Integrated pest and pollinator management – expanding the concept

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The objective of integrated pest and pollinator management (IPPM) is to co-manage for pest control and pollination goals. Departing from the well-established concept of integrated pest management, we include pollinator management in a hierarchical decision support system of management actions. We depict this support system as an IPPM pyramid. Priority is given to proactive measures at the base of the pyramid, which are undertaken through landscape and crop field management of mobile organisms, primarily arthropods. Farther up the pyramid, practices in the form of reactive use of biotic and abiotic inputs should align with basal actions. The goal of IPPM is to minimize trade-offs, and to maximize co-benefits and synergies between pest and pollinator management. We contend that IPPM has the potential to contribute to sustainable pest control and crop pollination, as well as provide broader environmental benefits.

Front Ecol Environ 2021; 19(5): 283–291, doi:10.1002/fee.2325

Integrated pest management (IPM) is a widely established decision support system that emphasizes the use of multiple methods to control pests (Kogan 1998). There are several definitions of IPM that can be broadly divided into two basic approaches, one that focuses on the judicious use of pesticides informed by monitoring and thresholds, and another more comprehensive form that emphasizes capitalizing on agroecosystem functions prior to intervention with reactive pest control options, such as chemical control (Zalucki *et al.* 2009). Integrated crop pollination (ICP) – a more recent concept that is analogous to IPM but applies to pollinators – emphasizes the integration of multiple strategies to achieve reliable and sustainable crop pollination (Isaacs *et al.* 2017). Integrated pest and pollinator management (IPPM) has been proposed to integrate pollinator management into IPM (Biddinger and Rajotte 2015). Initially, IPPM was essentially analogous to the first general IPM approach mentioned above because it focused on adapting chemical control to protect pollinators, but bypassed more comprehensive opportunities for co-managing pest control and pollination. Here, we expand the IPPM concept by emphasizing proactive landscape and crop field management as a crucial basis of IPPM (see also Egan *et al.* 2020), which can be supplemented with reactive human-based inputs like pesticides.

In a nutshell:

- There are numerous reasons to co-manage for pest control and pollination based on the often overlapping ecology of pests, natural enemies, and pollinators, and their non-independent effects on crop yield
- Integrated pest and pollinator management (IPPM) is a framework that can be used to co-manage for ecosystem functions driven by pests, natural enemies, and pollinators
- The IPPM pyramid represents a hierarchical decision support system that prioritizes base-level, proactive actions over apex, reactive actions to achieve both pest and pollinator management goals
- Strategies for simultaneously managing for pest control and pollination goals through IPPM are presented

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A broadened IPPM concept entails management of agroecosystem functions driven by pests, natural enemies, and pollinators, with arthropods as the central group of organisms responsible for each function (Losey and Vaughan 2006; Oerke 2006; Klein *et al.* 2007). Although traditionally considered separately, there are numerous reasons for co-managing crop pollination and pest control. The overlapping phylogeny and ecology of arthropod pests, natural enemies, and pollinators create potential – as well as challenges – for co-management. The three functional groups, of which one (pests) provides disservices, share many environmental and anthropogenic drivers (Figure 1). For example, habitat complexity at local and landscape scales can benefit both pollinators and natural enemies that use alternative habitats and resources at different times in their life cycles (Shackelford *et al.* 2013). The importance of co-management is magnified by the fact that the same species can be responsible for herbivory, predation, and pollination; for example, larval hoverflies are predators but adult hoverflies are pollinators, and some bee species (eg *Trigona spinipes*) can be either pollinators or pests depending on the type of crop (Saunders *et al.* 2016). Challenges for IPPM are clearly evident, particularly in terms of pesticide use that could harm beneficial non-target arthropods. IPPM approaches comprise strategies that tip the balance in favor of shared benefits for pollination and pest control.

An additional reason to co-manage pests and pollinators is that the yield of crops pollinated by animals is often interactively determined by both pollination and pest control

