Barbosa 1998).

In commercial cranberries (*Vaccinium macrocarpon* Aiton (Ericaceae)) in Wisconsin (United States of America), most growers use pest thresholds and pesticide alternatives in their integrated pest management programmes (Colquhoun and Johnson 2010). However, Wisconsin cranberry growers have not intentionally implemented biological control to any significant degree (Singleton 2010), despite observations that many native natural enemies exist in the cranberry system, including egg parasitoids, larval parasitoids, and generalist predators (Mahr 1999; Singleton 2010). Of these, the most efficient parasitoids have been shown to affect up to 97% of their pest hosts in a field population (Mahr 1999). It appears, therefore, that conservation biological control could provide significant pest suppression in cranberry systems (Marucci and Moulter 1992; Li *et al.* 1994; Simser 1994; Mahr 1999; Singleton 2010).

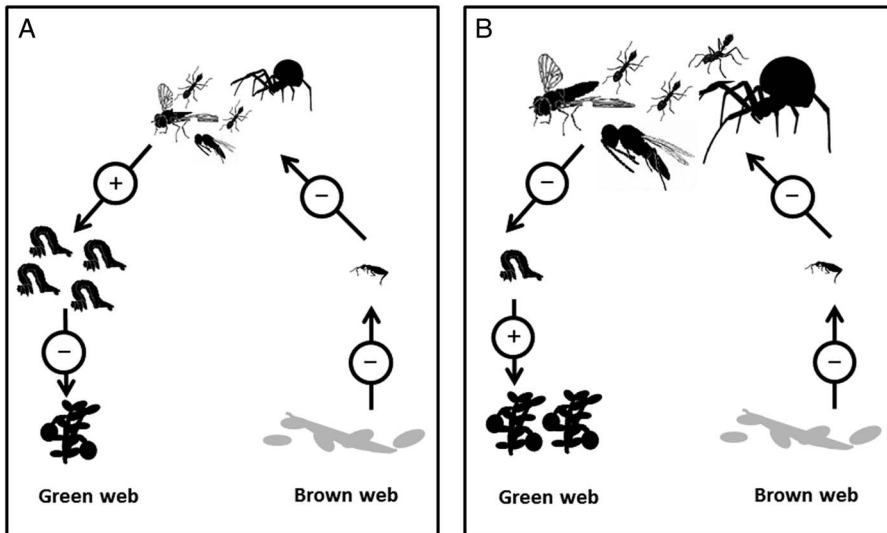
About half of Wisconsin cranberry growers flood their beds for one to two days in late spring, as a cultural pest control technique, as well as to remove significant quantities of detritus and detritivores (Steffan *et al.* 2012a). This flood takes advantage of the fact that cranberries are primarily a dry, irrigated crop, but the plant can withstand several days of submergence during cooler weather. The flood effectively replaces a corresponding insecticide application, and has been shown to control for the most economically important pests in cranberry

(Steffan *et al.* 2012b). However, it remains unclear through what mechanisms the flood controls these pests. It is unlikely that most caterpillar suppression is a result of the flood itself, given past work showing low caterpillar mortality in flood waters (Teixeira and Averill 2006; Steffan *et al.* 2012a).

We propose two other ways in which the flood may manifest an effect on pest caterpillar population densities. First, by replacing an insecticide application, the flood may conserve biological control agents (Marucci and Moulter 1992; Singleton 2010). Second, the flood may suppress pest populations through an indirect effect on generalist predator feeding habits (Fig. 1). The removal of large amounts of detritus and many detritivores, which represent an alternative prey source, may force hungry generalist predators to prey-switch. If this is the case, predators will consume proportionally more pest herbivores (which come from a “green”, or plant-based, food web) than they would in a situation with abundant detritivorous prey (which come from a “brown”, or detritus-based, food web, Birkhofer *et al.* 2008; Kuusk and Ekbohm 2010). If either of these situations are found to occur following flooding in cranberry production, then the flood would in fact represent conservation biological control, wherein changes to management practices preserve the native natural enemy populations.

