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RESEARCH ARTICLE

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Pollinators, pests and yield—Multiple trade-offs from insecticide use in a mass-flowering crop

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Abstract

1. Multiple trade-offs likely occur between pesticide use, pollinators and yield (via crop flowers) in pollinator-dependent, mass-flowering crops (MFCs), causing potential conflict between conservation and agronomic goals. To date, no studies have looked at both outcomes within the same system, meaning win-win solutions for pollinators and yield can only be inferred.
2. Here, we outline a new framework to explore these trade-offs, using red clover (*Trifolium pratense*) grown for seed production as an example. Specifically, we address how the insecticide thiacloprid affects densities of seed-eating weevils (*Protapion* spp.), pollination rates, yield, floral resources and colony dynamics of the key pollinator, *Bombus terrestris*.
3. Thiacloprid did not affect the amount of nectar provided by, or pollinator visitation to, red clover flowers but did reduce weevil density, correlating to increased yield and gross profit. In addition, colonies of *B. terrestris* significantly increased their weight and reproductive output in landscapes with (compared with without) red clover, regardless of insecticide use.
4. *Synthesis and applications*. We propose a holistic conceptual framework to explore trade-offs between pollinators, pesticides and yield that we believe to be essential for achieving conservation and agronomic goals. This framework applies to all insecticide-treated mass-flowering crops (MFCs) and can be adapted to include other ecological processes. Trialling the framework in our study system, we found that our focal insecticide, thiacloprid, improved red clover seed yield with no detected effects on its key pollinator, *B. terrestris*, and that the presence of red clover in the landscape can benefit pollinator populations.

KEYWORDS
bee, *Bombus*, mass-flowering crop, pesticide, pollination, pollinator, red clover, trade-off, yield

1 | INTRODUCTION

Insect-mediated pollination and pest control are vital regulating services for pollinator-dependent mass-flowering crops (MFCs) (Bommarco et al., 2013). However, intensive agricultural practices have increased the use of agrochemicals and reduced the availability of non-crop habitats, to the detriment of the beneficial insects that provide these services (Goulson et al., 2015; Vanbergen, 2013); causing potential conflict between their needs and those of the farmer. Indeed, farmers need pollinators to visit MFCs to maximise yield (Klein et al., 2007) and partially compensate for yield losses caused by high pest densities (Lundin et al., 2013). In return, MFCs can be an important forage resource for pollinators, particularly generalist flower visitors such as bumblebees (*Bombus* spp.) (Rundlöf et al., 2014; Westphal et al., 2003) that benefit from their abundant, yet transient, floral resources.

Pesticides, particularly neonicotinoid insecticides, can reduce pest densities (Elbert et al., 2008; Jeschke et al., 2011), pollination services (Park et al., 2015; Stanley et al., 2015) and negatively affect pollinator populations (Rundlöf et al., 2015; Woodcock et al., 2016), to potentially affect yield and profit (Lundin et al., 2020). From an agronomic perspective, pollinator risk may be warranted if the benefit of improved pest control outweighs the cost of less pollination in a pollinator-dependent crop. This could be the case if a pest problem is particularly severe or if the cost of reduced pollination is not particularly high for a given crop, for example, oilseed rape which only has a modest requirement for pollination (Klein et al., 2007; Lindström et al., 2015). However, management decisions are frequently based on the *perceived* cost of pest damage relative to the perceived benefit of improved pollination, which, consistent with loss aversion theory, emphasises losses and disadvantages over gains or advantages (Pannell, 1991; Tversky & Kahneman, 1991), contrary to principles of integrated pest management (Gross, 2016). Thus, following a perturbation to the system, such as a pesticide product ban, farmers may use an alternative, potentially less well-studied pesticide, or grow alternative, less pest-sensitive crops that may not be as beneficial to pollinators (Godfray et al., 2014; Kathage et al., 2018; Klatt et al., 2016). On the other hand, if the *perceived* benefits of pollination outweigh the perceived costs of pest damage, farmers may choose to practice integrated pest and pollinator management (IPPM) (Egan et al., 2020; Lundin et al., 2021) or grow organically.

Although previous studies have explored ways that insecticides may affect yield (Catarino et al., 2019; Motzke et al., 2015; Sutter & Albrecht, 2016), or pollinator-populations (Rundlöf & Lundin, 2019), none have looked at both outcomes within the same system; meaning that one can only *infer* win-win solutions for pollinators and yield as either pollinator population or yield dynamics have been overlooked. For example, it is impossible to know if enhanced pollinator visitation to crop flowers (pollination) benefits pollinator populations unless their reproductive output is also measured. Similarly, studies may overlook the relationships that underpin trade-offs, such as between pest density and nectar availability (Lindström et al., 2018; Muola et al., 2017; Sutter & Albrecht, 2016) by only comparing landscapes with and without an insecticide-treated MFC for pollinator populations (Rundlöf & Lundin, 2019).