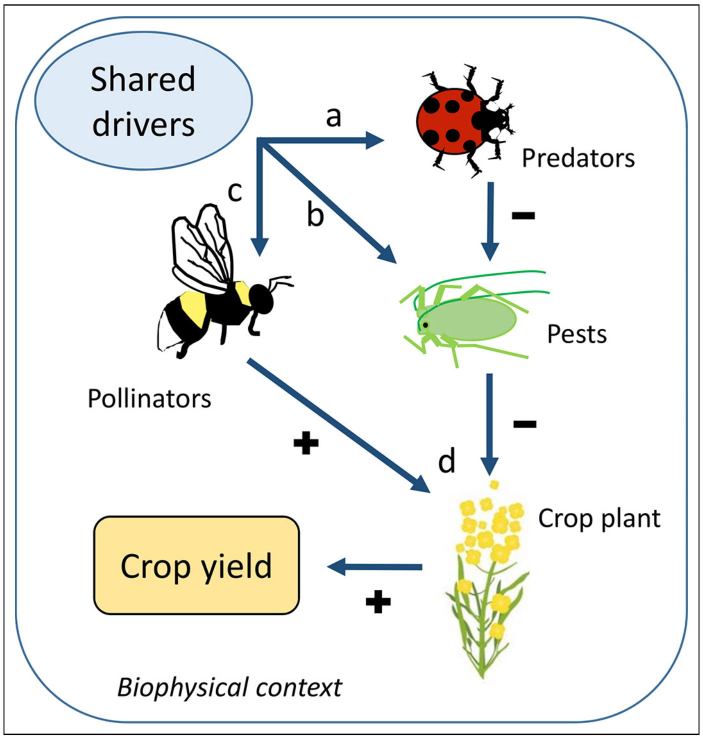

Figure 1. Ecological interactions among pests, natural enemies (predators), pollinators, and crop plants influence crop yield. Interdependence of pest and pollinator management is created by two distinct mechanisms: (a–c) shared drivers and (d) effects of the organism groups on one another's functioning. These interactions can be modified by the biophysical context (eg climate or geographic region). Arrows indicate links between drivers, organisms, and crop yield. Plus (+) and minus (–) signs indicate positive and negative relationships, respectively. Additional details about shared drivers are presented in Figure 2 and Table 1.

(Figure 1; Tamburini *et al.* 2019). More specifically, pollination benefits are often enhanced under effective pest control, and this appears to be especially true for pest damage to reproductive structures of crop plants (Tamburini *et al.* 2019). For this reason, the potential economic gains of enhancing crop yield that result from either pest or pollinator management are not determined independently. IPPM approaches take this non-independence into account and harness the synergistic opportunities presented by effective co-management. Crop yield is impacted by both pest damage and pollination, and provides a common currency for uniting the two processes (Figure 1; Saunders *et al.* 2016). Conducting yield-based analyses allows consideration of net benefits or costs by quantifying the marginal gains or losses of various strategies and actions that support pest control and pollination or increase one at the expense of the other.

The IPPM pyramid

A comprehensive IPM program is commonly depicted in the form of a pyramid (eg Hokkanen 2015). The pyramid shape illustrates a tiered decision support system, with priority given to proactive actions at the base and reactive actions at the top, which are implemented only if proactive actions are insufficient for managing pests or keeping damage below defined thresholds. A parallel hierarchical decision structure can be used for managing pollination, where pest and pollinator co-management form an IPPM pyramid (Figure 2; see also Egan *et al.* 2020). Actions at the base of the IPPM pyramid make greater use of ecological processes (eg ecosystem services delivered by natural enemies and pollinators; Dainese *et al.* 2019) or of the structure and design of managed and natural elements of landscapes that directly suppress pests (Gurr *et al.* 2017). Actions at the top replace biodiversity-based practices with synthetic management alternatives, such as pesticides. In the following sections, we review pest and pollinator management practices and highlight potential IPPM synergies, co-benefits, or trade-offs at each level of the pyramid. A summary of the evidence for effects of actions on pests, natural enemies, and pollinators at each level of the pyramid is presented in Table 1.

Landscape management

Pest management at the bottom of the IPPM pyramid targets actions at the landscape scale that directly suppress pests and support diverse and abundant communities of natural enemies that promote biodiversity-based pest control (Gurr *et al.* 2017). Similarly, landscape-scale actions can support pollinators and pollination services (Isaacs *et al.* 2017). Protecting or restoring natural or semi-natural habitat, increasing the diversity of both wild and crop plants, and ensuring resource continuity for natural enemies and pollinators forms the base of the IPPM pyramid.

Abundance of semi-natural habitat within the landscape can in some cases benefit natural enemies and pest control (Chaplin-Kramer *et al.* 2011; Rusch *et al.* 2016). However, responses among natural enemies differ depending on the type of semi-natural habitat; moreover, pests can also benefit from semi-natural habitat, resulting in variable outcomes for pest control (Karp *et al.* 2018). Semi-natural habitats in agricultural lands tend to benefit pollinators more consistently (Kennedy *et al.* 2013). The more idiosyncratic response of pest control might be due to the higher tri-trophic complexity (eg Snyder and Wise 2001) and taxonomic diversity of functionally important organisms involved in determining pest control versus pollination outcomes (Karp *et al.* 2018).