This study provides foundational information on the impacts of spring flooding on cranberry arthropods, illuminating mechanisms through which flooding suppresses pest caterpillars by showing the effects of the flood, compared with an insecticide application, on natural enemy abundance. In addition, comparing pest control methods is valuable from a practical standpoint to the cranberry growers. The moth species investigated, *Sparganothis sulfureana* Clemens (Lepidoptera: Tortricidae), *Rhopobota naevana* Hübner (Lepidoptera: Tortricidae), and *Acrobasis vaccinii* Riley (Lepidoptera: Pyralidae), are among the most damaging cranberry pests. *Acrobasis vaccinii* is a direct pest, feeding on up to six berries during their single larval generation each year. *Rhopobota naevana* has two generations per year, and can decrease photosynthetic capacity of the plant as well as damaging buds and flowers. *Sparganothis sulfureana* has two generations, with the first feeding on cranberry foliage in the spring, and the second feeding

**Fig. 1.** Two hypothetical consequences of the removal of detritus in a cranberry ecosystem, depicting energy moving up the “green” (plant-based) and the “brown” (detritus-based) food webs. **A**, Detritus removal leads to starvation of and decreased numbers of detritivores, and correspondingly also decreased numbers of predators. The few remaining predators consume fewer herbivores, leading to increased pest populations and having a detrimental effect on the crop. **B**, Detritus removal leads to starvation of and decreased numbers of detritivores. However, the generalist predators prey-switch, maintaining population numbers, but consuming proportionally more herbivores. This leads to a decreased pest population, and has a beneficial effect on the crop.



inside the fruit. Although the cost of both implementing the flood and applying an insecticide are highly variable, flooding is in general the cheaper pest control strategy.

To address the mechanisms through which flooding may affect pest caterpillar abundances, we looked at the abundances of herbivores, detritivores, parasitoids, and predators following the flood or the spray. We hypothesise that biological control and the cultural control strategy of flooding are compatible, because the flood conserves natural enemies, and that together they can provide pest suppression equivalent to or greater than a conventional insecticide spray.

## Methods

A total of 12 1.4-ha cranberry beds (Stevens variety, ~25 years old) were identified from within a single commercial marsh in central Wisconsin, United States of America. Each of the 76 beds is ~340 × 50 m, and separated from the next bed by either a dirt road or a dirt road and an ~25 m wide water reservoir. Study beds were separated from each other by at least 120 m. In all,

34 of the beds (including six study beds) received an ~30 hours spring flood on 28–29 May 2014, and did not receive any spring insecticide application (designated as “Flood”). Flood waters came from nearby water reservoirs. The other 42 beds (including six study beds) were not flooded, and were treated with the insecticide Hatcher (active ingredient chlorpyrifos) (Dow Agro-Sciences; Indianapolis, Indiana, United States of America) on 30 May 2014 (designated as “Spray”). All insecticide applications were administered at the registered label rates, and were applied using a tractor-mounted boom spraying method, in accordance with conventional cranberry cultivation practices. Blocks to flood or spray were constrained by the marsh layout; however, the location of the study beds was randomised from within available beds.

## Sampling

Beginning in May 2014, arthropod communities were sampled weekly for seven consecutive weeks. Depending on weather conditions and marsh spray schedules, actual sampling intervals ranged from six days to 10 days between sampling events.

The initial sampling period took place seven days before flooding or spraying. Before the seventh week, all beds received an application of the insecticide Altacor (active ingredient chlorantraniliprole) (DuPont, Wilmington, Delaware, United States of America). Each sampling event used three separate methods: pitfall traps, sweep netting, and pheromone-baited traps. Voucher specimens are being archived within the University of Wisconsin Insect Research Collection (Madison, Wisconsin, United States of America).