Here, we present a new framework to explore trade-offs (and underlying relationships) between insecticide use, pollinator populations *and* yield (Figure 1A). In a pollinator-dependent MFC affected by pests, we expect high pest control and pollinator visitation to increase yield (Figure 1B). Furthermore, floral resources (determined by pest damage or the absence of the crop) and insecticide risk (exposure scaled by toxicity) may affect pollinator densities (Figure 1C). Thus yield *and* pollinator populations could benefit from insecticides that effectively control pests (and their potential crop damage), providing they are not too toxic to pollinators (Figure 1B,C).

We chose red clover *Trifolium pratense*, grown for seed production, as our focal pollinator-dependent MFC to exemplify this framework. During crop flowering and maturation, *Protapion* spp., weevil larvae feed on developing clover seeds (Lundin et al., 2012), potentially reducing floral resources for pollinators and seed yields (Figure S1, Appendix S1). We selected thiacloprid as our focal insecticide because it controls weevils in 'conventionally-managed' clover (Lundin et al., 2012). Finally, we chose *B. terrestris* L. as our focal pollinator species as they are important pollinators of clover (Rundlöf et al., 2018) and other crop species (Kleijn et al., 2015). Furthermore, *B. terrestris* are the proposed test species for *Bombus* spp. in European Risk Assessment (EFSA, 2013) and the availability of commercial colonies makes it possible to monitor colony performance with high replication.

For *pollinators*, we hypothesised (1) that insecticide use would increase crop floral resources as pest pressure is controlled, balancing the negative effects of insecticide exposure. Since our focal insecticide, thiacloprid, is relatively low in toxicity to pollinators, we did not anticipate strong negative effects on pollinator populations (Rundlöf & Lundin, 2019). We, thus, expected an overall benefit of clover, regardless of insecticide use, compared with landscapes without clover as there would be more flowers in the landscape. Furthermore, for *yield*, we hypothesised (2) that insecticide use would lower pest densities but not affect pollinator visitation, as pollinators would be unaffected by insecticide use. Thus, the yield would be lower in untreated clover as pollination levels cannot compensate for higher pest densities.

2 | MATERIALS AND METHODS

We used a triplicated landscape design, centred around: (a) clover treated with thiacloprid (flowers + insecticide) with an unsprayed plot, (b) clover *not* treated with thiacloprid (flowers + no insecticide), and (c) non-flowering 'control' sites (no flowers + no insecticides) (Figure 2A). Sites were conventionally managed, except for five 'untreated' clover sites that were organically managed (see Figure 1, Appendix S1). Control sites were apple orchards ($n = 3$) or oilseed rape fields ($n = 4$) that had stopped flowering. No crops other than red clover were in bloom during our study, and no red clover was present in control landscapes (Table S1, Appendix S1). Landscapes