Crop type and diversity along with landscape configuration affect pest and pollinator management. Reducing the spatio-temporal continuity of a host crop could effectively reduce pest abundance, particularly of host-specialized pests (Figure 3; Root 1973; Delaune *et al.* 2019), whereas increased crop diversity benefits biological pest control by naturally occurring predators (Redlich *et al.* 2018). The effects of crop diversity on pollinators may be more complex and depend on crop identities and management intensity, where mass-flowering crops (but not intensively managed cereals) promote pollinator populations (Figure 3; Rundlöf *et al.* 2014; Hass *et al.* 2018).

Achieving IPPM co-benefits may therefore require more nuanced selection of crop composition rather than simply increasing crop diversity. Landscape configurations in the form of landscapes with small and irregularly shaped fields and patches of semi-natural habitat benefit both pollination and pest control (Martin *et al.* 2019).

Advancing IPPM at the landscape scale will require a deeper understanding of the ecology of pests, natural enemies, and pollinators. The goal at the landscape scale should be to ensure resource continuity for pollinators and natural enemies while decoupling resources for pests. Taking advantage of differences in mobility among organism groups might render co-management opportunities by ensuring resource continuity in time and space at scales suitable for beneficial arthropods but not for species that damage crops (Figure 3; Thies *et al.* 2005). Another opportunity is to take advantage of differences in host-plant and habitat preferences between pests and pollinators, for instance by substituting host crop cover with alternative non-host plants to disrupt resource continuity for pests while ensuring that substituted crops provide resources for pollinators and natural enemies (Schellhorn *et al.* 2015; Delaune *et al.* 2019). At the landscape scale, this can be achieved for multiple crops that benefit from generalist pollinators and natural enemies but suffer primarily from specialized pests.

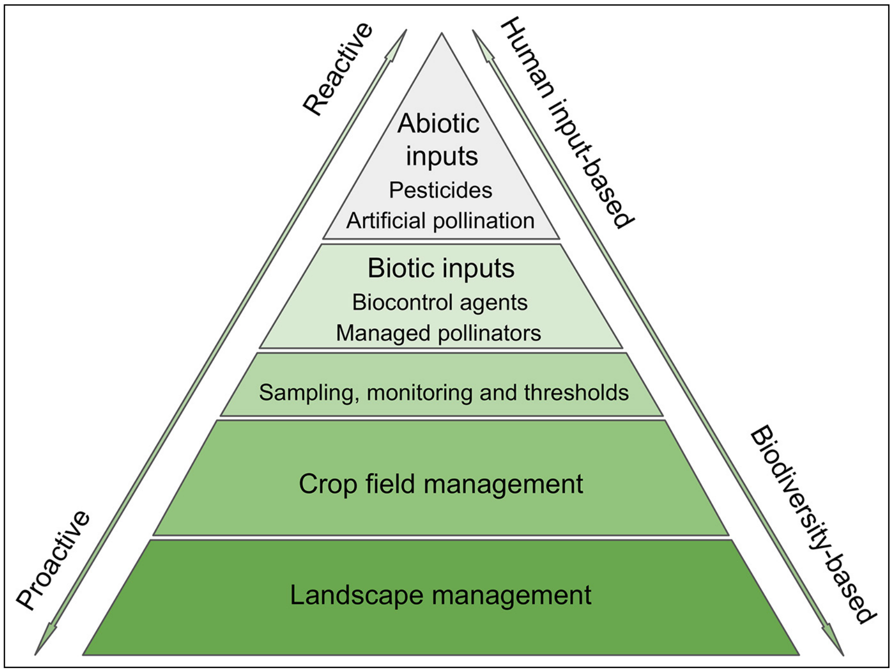

Figure 2. The integrated pest and pollinator management (IPPM) pyramid. The pyramid represents a hierarchical decision support system, prioritizing base level, proactive actions over apex, reactive actions to achieve pest and pollinator management goals. Actions at the base utilize ecosystem functions to a greater degree, whereas human inputs dominate at the apex. Sampling, monitoring, and thresholds occupy the center of the pyramid and guide which actions to implement.

Crop field management

A wide variety of field-based actions have been developed to prevent pest outbreaks, collectively referred to as "cultural control" approaches (Bajwa and Kogan 2004). Cultural control includes such actions as increasing within-field plant diversity, planting pest-resistant cultivars, and modifying soil tillage and agronomic inputs like fertilization and irrigation. For several of these practices, impacts on pollinators are poorly understood and considerable research is needed before IPPM can be implemented successfully.