Pitfall traps were non-baited and measured the activity-density of arthropods in the understorey. Two pitfall traps were placed in each bed, located on opposite ends approximately one-quarter of the long length into the bed and ~2 m from the side of the bed. Each pitfall trap was constructed from a 500-mL plastic cup (Dart Container, Mason, Michigan, United States of America) buried to soil-surface level in the cranberry bed and covered with a plastic roof to prevent rainfall from entering the trap. Each cup contained ~150 mL of 100% propylene glycol (ChemPoint, Bellevue, Washington, United States of America). Traps remained in the field for seven days at a time, contents were collected weekly, and propylene glycol was added as needed. Arthropods were strained and stored in 95% ethyl alcohol (Pharmco-Aaper, Brookfield, Connecticut, United States of America).

Sweep-netting measures the density of arthropods in the cranberry canopy. Each sweep sampling event consisted of six sets of 20 sweeps with a 38-cm-diameter sweep net (BioQuip, Rancho Dominguez, California, United States of America). Sweep sampling took place across the width of the bed, with two sets of 20 sweeps each to transverse the 50-m bed. This was repeated three times moving down the length of the bed. All sweep netting occurred between 10:00 AM and 04:00 PM, with no precipitation. Arthropods were stored in airtight bags on ice in a cooler, and then transferred to vials of 95% ethyl alcohol. All arthropods in the pitfall and sweep-netting samples were identified to order. In order to separate each into functional trophic guilds, some orders were identified to family or genus.

Pheromone-baited traps consisted of P2 diamond-shaped sticky-traps (Great Lakes IPM, Vestaburg, Michigan, United States of America), placed ~0.5 m above the cranberry canopy, and

baited with lures for adult male moths of *S. sulfureana*, *A. vaccinii*, and *R. naevana* (ISCA Technology, Riverside, California, United States of America). Each bed contained six total traps in two groups of three placed at opposite ends of the beds near the pitfall traps, such that one baited for each moth species was placed at each end. The number of moths in each pheromone-baited trap was counted and recorded in the field. Traps were replaced as necessary and lures were replaced every three weeks.

### Statistical analyses

All statistical analyses were conducted using repeated measures analysis of variance (ANOVA), except for parasitoids due to their low abundance. Repeated measures ANOVA analyses were used to compare treatment effects across all seven weeks of sampling. Parasitoid wasp pitfall trap data were analysed using a Mann–Whitney Rank Sum test, in which samples from week 2 through week 6 were summed for analysis. Week 1 was excluded from parasitoid analysis because it took place before flood or spray events, and week 7 was excluded because all beds were sprayed the previous week. Insufficient parasitoid wasps were found in sweep samples (0–15 per bed), so these data were not analysed.

For pheromone-baited traps, counts for each of the three pest moth species were analysed individually, with the two trap counts for each species in each bed summed. For pitfall and sweep-netting samples, analyses were first conducted at the taxonomic level of order. These were then assigned to feeding guilds (herbivore, detritivore, predator, or parasitoid) based on extension publications and grower expertise. The most abundant order from each guild was considered an indicator of overall guild population dynamics; these were the orders that were used for analyses.

The trap catch for each order from the two pitfalls traps in each bed was summed. In week 4, extensive rain flooded most of the pitfall traps, so pitfall data from week 4 was excluded. For sweep netting, the total number of insects in each order per bed was added together. Arthropod abundances that were not normally distributed were  $\log(x+1)$  transformed (sweep net samples of Collembola and spiders).

All statistical analyses were conducted in SigmaPlot 12.5 (Systat Software 2013).

## Results

During the seven weeks of sampling, 7122 arthropods were collected in sweep netting, and 46 000 arthropods and mollusks were collected in pitfall traps. Throughout their flight, 2288 moths were caught in pheromone-baited traps. Across all sampling methods, the majority of arthropods collected belonged to the Acari (25 000) and Collembola (22 000). Other frequently captured taxa included Lepidoptera (2300), Diptera (2000), and Araneae (1000). Hymenoptera were much less frequently captured (225).