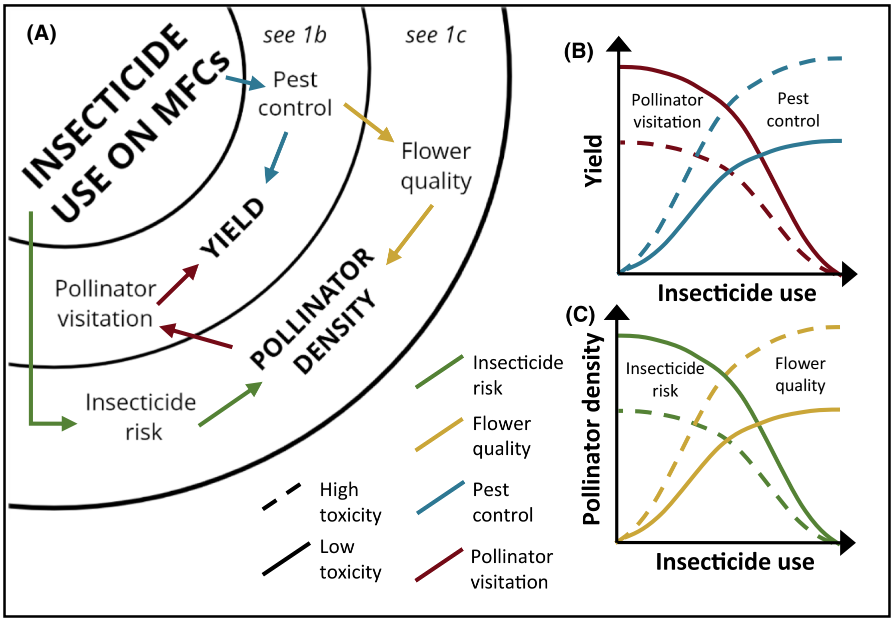

FIGURE 1 To safeguard the yield of mass-flowering crops (MFCs), farmers can use insecticides to control pests (blue lines in A and B). However, in pollinator-dependent MFCs, several other consequences of this insecticide use exist, affecting pollinator density and yield (yellow, green and red lines in A, B and C). Here, we depict the insecticide use trade-offs that emerge from its direct and indirect relationships with pollinator density and yield in a pollinator-dependent MFC (A). Specifically, the modifying effects of pest control and pollinator visitation on the relationship between insecticide use and yield (B) and insecticide risk (exposure scaled by toxicity) and flower quality on the relationship between insecticide use and pollinator density (C). Insecticide toxicity (to both pests and pollinators) may change the shape of these relationships (dashed and solid lines in B and C). However, pest control and pollinator visitation must be similarly affected by the insecticide use not to change the consequences for pollinator density or yield (intersect of dashed versus solid lines on B and C). Thus an insecticide should have high toxicity to pests (dashed blue and yellow lines in B and C) and simultaneously low toxicity to pollinators (solid red and green lines in B and C) to benefit yield and pollinator populations. Figure simplified for brevity; we only consider pests that affect crop flowers and not pest natural enemies.

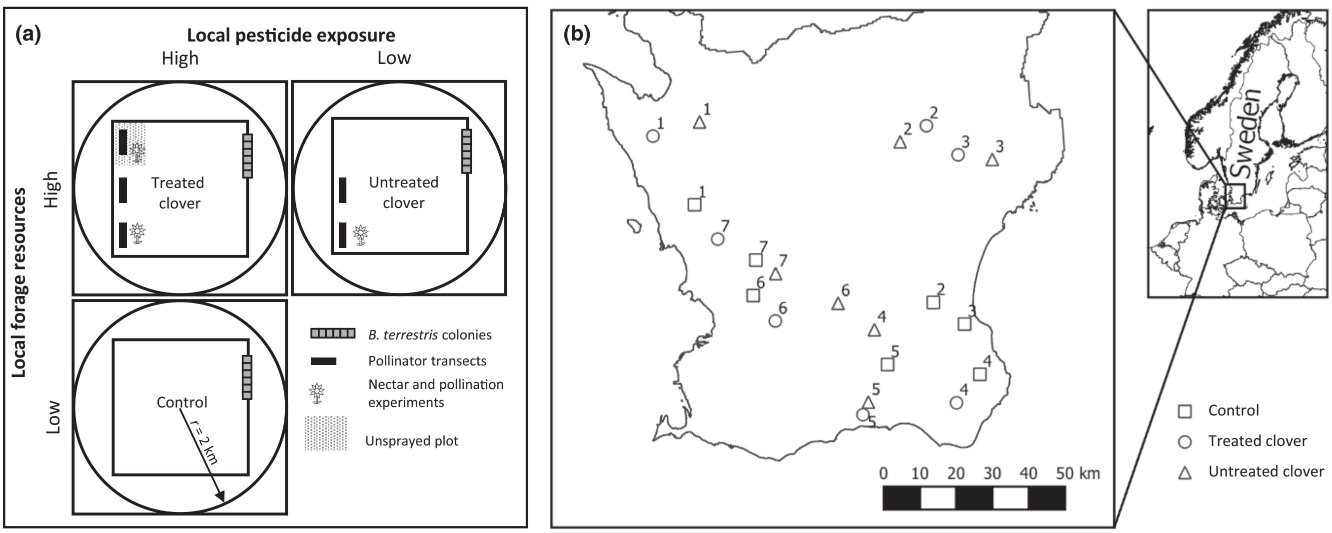

FIGURE 2 A triplicated landscape design centred around (1) clover treated with thiacloprid (flowers + insecticide) with an unsprayed plot, (2) clover not treated with thiacloprid (flowers + no insecticide), and (3) control landscapes with no flowering crops within 2 km (no flowers + no insecticides) to vary the local insecticide exposure and availability of floral resources. (A) Each site had sentinel *Bombus terrestris* colonies, and all clover sites had pollinator transects and nectar and pollination plots. Red clover sites treated with thiacloprid contained an unsprayed plot (12–24 m by 50 m). (B) We replicated this landscape design seven times across southern Sweden; numbers indicate triplet identity. We created our maps in QGIS 3.6.0 based on shapefiles from gadm.org and naturalearthdata.com.