Plant diversity can be increased in the cropped field or along its borders to promote pest control, through both bottom-up and top-down paths (Root 1973); examples include intercropping (Iverson *et al.* 2014); cover cropping (Schipanski *et al.* 2014); addition of non-cropped vegetation, such as flower strips or hedgerows (Tschumi *et al.* 2015; Morandin *et al.* 2016); and reducing weed control (DiTommaso *et al.* 2016). Flower strips and hedgerows (Blaauw and Isaacs 2014; Morandin *et al.* 2016) and reduced weed control (DiTommaso *et al.* 2016) can also promote pollinators and crop pollination. Although the effects of intercropping and cover cropping on pollinators are less well understood, these approaches show promise when the cropping system is diversified through the addition of flowering herbs (Mallinger *et al.* 2019). Cropping systems containing greater plant diversity have often been developed separately for pest control and pollination. Careful selection of plants characterized for their effects on pests, natural enemies, and pollinators (Lundin *et al.* 2019), as well as

Table 1. Summary of effects of actions across the levels of the integrated pest and pollinator management pyramid on pests, natural enemies, and pollinators

	Pests	Natural enemies	Pollinators
Artificial pollination	↔	↔	↔
Pesticide use	↓	↓	↓
Biocontrol agents	↓	↑	↔
Managed pollinators	↔	↔	↑
Irrigation	↑↓	↓	↑
Organic fertilizer	↓	↑	↔
Flower strips	↑↓	↑	↑
Crop diversity	↓	↑	↔
Semi-natural habitat	↑↓	↑↓	↑

Notes: upward pointing arrows = positive effects; downward pointing arrows = negative effects; sideways arrows = neutral effects. Upward and downward pointing arrows in the same cell indicate both positive and negative effects. Arrows represent generalizations and should not be interpreted as universally true (see also Panel 1).

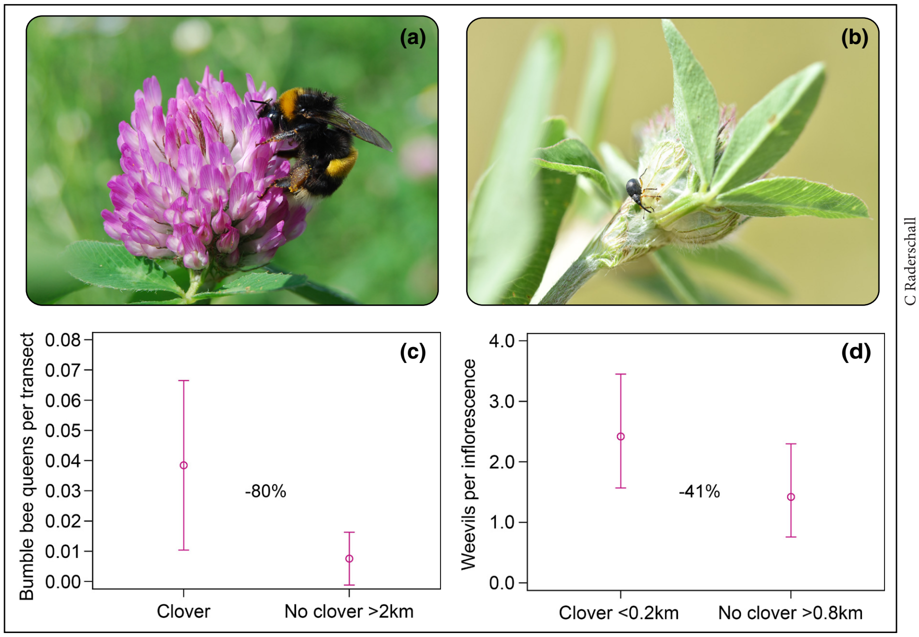

Figure 3. Landscape-scale trade-offs between promoting pollinators and limiting pests. In fields of red clover (*Trifolium pratense*) grown for seed, (a) bumblebees (*Bombus* spp) are pollinators, and (b) clover seed weevils (*Protapion* spp) are pests. (c) Greater numbers of bumblebee queens are detected at sites within 2 km of clover fields than at sites lacking clover (80% fewer bumblebee queens in sites lacking clover; Rundlöf *et al.* 2014), whereas (d) seed weevil abundance tends to be higher and lower at sites where the nearest clover field is <0.2 km and >0.8 km away, respectively (41% fewer weevils in fields without clover within 0.8 km; Lundin *et al.* 2016). Therefore, it may be possible to limit pests by spacing fields far enough apart so that pest movement is restricted while still promoting pollinators. Error bars indicate 95% confidence intervals (CI) around the means.

their weediness, would allow for diversification strategies that support natural enemies and pollinators without benefitting crop pests or exacerbating weed-associated problems. Improving our general understanding of resource use of functionally important arthropods is needed to fully capture the potential of plant diversification at the field scale as an IPPM tool.