### Herbivores

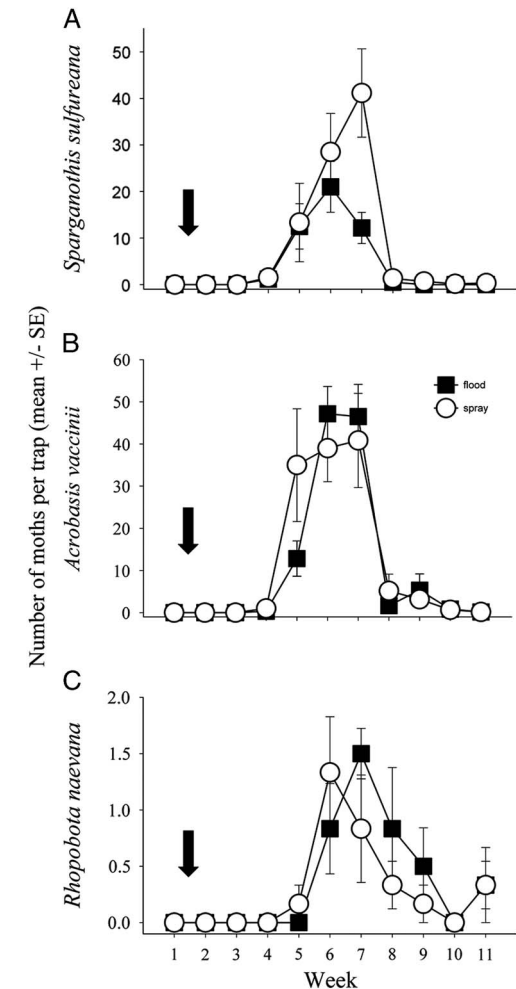
There was no significant difference in pheromone trap catch between flooded and sprayed beds for any of the key pest species (*S. sulfureana*:  $F(1,10) = 1.655$ ,  $P = 0.227$ ; *A. vaccinii*:  $F(1,10) = 0.763$ ,  $P = 0.403$ ; *R. naevana*:  $F(1,10) = 0.335$ ,  $P = 0.575$ ; Fig. 2). Adult moth trap catches for all species in both flood and spray beds followed a typical flight pattern, with a mid-summer pulse in trap counts, and all populations peaking in early July. However, for *S. sulfureana* there were fewer moths caught in flooded beds than in sprayed beds during peak flight week, as indicated by a significant treatment  $\times$  week interaction ( $F(5,50) = 4.566$ ,  $P = 0.002$ ; pairwise contrast week 7:  $t = 4.133$ ,  $P < 0.001$ ).

Fewer than eight caterpillars were captured in either pitfall traps or sweep net samples, so these data were not analysed. Other herbivores caught using pitfall traps and sweep netting were in the subclass Acari, and insects from the orders Coleoptera (Chrysomelidae and Curculionidae), Hemiptera (Cicadellidae, Cercopidae, and Miridae), and Thysanoptera. These groups were not analysed, as they are not considered to be important pests of cranberry.

### Detritivores

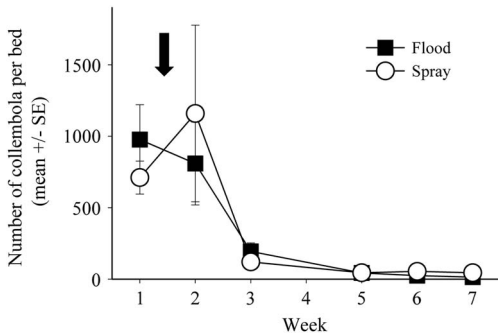
In the pre-treatment sample, the most abundant group of detritivores was Collembola, with captures up to 2000 per pitfall trap. There was a significant effect of week on Collembola numbers from both sweep net samples and pitfall traps (sweep:  $F(6,60) = 4.703$ ,  $P < 0.001$ ; pitfall:  $F(6,60) = 41.302$ ,  $P < 0.001$ ): initial population densities were high, then decreased to near zero

by week 3, and subsequently stayed very low for the remainder of the sampling period (Fig. 3). In sweep net samples, Collembola abundance dropped by week 2, while in the understory abundances stayed high for week 2, but decreased by week 3. There was no effect of treatment on Collembola density (pitfall:  $F(1,10) = 0.053$ ,  $P = 0.823$ , Fig. 3; sweep:  $F(1,10) = 0.232$ ,  $P = 0.64$ ).