(r = 2 km) were matched within each triplet based on their geographical proximity, the proportion of agricultural land use and semi-natural grassland, focal field size, and for clover sites only, the total amount of mass-flowering clover (Table S1, Appendix S1). Triplets were replicated seven times (in total 21 field sites) and evenly distributed across a gradient of agricultural land (40%–95%) dominated by annual crops such as cereals, typical landscapes for our study area (Figure 2B). All sites (n = 21) were spaced more than 6 km apart, except for two sites 2 km apart, to ensure independent pollinator populations (Vaissière et al., 2011). Within a triplet clover sites were matched (where possible) by clover ploidy (diploid or tetraploid) since ploidy can influence flower size, flower resources and seed production (Boelt et al., 2015; Hederström et al., 2021; Rundlöf et al., 2018). Eight clover cultivars were included in this study: three unique to treated sites, three unique to un-treated sites, and two shared between treated and untreated sites (Appendix S1). According to recommendations, farmers sprayed 'thiacloprid-treated' sites before or during bloom (Table S3, Appendix S1).

2.1 | Data collection

We conducted fieldwork from early June until late August 2019. At all clover sites and in the unsprayed plot at treated sites (Figure 2A), we quantified nectar sugar per flower, weevil, pollinator and flower densities, and experimental seed yields. At all sites (Figure 2A), we quantified pesticide exposure and the growth and reproduction of *B. terrestris* colonies. We needed no ethical approval or licences for our research, and farmers provided permission to access field sites.

2.2 | From clover sites

We quantified the volume (μl) and sugar concentration (g of sugar in 100 g solution) of nectar and thus the total amount of sugar produced over 24 hr from 10 clover flowers, following the formula provided in Prŷs-Jones and Corbet (2011) (Appendix S2). Clover flower head density was estimated from two 0.25 m^2 quadrats randomly positioned along transects in each field (Figure 2A) during early, mid and late bloom and multiplied to give a value per m^2 (Appendix S2).

We quantified the density of the main seed-eating pests, *Protapion* spp., weevils, from 80 flower heads (Figure S3, Appendices S1 and S2).

We recorded bee visitation (from all bee species) to clover flowers from 50 m transects during early, mid, and late bloom (Figure 2A). Transects were walked at a steady pace (~5 min each) with observations made 1 m either side and in front of the recorder. Clover sites within a triplet were surveyed on the same day (Appendix S2).

We estimated experimental seed yield from the number of intact seeds in 10 open-pollinated flower heads 3 weeks after flowering (Appendix S2). Farmers provided the quantity of final seed yield (Table S6, Appendix S1). We combined farmers' income from seed yield with their expenditure on farming practices to estimate the value of red clover production under conventional and organic management at experimental (our site network) and national scales (Table S7, Appendix S1).

2.3 | From all sites

We housed six commercial colonies of *B. terrestris* (Biobest Biological Systems, Belgium) in two large ventilated wooden boxes along a shady boundary of each site, between the 12th and 15th of June, 1 to 24 days before thiacloprid treatment (at treated sites). We confirmed that each colony had a natal queen and recorded their initial 'starting' weight. All colonies were well established with >60 workers and at a similar stage of development with no pupated or emerged gynes. Colonies had no supplementary food.

During the mid-bloom of clover, we collected pollen from 20 *B. terrestris* foragers per site as they returned to their colonies. We sent one pollen pellet from one corbicula of each bee for pesticide residue analysis, including thiacloprid. The other pellet was used to estimate the proportion of red clover pollen in its diet to verify crop use (Appendix S2).

Colony growth, a highly correlated but less invasive metric to estimates of worker force and brood production (Lefebvre & Pierre, 2006; Westphal et al., 2009), was assessed by weighing colonies every 7 days until 26–28 July. We weighed all colonies within a triplet on the same day and systematically varied the site order to prevent temporal bias. We collected and terminated (by freezing) colonies after 6 weeks. Colonies were dissected to estimate reproductive output from the number of intact and eclosed worker/ male cocoons (castes cannot be distinguished without opening, which we did not have resources to do) and queen cocoons (>12 mm, Rundlöf et al., 2015). We quantified queen cocoons from all colonies and worker/male cocoons from four of the six colonies per site. Finally, using digital callipers, we measured the inter-tegular distance (ITD) (a measure of bee size) of up to 12 adult queens, workers and males per colony (in four of the six colonies) (Appendix S2).

2.4 | Statistical analysis

All data analyses and visualisation were carried out in R 3.6.1 (R Core Team, 2019), using linear mixed-effect models in LME4 (Bates et al., 2015) and NLME for colony weight gain only. Models were evaluated for overdispersion, normality and homoscedasticity using diagnostic functions from the 'DHARMA' package (Hartig, 2021).

2.5 | All sites

We compared thiacloprid concentrations in pollen (ng/g) between our landscape types (treated, untreated and control) using a non-parametric Kruskal–Wallis test with multiple pairwise comparisons using a Wilcoxon signed-rank test. We used this initial analysis to validate our assumption that landscape-level insecticide exposure (experienced by pollinators sampled at the focal site) aligned to insecticide use at the focal site. Consequently, we included landscape type (fixed effect, treated, untreated or control) as a proxy for exposure and local flower resource availability. We compared the proportion of red clover pollen in corbicular pollen between landscape types using a binomial generalised linear mixed model (GLMM) (with logit link) with triplet as a random effect.