Using crop cultivars that are resistant to pests is an essential tool for pest management (Stenberg 2017). For pollinator management, a similar strategy is to breed for or select cultivars that are attractive to pollinators. A key challenge for breeding and cultivar selection from an IPPM perspective would be the simultaneous mapping and consideration of multiple crop traits, including pest resistance, pollinator dependency and attraction, and crop yield.

Pest management for crops also entails modification of agronomic inputs, such as fertilizer and water. For example, organic fertilizers can improve top-down pest control via beneficial effects on predators and bottom-up control by enhancing crop defense against pests (Rowen *et al.* 2019) while at the same time increasing crop flower visitation by pollinators (Banaszak-Cibicka *et al.* 2019). Effects of water availability on pests, natural enemies, and pollinators are generally not well known. Irrigation, especially by flooding, can disturb predators (Baraibar *et al.* 2009), whereas water availability can have both positive and negative effects on crop pests and pest damage to crops (Daane and Williams 2003). Managing for adequate soil moisture and avoiding both under- and over-irrigation can benefit pollinator crop visitation through increased nectar production (Gillespie *et al.* 2015).

In addition to cultural control techniques, other approaches, such as physical control of insect pests (eg exclusion netting and row covers), have received greater attention in recent years, many of which can require integration with pollinators when the crop is pollinator dependent (Minter and Bessin 2014; Leach *et al.* 2016).

The effectiveness of IPPM practices at the field scale (eg addition of flower strips) on pollination and pest control depends on the landscape context, with some evidence that benefits are greater in simple than in complex or cleared landscapes (Jonsson *et al.* 2015; Grab *et al.* 2018). Field and landscape management actions sometimes overlap, as field actions employed over large areas scale-up to become landscape-level practices.

Sampling, monitoring, and thresholds

Monitoring and sampling are fundamental components of pest management that are used, along with thresholds, to determine control actions. The economic threshold (ET) defines the lowest pest density for which action must be taken to avoid reaching the economic injury level (EIL), which is the lowest pest density that incurs financial loss as a result of crop injury that exceeds the cost of the control action (Stern *et al.* 1959). In practice, however, ETs for specific pests and cropping systems are often unavailable, outdated, or lack scientific support, possibly due to the extensive amount of data needed for their determination. In contrast, the goal of pollination management is to maintain pollinator populations above a certain threshold such that economic losses due to insufficient pollination are avoided, necessitating the development of a pollinator economic impact level (PEIL) analogous to the EIL (Flöhr *et al.* 2020). The PEIL is a potentially useful metric to determine whether pollinator management actions are justified, but as with EILs, quantification of crop-specific PEILs requires substantial amounts of ecological and economic data. Specifically, more comprehensive knowledge of how to rapidly determine whether crops are pollen limited using field sampling data (but see Garibaldi *et al*. 2020) would be needed to increase the usefulness of the PEIL concept. In addition, although several pest management actions (eg pesticide application) can be performed quickly, management actions for pollinators may be logistically challenging to implement rapidly in response to monitoring (eg the ability to add managed bees may depend on the availability of surplus hives). EIL and PEIL can also be merged into a single decision metric – the joint economic impact level (jEIL) – that integrates crop yield limitation attributable to the actions and availability of both pests and pollinators (Flöhr *et al*. 2020).

Biotic inputs

Reared and released biological control agents, primarily consisting of invertebrates and microorganisms, are often used as biotic inputs for pest management. Historically, exotic biological control agents were typically introduced with the goal of achieving long-term pest control (ie classical biological control), but augmentative releases to strengthen existing natural enemy populations in the field (ie augmentative biological control) is becoming an increasingly common strategy (van Lenteren *et al*. 2018).

Managed bees are ubiquitous biotic inputs for crop pollination. As with biological control agents, bees are used to augment naturally occurring, service-providing organisms. Globally, the European honeybee (*Apis mellifera*) is the dominant managed crop pollinator, while several bumblebee (*Bombus* spp) and solitary bee species are also regionally employed (Isaacs *et al*. 2017). The contribution of managed honeybees to yield varies greatly among crops and regions (Garibaldi *et al*. 2013). Future research is needed to explore the potential of using species other than honeybees for crop pollination and to determine suitable stocking densities of managed pollinators (Isaacs *et al*. 2017).