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**Fig. 3.** Collembola activity-density, as a model for overall detritivore activity-density, as measured in pitfall traps across the seven-week sampling period. The open circles represent Collembola caught in spray beds, while the black squares represent Collembola caught in flood beds. The arrow signifies the time of the flood/spray treatment. No data were collected on week 4 due to traps flooding. SE, standard error.



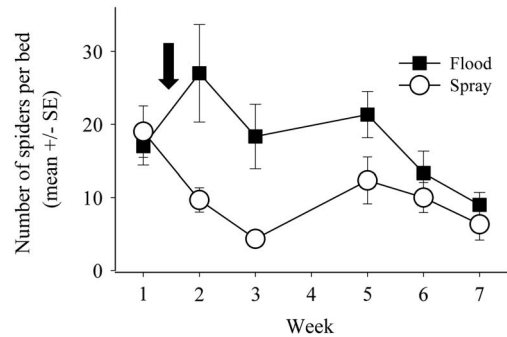
The second most abundant of the detritivores were Acari, whose population trends, like Collembola, did not differ between flood and spray beds (pitfall:  $F(1,10) = 0.364$ ,  $P = 0.56$ ; sweep:  $F(1,10) = 1.003$ ,  $P = 0.34$ ). Other detritivores caught, at much lower densities, included Gastropods, Orthoptera (Gryllidae), Diptera (Nematoceran larvae), and several species of Coleoptera larvae.

## Predators

The most abundant order of generalist predators in both pitfall traps and sweep net samples was Araneae (spiders). Although representing a complex and diverse group, for the purposes of this analysis all spiders were analysed together, and used as an indicator of generalist predators. This is based on the majority of feeding habits of spider species, and is used because specific classifications are not known for this agricultural ecosystem (Bardwell and Averill 1997).

A total of 330 individual spiders were caught in sweep net samples, and there was no treatment effect on spider abundance ( $F(1,10) < 0.001$ ,  $P = 0.995$ ). However, in pitfall traps there were 700 total spiders captured, with significantly more spiders in the flooded than in the sprayed beds ( $F(1,10) = 7.223$ ,  $P = 0.023$ ; Fig. 4). The significant treatment  $\times$  week interaction ( $F(5,50) = 3.298$ ,  $P = 0.012$ ) suggests that the

**Fig. 4.** Spider activity-density, as a model for overall generalist predator activity-density, as measured in pitfall traps across the seven-week sampling period. The open circles represent spiders caught in spray beds, while the black squares represent spiders caught in flood beds. The arrow signifies the time of the flood/spray treatment. No data were collected on week 4 due to traps flooding. SE, standard error.



effect of flooding on spider activity-density depended on the post-flood timing of sampling. Specifically, there was a significant difference in trap catch only during the first two weeks immediately following the flood/spray pest control event.

Other generalist predators caught included Chilopoda, Diptera (Syrphidae larvae), and Coleoptera (Staphylinidae, Carabidae, and Lampyridae). These were present at 20% lower density than the spiders, and were not analysed.

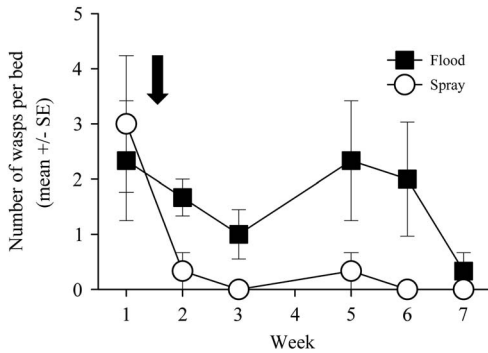
## Parasitoids

Throughout the summer, 79 parasitoid wasps were caught by sweep netting and 116 parasitoids were caught in pitfall traps. Most of the parasitoids analysed come from the families Ichneumonidae, Braconidae, and the superfamily Chalcidoidea. Because parasitoid abundances were low, week 2 through week 6 were summed together and analysed using a Mann–Whitney rank sum test. There were significantly more parasitoid wasps caught in the flooded than in the sprayed beds ( $U = 468.50$ ,  $n_1 = n_2 = 42$ ,  $P < 0.001$ ; Fig. 5).