We compared colony weight change since field placement (g) between landscapes using a linear mixed model (LMM) with week, and the interaction between landscape type and week, specified as fixed effects. Since colony weight change was a repeated measure of the same individual colony each week, a corAR(1) covariance structure was specified. We compared the number of queen cocoons between landscape types using a Poisson GLMM (with log link) with site and triplet as nested random effects. Since one untreated site had a high level of thiacloprid exposure, we conducted our analyses with and without this site (Table S5, Appendix S1).

2.6 | Clover sites

At clover sites, 'landscape type' (treated or untreated) was used as a proxy for exposure. We specified site as a random effect for data collected within sites (nectar, flower density, bee abundance, experimental seed yield) and triplet as a random effect for data collected at a site level (pest abundance, farmer-reported yield). We specified the blooming period as a fixed effect for data collected at multiple time points (flower density and bee abundance). We offset abundance data (bees and pests) by flower density estimated from quadrats and the number of flowers used to emerge the weevils, respectively, to create densities. Finally, we included ploidy as a fixed effect for yield data (experimental and farmer-reported yield). We included flower density as an offset in the bee and pest abundance models to account for the differences in blooming flowers in transects and flowers collected for weevil emergence, respectively. Following these principles, we analysed nectar sugar (g/flower) using a gamma GLMM (with an inverse link) and bee abundance and pest abundance using Poisson GLMMs (with log links). In addition, experimental yield (seeds per flower head), farmer-reported final yield (kg/ha) and flower density (m^2) were analysed with LMMs.

To further isolate thiacloprid's effect, while standardising clover cultivar, we compared nectar sugar, flower density, bee abundance, pest density and experimental seed yields between the sprayed and unsprayed areas of treated sites. These analyses were conducted as above, except that 'treatment' (sprayed or unsprayed) was specified instead of landscape type. Furthermore, ploidy was no longer included as a fixed effect for experimental yield because it overfitted the model.

3 | RESULTS

Thiacloprid residues in bee-collected pollen varied between landscape types (H_2 = 8.13, p = 0.02) and were greatest at colonies in sites treated with thiacloprid (Table 1). On the other hand, the proportion of clover pollen in the bee's diet during mid-bloom was significantly greater at colonies in untreated clover sites (Table 1). Despite there being significantly fewer *Protapion* spp., weevils in treated/sprayed clover flowers than untreated and unsprayed clover flowers (Table 2), there was no difference in the amount of sugar produced (g/flower) (although there was variation between cultivars, Figure S4, Appendix S1) or flower density (m^2) (Table 2). There was no difference in bee visitation, mostly from *Apis mellifera* and *B. terrestris* agg., 45% and 21%, respectively, to clover flowers between treated and untreated, or sprayed and unsprayed clover (Table 2).

Colonies of *B. terrestris* grew to similar weights (Figure 3A) and produced a similar number of queen and worker/male cocoons (Figure 3B) in landscapes with red clover, independent

TABLE 1 Mean (and range) of insecticide concentrations (ng/g) in pollen returned by *Bombus terrestris* foragers to colonies and the proportion of that pollen containing red clover in the three different landscape types

	Clover treated with thiacloprid	Untreated clover	Control without clover	LOD[a]	LOQ[b]
Thiacloprid[c]	44.37 (2-117)[a]	16.68 (<LOD-113)[b]	1.28 (<LOD-4.1)[b]	0.01	0.05
Acetamiprid	0.01 (<LOD-0.1)	0.09 (<LOD-0.65)	0.85 (<LOD-5.5)	0.01	0.05
Clothianidin	<LOD	0.04 (<LOD-0.27)	<LOD	0.04	0.2
Imidacloprid	<LOD	<LOD	<LOD	0.05	0.3
Thiamethoxam	<LOD	<LOD	<LOD	0.02	0.1
Indoxacarb	<LOD	<LOD	3.95 (<LOD-19)	0.4	2
Red clover[d]	0.07 ± 0.02[a]	0.22 ± 0.06[b]	0.01 ± 0.001[c]	—	—

[a]Limit of detection. Values below the LOD assumed zero when calculating means.

[b]Limit of quantification.

[c]Different letters indicate significant differences between landscapes (p < 0.05, paired samples Wilcoxon test).

[d]Model estimated marginal mean proportions (back-transformed from the logit scale) ± *SE*, different letters indicate significant differences between landscapes (p < 0.05, Tukey post hoc tests).