Pest management and pollinator management that both rely on biotic inputs operate largely independently from each other. One important exception is the entomovectoring technique, whereby insects (typically bees) serve as vectors to deliver microbial control agents against pathogens and insect pests (Mommaerts and Smagghe 2011). There is a potential for synergy between actions aiming to create landscapes and fields with robust populations of wild beneficial arthropods and using biotic inputs for pest and pollinator management. Released biological control agents benefit from complex, resource-rich landscapes (Perez-Alvarez *et al*. 2019); likewise, landscapes with diverse floral resources benefit managed pollinators (Smart *et al*. 2016). Conversely, releasing biotic IPPM agents into resource-poor landscapes may lead to increased competition between wild and managed pollinators (Herbertsson *et al*. 2016) or antagonistic interactions between naturally occurring and introduced natural enemies (Perez-Alvarez *et al*. 2019).

Abiotic inputs

Despite 60 years of IPM development, chemical pest control remains the standard method of pest management in intensive agricultural systems throughout much of the world (Zalucki *et al*. 2009; Hokkanen 2015). In Europe and North America, insecticide use patterns have changed over time, with lower quantities but more potent insecticides being applied (Douglas *et al*. 2020).

Analogous to the fully synthetic inputs in the form of pesticides used for controlling pests, several methods for artificial pollination (eg hand pollination, pollen spraying, other mechanical devices) are used for pollen transfer (Westerkamp and Gottsberger 2000; Potts *et al*. 2018). However, use of artificial pollination techniques has yet to reach the same level of ubiquity as that of chemical pesticides, and such techniques are unlikely to serve as substitutes for bees or other pollinators on a large scale. However, artificial pollination techniques could play a niche role for crops grown in settings where managing for pollinators in sufficient numbers is not possible (Potts *et al*. 2018).

The overlapping physiologies, activity patterns, and habitats of pests, natural enemies, and pollinators underscore how the use of insecticides may be potentially disruptive for IPPM co-benefits. Insecticide use for pest control is linked with risks for trade-offs both in terms of negative effects on natural enemies and pollinators (Figure 4; Bommarco *et al*. 2011; Rundlöf *et al*. 2015). Indiscriminate insecticide application can lead to negative effects on biological control that are greater than the targeted effect on the pest (Bommarco *et al*. 2011), and can also detrimentally affect pollinators (Rundlöf *et al*. 2015), which in turn can have negative repercussions for crop yield (Stanley *et al*. 2015). On the other hand, use of low-risk insecticides on flowering crops may also benefit bees by protecting their food resources from pest damage (Rundlöf and Lundin 2019).

It is unclear how the landscape context moderates negative effects of pesticides on natural enemies and pollinators. A complex and resource-rich landscape can buffer for negative effects of pesticides on pollinators (Park *et al*. 2015), but pesticides can also negate positive effects of landscape complexity on biological control (Ricci *et al*. 2019). Research on how pesticides affect both pest control and pollination, and how these functions in turn affect yield, is urgently needed to calibrate pesticide use to levels that maximize farmers' economic returns while reducing the risk of adverse impacts on ecosystem functioning (Catarino *et al*. 2019). An integral part of IPPM is to reduce insecticide use by exploring effects on pests and pollinators of alternative control methods from more basal parts of the IPPM pyramid (Figure 4), or evaluating alternative abiotic inputs such as biotechnological options (eg RNA interference; Zotti *et al*. 2018). Research and innovation that contribute to insecticide applications targeting pests over natural enemies and pollinators are also central to IPPM development (Biddinger and Rajotte 2015), and this could be achieved by applying pesticides at