## Discussion

In a Wisconsin commercial cranberry system, flooding was shown to be similar to a broad-spectrum insecticide application at controlling the three most economically important cranberry pest

**Fig. 5.** Parasitoid wasp activity-density as measured in pitfall traps across the seven-week sampling period. The open circles represent parasitoid wasps caught in spray beds, while the black squares represent parasitoid wasps caught in flood beds. The arrow signifies the time of the flood/spray treatment. No data were collected on week 4 due to traps flooding. SE, standard error.



moths, *S. sulfureana*, *A. vaccinii*, and *R. naevana* (Fig. 2). This upholds findings from previous studies (Cockfield and Mahr 1992; Steffan *et al.* 2012b), and provides evidence that flooding is similar to a spring insecticide application in terms of pest suppression. Thus, we provide evidence in support of our hypothesis that biological and cultural control strategies are compatible with each other, and that, together, they are equivalent in efficacy to conventional insecticide use.

Another salient finding of this study is that the spring flood elevated the activity-density of natural enemies, specifically of spiders and parasitoid wasps, compared with the use of a spring insecticide application (Figs. 4–5). This finding offers insight into the mechanism through which flooding affects pest management, by looking at trophic dynamics in the marsh community. One possible mechanism through which pests are suppressed by the flood is indirectly, through the relative increase in the number of natural enemies present when using the spring flood compared with the traditional insecticide-based pest management programmes. Multiple studies have supported the notion that natural enemies, especially parasitoid wasps, are potentially important drivers in cranberry pest suppression (Marucci and Moulter 1992; Mahr 1999). Observations suggest that 33–50% of *S. sulfureana* larvae are parasitised in Wisconsin commercial

cranberry (Deutsch 2014). Our finding that the cultural practice of spring flooding conserves natural enemies, more than the conventional practice of an insecticide application, suggests that the increased numbers of natural enemies had some influence on the impact of the flood on pest numbers.

Compatibility between flooding and natural enemy abundance, however, does not necessarily equate with pest suppression, given that many natural enemies also feed on detritivores as well as other predators (Straub *et al.* 2008). Many factors may undermine herbivore control, making it possible that greater predator abundance and diversity would not result in an increase in herbivore suppression – predator community compositions often change, and with these shifts, the prey targeted may shift as well. Factors affecting herbivore control include predator-predator interference (Sih *et al.* 1998), intraguild predation (Polis 1991; Finke and Denno 2005), and variable predator hunting modes and ranges (Preisser *et al.* 2007). However, given that the insecticide application itself controlled pests in the spray treatment, it is likely that the increased numbers of natural enemies in the flood treatment did in fact work to some extent in reducing pest pressure.

Spiders were by far the most abundant predators found, and were more common in flooded than sprayed beds. Because the feeding habits of spiders in commercial cranberry systems have not been well documented, it is unclear to what extent increased spider density would lead to a decrease in pest caterpillars. While many spiders are generalist predators and are likely to consume caterpillars opportunistically, some species of spiders are unlikely to encounter caterpillars on a regular basis (Bardwell and Averill 1997). Identifying spiders to a finer taxonomic resolution, as well as directly studying their feeding habits or using gut-content analyses, would clarify the link between spider density and pest suppression.

The parasitoid wasps we collected belong largely to the superfamily Chalcidoidea, as well as several members of the Ichneumonidae and Braconidae. Because many parasitoids are host-specific or attack only a narrow group of species (Van den Bosch and Telford 1964), they are unlikely to prey-switch away from consuming

their target prey, and thus might not be strongly affected by the abundance or paucity of alternate prey species. Although the majority of these wasps parasitise moth larvae, they were not identified to a level of specificity to be sure of their host breadth. Pest caterpillar parasitism rates in flooded versus sprayed cranberry systems might be better assessed by rearing parasitoids from sentinel or wild-caught pest caterpillars. Rearing parasitoids in this way would control for variability in arthropod movement or differences in prey/host availability, and thereby demonstrate more accurately whether flooding conserves the specific parasitoids that target cranberry pest caterpillars.