TABLE 2 Model results testing for differences in nectar sugar, flower density, bee visitation, pest densities, colony metrics and yield between landscape types as well as within thiacloprid-treated fields, between the sprayed and unsprayed area. Post-hoc Tukey tests show significant differences

	Model estimated marginal mean ± *SE*	Effect of insecticide treatment/ crop		Tukey post hoc tests	
		χ^2	*p*	Direction	*p*
Nectar sugar (mg/flower)[a]	***TC*** 1.40 ± 0.35 ***UC*** 1.09 ± 0.23	0.64	0.43	–	–
Nectar sugar (mg/flower)[b]	***S*** 1.52 ± 0.26 ***US*** 1.74 ± 0.33	1.63	0.20	–	–
Flower density (m^2)[a]	***TC*** 469 ± 39 ***UC*** 405 ± 39	1.33	0.25	–	–
Flower density (m^2)[b]	***S*** 469 ± 43.5 ***US*** 446 ± 43.5	0.21	0.65	–	–
Bee abundance per flower head[a]	***TC*** 0.39 ± 0.07 ***UC*** 0.41 ± 0.08	0.11	0.74	–	–
Bee abundance per flower head[b]	***S*** 0.37 ± 0.07 ***US*** 0.37 ± 0.07	0.02	0.88	–	–
Protapion spp. weevils per flower head[a]	***TC*** 0.14 ± 0.08 ***UC*** 1.15 ± 0.63	698.43	**<0.001**	–	–
Protapion spp. weevils per flower head[b]	***S*** 0.04 ± 0.04 ***US*** 0.24 ± 0.22	500.91	**<0.001**	–	–
Colony weight change (g)[c]	***TC*** 209.8 ± 21.8 ***UC*** 188.0 ± 21.8 ***C*** 55.2 ± 21.8	24.43	**<0.001**	TC > C UC > C	**<0.001** **0.001**
Worker/male cocoons[c]	***TC*** 403 ± 73 ***UC*** 492 ± 89.1 ***C*** 190 ± 34.4	43.47	**<0.001**	TC > C UC > C	**<0.001** **0.001**
Queen cocoons[c]	***TC*** 84.2 ± 23.05 ***UC*** 79.9 ± 21.88 ***C*** 21.3 ± 5.92	25.91	**<0.001**	TC > C UC > C	**<0.001** **<0.001**
Experimental yield (seeds/flower head)[a]	***TC*** 54.5 ± 15.6 ***UC*** 47.0 ± 11.1	0.22	0.65	–	–
Experimental yield (seeds/flower head)[b]	***S*** 41.0 ± 7.94 ***US*** 27.4 ± 8.01	14.83	**<0.001**	S > US	**<0.001**
Farmer-reported yield (kg/ha)[a]	***TC*** 446 ± 70.1 ***UC*** 266 ± 49.8	***F*** = 4.81	**0.05**	TC > UC	**0.05**

Statically significant values are in bold ($p < 0.05$).

[a]Clover treated with thiacloprid (TC) and untreated clover (UC) (1 *df*).

[b]Sprayed (S) and unsprayed (US) clover at sites treated with thiacloprid (1 *df*).

[c]Clover treated with thiacloprid (TC), untreated clover (UC) or control without clover (C) (2 *df*).

of insecticide treatment, compared with landscapes without red clover (Table 2), and landscape type had no effect on ITD (Table S4, Appendix S1). Including data from the untreated site with high thiacloprid exposure did not affect our results (Table S5, Appendix S1); thus, we chose to retain our full dataset to increase our statistical power.

Although there was no difference in experimental yield between thiacloprid-treated and untreated sites, sprayed clover had significantly greater yields within thiacloprid-treated sites than unsprayed clover (Table 2). Final yields were also greater at thiacloprid-treated than untreated sites (Table 2, Table S6, Appendix S1) and associated conventional management increased gross profit by €242/ha (Table S7, Appendix S1).

4 | DISCUSSION

In our system, greater exposure to thiacloprid did not affect bumblebee colony performance. Although this result was expected (hypothesis 1), it was not achieved via the positive effect of improved resources balancing the negative effect of exposure that we had hypothesised. Instead, it appears to have been achieved by the low toxicity (despite higher exposure) and similar amount of floral resources (both nectar sugar and flower density) at thiacloprid-treated, relative to untreated clover sites. These findings resulted in an overall benefit from clover, irrespective of insecticide use, compared to landscapes without clover, evidenced by heavier colonies with more reproductives. Indeed, late-flowering MFCs such as red clover may particularly