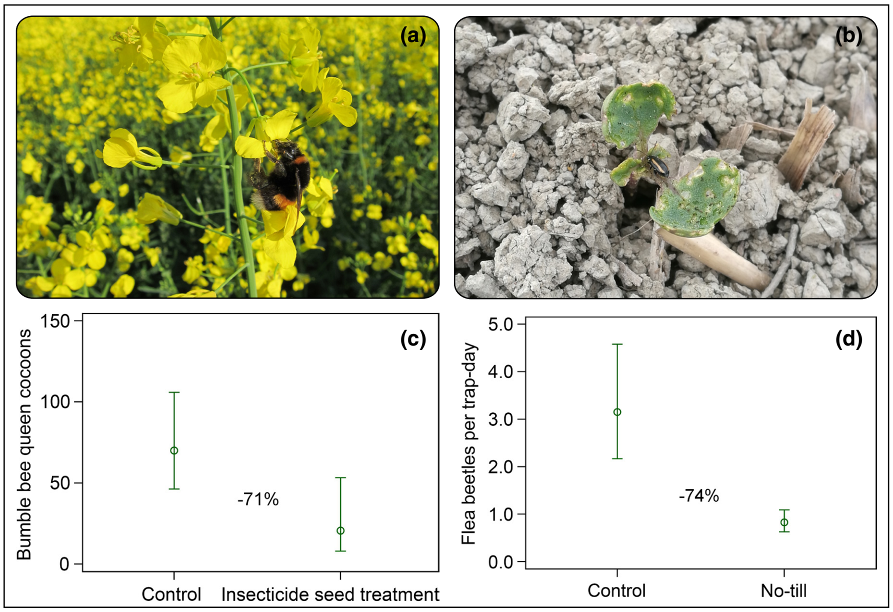

Figure 4. Shifting to pollinator friendly pest control practices. In spring rapeseed (*Brassica napus*) fields, (a) bumblebees are pollinators and (b) flea beetles (*Phyllotreta* spp) are pests that attack seedlings. Flea beetles were formerly controlled with neonicotinoid seed treatments, (c) but neonicotinoids translocate into pollen and nectar with subsequent negative effects on bumblebee colony reproduction (71% fewer bumblebee queen cocoons; Rundlöf *et al.* 2015). (d) In contrast, switching from conventional to no-till approaches offers effective flea beetle control without the need for seed treatments (the no-till value shown in the figure, 74% fewer flea beetles, is the average of two no-till treatments presented in Lundin [2019]). Error bars indicate 95% CI around the means.

times (eg pre-flowering) and locations within the crop where pest activity is high relative to beneficial arthropod activity.

Advancing IPPM in practice

Within our IPPM framework (Figure 2), current common practice essentially takes the form of an inverted pyramid, with pesticide use and a single managed pollinator species (*A mellifera*) dominating pest and pollinator management, respectively. Although recognition of the need to integrate pest control and pollination has grown, the inverted perspective has been largely retained through consideration of adaptive pesticide use to minimize risks to a single pollinator species (ie *A mellifera*; Biddinger and Rajotte 2015; Curtis *et al.* 2019). However, dwindling options for chemical pest control and increasing pressure on honeybee health will likely necessitate more diversified strategies in the future. Important research priorities to further advance the development of IPPM are listed in Panel 1.

Public and private crop advisors, pest control specialists, and educators play important roles in linking pest management research with practice (Lamichhane *et al.* 2016). To develop IPPM in practice, we believe that the focus of agriculture extension services must be expanded to take into account pollinator management based on the IPPM framework. Likewise, advancing IPPM in practice would benefit from pest management being considered in services provided by apiculture extension officers and experts in pollinator conservation (Sponsler *et al.* 2019). An important first step toward facilitating IPPM adoption would be the development of guidelines for the practical implementation of elements within the holistic IPPM framework (Figure 2). Shifting practice from an inverted to an upright model will require formulation of clear guiding principles, well-designed messaging, and a delivery system for advisors and practitioners. Because specific IPPM goals will vary among regions, farming systems, and practitioners, adoption of IPPM will require tiered practices that allow flexibility in employing alternative or selected parts, backed by clear economic validation that also recognizes risk and uncertainty of practices.

One potential complicating factor for implementation of IPPM at the landscape scale is that pests, natural enemies, and pollinators are generally affected by management practices beyond the scale of the individual field or farm (the typical management unit for these organisms). This can create a spatial mismatch whereby benefits deriving from IPPM management at the field or farm level accrue beyond the management unit. Furthermore, agri-environmental policies typically target individual fields or habitats, such that policy instruments facilitating efficient management of agricultural landscapes are often lacking (Goldman *et al.* 2007). A combination of policy development and voluntary engagement of communities of land managers (Goldman *et al.* 2007; Brewer and Goodell 2012) holds promise to advance landscape-scale IPPM. Such

Panel 1. Research priorities for integrating pest and pollinator management

- Developing a deeper understanding of the ecology (especially movement ecology) of pests, natural enemies, and pollinators in agricultural landscapes.
- Developing a stronger evidence base for biodiversity-based landscape and field management actions at the base of the integrated pest and pollinator management (IPPM) pyramid (Figure 2), focusing particularly on the actions' potential to contribute to crop yield and economic profit.
- Exploring how pesticide use can be incorporated into IPPM in ways that are highly effective in controlling pests but that have minimal effects on pollinators and natural enemies.
- Developing and evaluating IPPM strategies that incorporate multiple management actions targeting both crop pests and pollinators.

policy instruments and partnerships could enable coordination of local interventions among farmers or contribute to landscape-scale crop rotations that favor pollinators and natural enemies over pests (Figure 3).