We had expected that, by removing significant numbers of detritivores, the flood would eliminate this alternate prey resource and force hungry generalist predators to consume proportionally more herbivores, which is likely to include pest caterpillars (Fig. 1). Specifically, we had expected that the decline to near zero in Collembola populations, following both flood and spray treatments, would force spiders to prey-switch and drive down herbivore populations, most dramatically in the flooded beds that exhibited higher spider densities. However, we did not find any treatment effect on the abundance of herbivores or detritivores in this study. However, it is likely that, had we been able to distinguish between the direct effects of the flood and the spray, compared with indirect effects from the increase in natural enemies following the flood (such as with a no-flood, no-spray treatment), we may have found fewer herbivores in treatments with increased natural enemies present.

Altogether, our data show that there were greater numbers of natural enemies in flooded compared with sprayed beds, with both treatments leading to similar trends in pest moth and detritivore densities. Increased numbers of natural enemies in flooded beds is likely to increase biological control efforts, keeping herbivore populations in check and strengthening integrated pest management programmes. Thus, the spring flood in cranberries is not only compatible with biological control, but also appears to be similar in effectiveness to an insecticide application. Replacing a chemical control tactic with a cultural control tactic, which promotes carnivore survival, represents an example of a sustainable,

best-management strategy. Further work in this vein may more directly elucidate the mechanisms driving the effect, and thereby provide evidence of conservation biological control.

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## References

- Barbosa, P. 1998. Agroecosystems and conservation biological control. *In* Conservation biological control. *Edited by* P. Barbosa. Academic Press, San Diego, California, United States of America. Pp. 39–54.
- Bardwell, C.J. and Averill, A.L. 1997. Spiders and their prey in Massachusetts cranberry bogs. *Journal of Arachnology*, **25**: 31–41.
- Birkhofer, K., Wise, D.H., and Scheu, S. 2008. Subsidy from the detrital food web, but not microhabitat complexity, affects the role of generalist predators in an aboveground herbivore food web. *Oikos*, **117**: 494–500.
- Bommarco, R., Miranda, F., Bylund, H., and Björkman, C. 2011. Insecticides suppress natural enemies and increase pest damage in cabbage. *Journal of Economic Entomology*, **104**: 782–791.
- Cockfield, S.D. and Mahr, D.L. 1992. Flooding cranberry beds to control blackheaded fireworm (Lepidoptera: Tortricidae). *Journal of Economic Entomology*, **85**: 2383–2388.
- Colquhoun, J. and Johnson, H. 2010. Sustainable cranberry production for a vibrant future: the Wisconsin experience. University of Wisconsin-Madison Horticulture Department, Madison, Wisconsin, United States of America.
- DeBach, P. 1947. Predators, DDT, and citrus red mite populations. *Journal of Economic Entomology*, **40**: 598–599.
- DeBach, P. 1964. The scope of biological control. *In* Biological control of insect pests and weeds. *Edited by* P. DeBach. Reinhold Publishing Corporation, New York, New York, United States of America. Pp. 3–20.
- DeBach, P. and Rosen, D. 1991. Biological control by natural enemies. Cambridge University Press, Cambridge, United Kingdom.