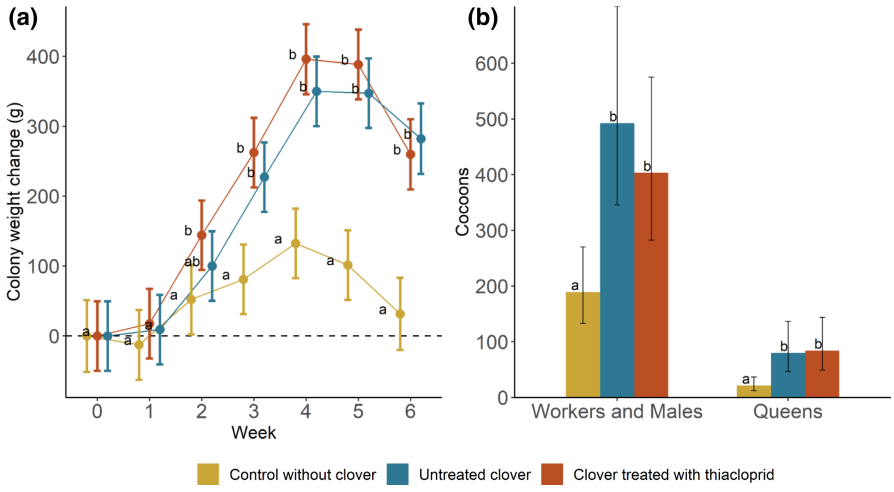

FIGURE 3 Average (A) weekly weight change of *Bombus terrestris* colonies since field placement, and (B) production of workers/ males and new queens in relation to landscape type ($n = 6$ colonies per site). Control landscapes were apple or oilseed rape that was no longer flowering; these sites had no flowering crops within 2 km radius. Means and 95% confidence intervals are based on model-estimated least-square marginal means. Different letters indicate significant differences between landscapes ($p < 0.05$, Tukey post hoc test).

benefit the production of reproductives (Knapp et al., 2018; Riggi et al., 2021; Rundlöf et al., 2014), especially if flowering coincides with when colonies are at their peak in worker numbers (Hovestadt et al., 2019), as was the case with our commercial colonies.

As expected (hypothesis 2), weevil densities were lower where thiacloprid was used. However, bee visitation rates remained similar - as pollinators appeared unaffected by weevils or thiacloprid use (hypothesis 1). High weevil density reduced the experimental yield of unsprayed clover (within treated sites) and, to a lesser extent, final yield in untreated relative to treated clover. This little difference in final yield may be because diploid cultivars, unique in our study to untreated, organically-managed sites, are more able to set seed than tetraploid cultivars (Boelt et al., 2015; Hederström et al., 2021; Jing et al., 2021; Vleugels et al., 2015) and thus able to compensate (to some extent) for pest damage. Fertile cultivars, also observed within oilseed rape (Lankinen et al., 2018), are important for farmers wishing to maximise their yields (Boelt et al., 2015; Knapp et al., 2016), and fertility should be considered as an additional trait alongside pest-resistance and pollinator-dependency/attraction within the IPPM framework (Egan et al., 2020; Lundin et al., 2021). Red clover growers of tetraploid (lower seed set and fertility) or organic (higher pest density) cultivars are paid a higher yield price (per kilo) to compensate for lower potential yields (Jordbruksverket, 2020; Reganold & Wachter, 2016). However, our results show conventional management to be 37% (€242/ha) more profitable than organic management (Table S7, Appendix S1), suggesting that organic red clover farmers are not adequately compensated for their lower yields. The difference in profit between management types is even larger at a national scale (Table S7, Appendix S1), but this may be influenced by the distribution of organic production to more unproductive land (Rundlöf & Smith, 2006). Furthermore, weed control and harvest technique and conditions, in addition to pollination, insect pest control and cultivar choice, are also highly likely to influence yield (Langer & Rohde, 2005), and these factors were not investigated in this study.

Since clover seed yields tend to be higher and more profitable when there are fewer seed-eating weevils and weevils are effectively controlled by thiacloprid, its use (as part of IPPM) could be considered. Indeed, thiacloprid had no adverse effect on bee visitation or colony dynamics and is relatively low in toxicity to bumblebees in our system (Rundlöf & Lundin, 2019), unlike other neonicotinoids such as clothianidin and thiamethoxam (Rundlöf et al., 2015; Woodcock et al., 2017). However, field-realistic studies on the effects of thiacloprid on pollinators are variable (Ellis et al., 2017; Havstad et al., 2019) and dependent on the spatiotemporal patterns of pesticide use and pollinator activity (Sponsler et al., 2019). Likewise, effects on individual bumblebees are likely obscured by the colony's organisational redundancy (e.g. Stanley & Raine, 2016), similar to honeybees (Franklin & Raine, 2019). Furthermore, the timing of exposure relative to the bumblebee's colony cycle can also lead to different effects. For example, queen bumblebees are particularly sensitive during nest initiation (Baron et al., 2017; Leza et al., 2018), which was not investigated in our study. Nonetheless, the vulnerability of bumblebees in their solitary life-history stage demonstrates how harmful pesticides could be to solitary pollinator species due to the direct link between their survival and reproductive success. Thus, crop systems that are more dependent than ours on solitary bee pollination, such as apple (Blitzer et al., 2016), may experience more negative effects from pesticide use.