Conclusions

We present here a framework for expanding IPM to include pollinator management, resulting in IPPM. This approach creates opportunities for increasing synergies while limiting trade-offs of proactive actions to simultaneously achieve pest control and pollination goals through largely biodiversity-based landscape and field management actions at the base of the IPPM pyramid. Several field and landscape management actions within IPPM are likely to enhance additional ecosystem services, such as those delivered by belowground biotic communities, making it possible to align IPPM with the wider concept of ecological intensification (Kleijn *et al*. 2019). Proactive IPPM would also enhance environmental benefits by reducing input use and increasing biodiversity. In conclusion, implementing an expanded IPPM concept will contribute to sustainable pest control and crop pollination by capitalizing on co-management potentials.

Acknowledgements

NMW and RB were supported by the August T Larsson Guest Researcher Programme at the Swedish University of Agricultural Sciences (SLU). MJ was supported by the Centre for Biological Control at SLU. MR was supported by the Swedish Research Council VR (grant 330-2014-6439) and Formas (grant 2018-01020). The manuscript benefitted from conceptual discussion with E Lonsdorf.

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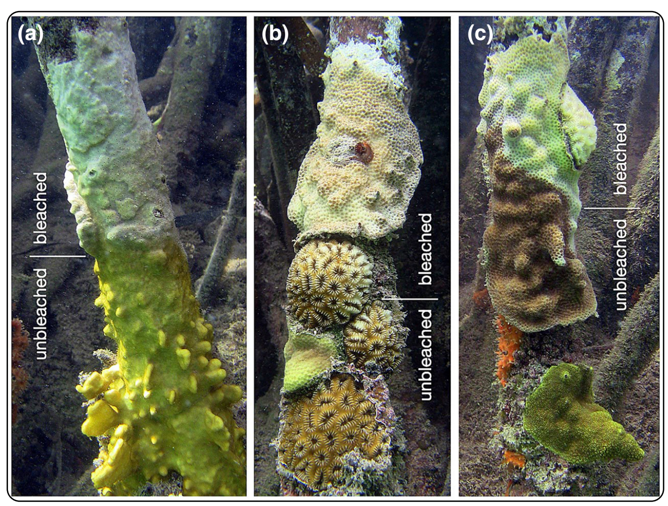
FrontiersEcoPics

Bleaching in mangrove corals

Roughly half of coral species inhabiting Caribbean reefs also inhabit mangroves. Two alternative hypotheses suggest mangroves could promote coral survival under climate change: mangroves may serve as an "ecological refuge" for corals from heat extremes, or variable mangrove environments may select for resilience in corals to future perturbations (*Biogeosciences* 2014; doi.org/10.5194/bg-11-4321-2014). Both hypotheses presume different conditions in mangroves versus reefs and imply mangrove corals experience less heat-induced bleaching than reef conspecifics.

Observations made during longitudinal monitoring of corals inhabiting mangrove prop roots in Belize (*Front Mar Sci* 2020; doi.org/10.3389/fmars.2020.00377) suggest (1) bleaching is rarer in mangrove corals than in reef corals, and (2) bleaching in mangroves and bleaching in reefs may be driven by different environmental stressors. During four of five annual field seasons, we observed only one bleached colony among hundreds of mangrove corals, even as bleaching of the same species was widespread on nearby reefs during two of those field seasons. However, in one of the five field seasons, multiple coral species (such as *Millepora alcicornis*, *Porites astreoides*, and *Favia fragum*) inhabiting mangrove roots were bleached, specifically the shallowest corals (< 20 cm deep). In this instance, we suspect bleaching resulted from a surface lens of cold, hyposaline water generated by a rain-producing cold front that enveloped the site for ~5 days. Corals located below this lens did not bleach.

If different stressors trigger bleaching in reef and mangrove habitats, coral species that occur in both habitats may be better able to survive fluctuating temperature extremes. Given the potential importance of mangroves for coral survival, a key question is why some coral species can exploit mangrove habitats while others cannot.



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doi:10.1002/fee.2353