- Deutsch, A. 2014. Integrating pest management in Wisconsin cranberry marshes: pheromone-based mating disruption and insect phenology models. M.Sc thesis. University of Wisconsin, Madison, Wisconsin, United States of America.
- Fagan, W.F., Hakim, A.L., Ariawan, H., and Yuliyantiningsih, S. 1998. Interactions between biological control efforts and insecticide applications in tropical rice agroecosystems: the potential role of intraguild predation. *Biological Control*, **13**: 121–126.
- Finke, D.L. and Denno, R.F. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters*, **8**: 1299–1306.
- Kuusk, A.-K. and Ekbohm, B. 2010. Lycosid spiders and alternative food: feeding behavior and implications for biological control. *Biological Control*, **55**: 20–26.
- Li, S.Y., Henderson, D.E., and Myers, J.H. 1994. Selection of suitable *Trichogramma* species for potential control of the blackheaded fireworm infesting cranberries. *Biological Control*, **4**: 244–248.
- Mahr, D.L. 1999. Biological control in a high-value native crop: status, opportunities, and constraints in cranberry. In *Biological control of native or indigenous insect pests: challenges, constraints, and potential*. Edited by G.J. Brewer and L.D. Charlet. Thomas Say Publications, Lanham, Maryland, United States of America. Pp. 64–90.
- Marc, P., Canard, A., and Ysnel, F. 1999. Spiders (Araneae) useful for pest limitation and bioindication. *Agriculture, Ecosystems & Environment*, **74**: 229–273.
- Marucci, P.E. and Moulter, H.J. 1992. Biological control of sparganothis fruitworm on cranberries in New Jersey, part II. Cranberries, **56**: 14–15.
- Polis, G. 1991. Complex trophic interactions in deserts: an empirical critique of food-web theory. *American Naturalist*, **138**: 123–155.
- Preisser, E.L., Orrock, J.L., and Schmitz, O.J. 2007. Predator hunting mode and habitat domain alter nonconsumptive effects in predator-prey interactions. *Ecology*, **88**: 2744–2751.
- Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., and Lestari, A.S. 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology*, **77**: 1975–1988.
- Sih, A., Englund, G., and Wooster, D. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, **13**: 350–355.
- Simser, D. 1994. Parasitism of cranberry fruitworm (*Acrobasis vaccinii*; Lepidoptera: Pyralidae) by endemic or released *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae). *Great Lakes Entomologist*, **27**: 189–196.
- Singleton, M. 2010. Biological impacts of insecticide use in the Wisconsin cranberry industry. M.Sc thesis. University of Wisconsin, Madison, Wisconsin, United States of America.
- Smith, R.F., Apple, J.L., and Bottrell, D.G. 1976. The origins of integrated pest management concepts for agricultural crops. In *Integrated pest management*. Edited by J.L. Apple and R.F. Smith. Springer United States Plenum Press, New York, New York, United States of America. Pp. 1–16.
- Steffan, S., Singleton, M., Sokja, J., and Zalapa, J. 2012a. Removal of arthropods in the spring “trash floods”. *Cranberry Crop Management Newsletter*, **25**: 3–4.
- Steffan, S., Singleton, M., Sokja, J., Zalapa, J., Dittl, T., and Harbut, R.D. 2012b. Early-season flooding for insect pest control. In *Wisconsin Cranberry School 2012 Proceedings*, Stevens Point, Wisconsin, 11–12 January 2012. Edited by R. Harbut. Wisconsin State Cranberry Growers Association, Wisconsin Rapids, Wisconsin, United States of America. Pp. 24–28.
- Stern, V.M., Smith, R.F., van den Bosch, R., and Hagen, K.S. 1959. Integrated control concept. *Hilgardia*, **29**: 81–101.
- Straub, C.S., Finke, D.L., and Snyder, W.E. 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control*, **45**: 225–237.
- Systat Software. 2013. SigmaPlot 12.5 user’s guide. Systat Software Incorporated, San Jose, California, United States of America.
- Teixeira, L.A.F. and Averill, A.L. 2006. Evaluation of flooding for cultural control of *Sparganothis sulfureana* (Lepidoptera: Tortricidae) in cranberry bogs. *Environmental Entomology*, **35**: 670–675.
- Van den Bosch, R. and Telford, A.D. 1964. Environmental modification and biological control. In *Biological control of insect pests and weeds*. Edited by P. DeBach. Reinhold Publishing Corporation, New York, New York, United States of America. Pp. 459–488.