Consequently, it would be precautionary for pollinators and yield to avoid using insecticides during crop bloom (Egan et al., 2020; Lundin et al., 2021) or grow organically. Organic management is particularly precautionary for beneficial insects as pesticide exposure is reduced over space, as less of the landscape is treated, and time, as fewer flowering (crop and non-crop) species are treated during the season (Botías et al., 2015; Reganold & Wachter, 2016). Although this precautionary approach may have little justification from a neoclassical short-term economic perspective (i.e. under profit maximisation), it may benefit farmers of pest and pollinator-dependent crops in the long term if the value of sustaining insect-mediated pollination and pest control are high. However, perceptions of these values may vary with growers' discount rates (intertemporal preferences) (Soman et al., 2005). Organic landscapes are also less likely to expose beneficial insects to multiple pesticides that may have synergistic, negative effects on their populations, for example, between some insecticides and fungicides that commonly co-occur in various crop systems (Raimets et al., 2017; Sgolastra et al., 2016). Indeed, organic management has been shown to benefit pollinators (Carrié et al., 2018; Rundlöf et al., 2008), natural enemies (Crowder et al., 2010; Garratt et al., 2011) and yield (Blitzer et al., 2016; Woodcock et al., 2019). However, findings are dependent on landscape context, and, on a global scale, yield is higher in conventional systems (Seufert et al., 2012; Smith et al., 2020). Indeed, organic production is not a panacea for pollinators; diversified cropland, reduced field size and semi-natural habitat may outweigh the benefits of no synthetic pesticides to increase biodiversity and multi-functionality in all landscapes (Tscharntke et al., 2021).

While quantifying insecticide effects on pollinators is vital, there are likely to be many more unintended effects in the ecosystem. Indeed, thiacloprid has been shown to have a negative impact on aquatic systems (Englert et al., 2012), and this, combined with concerns over human health (EFSA et al., 2019), has meant that the approval of thiacloprid will not be renewed in the European Union in 2020 (European Commission, 2021). Although acetamiprid, another relatively bee-safe neonicotinoid (EFSA, 2016), is a likely substitute, farmers may consider entirely different management strategies. These could include using an alternative, potentially less well-studied insecticide, cultivating less pest-sensitive crops that may not be as beneficial to pollinators (Godfray et al., 2014; Ratnieks et al., 2018) or relying on non-insecticidal weevil control options such as spatial planning (Lundin et al., 2021). Mass-flowering clover benefits bumblebee colonies; thus, using a (potentially) more toxic insecticide or replacing it with a less bee-attractive crop could negatively affect bumblebee colonies in the landscape.

5 | CONCLUSIONS

Insecticide, pollinator and yield trade-offs are underpinned by several factors: toxicity and patterns of insecticide use, pollinator dependency and pest susceptibility of the crop, the life history of the focal pollinator and pest species, and the surrounding landscape, which are likely to vary between crop fields even within a season. Thus, the value of our framework lies in its realistic simplicity that makes it adaptable to any pollinator-dependent insecticide-treated MFC, regardless of the focal insecticide, pollinator or pest. Consequently, our framework is a valuable tool for scientists and practitioners wishing to understand insecticides' biological or social trade-offs for yield, profit and bee colony performance – key agronomic and conservation concerns. For yield, balancing losses from pest damage against gains from pollination is vital to ensure that on-farm management does not preferentially focus on remedying losses from pests at the potential expense of gains from pollinators and other beneficial insects. For pollinator populations, balancing the crop's nutritional value at the flower and landscape scales against the disadvantages of insecticide exposure and impacts is vital to ensure that scientists conduct holistic research on the socially and ecologically complex issue of insecticide use in MFCs. Finally, our framework can evolve to include additional environmental factors that indirectly, for example, natural pest control, or directly, for example, soil quality, influence yields so that farmers can prioritise key regulating services in their management for optimal crop yields.

AUTHOR CONTRIBUTIONS

Jessica L. Knapp substantial contributions to conception and design, acquisition of data, analysis and interpretation of data and drafted the article; Adam Bates, Theresia Krausl, Glenn P. Svensson acquisition of data; Ove Jonsson acquisition of data, analysis and interpretation of data; Björn Klatt acquisition of funding and interpretation of data; Ullrika Sahlin acquisition of funding, analysis and interpretation of data; Maj Rundlöf acquisition of funding, substantial contributions to conception and design, acquisition of data and interpretation of data. All authors critically revised the manuscript for important intellectual content.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.cfxpnvx84 (Knapp et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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