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Flowering resources distract pollinators from crops: Model predictions from landscape simulations

Charlie C. Nicholson[1] [iD] | Taylor H. Ricketts[1] [iD] | Insu Koh[2] | Henrik G. Smith[3] |
Eric V. Lonsdorf[4] | Ola Olsson[5] [iD]

[1]The Gund Institute for Environment and Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont

[2]The Department of Pathology and Laboratory Medicine, University of Vermont, Burlington, Vermont

[3]Centre for Environment and Climate Research, Lund University, Lund, Sweden

[4]Institute on the Environment, University of Minnesota, St. Paul, Minnesota

[5]Biodiversity Unit, Department of Biology, Lund University, Lund, Sweden

Correspondence
Charlie C. Nicholson
Email: ccnichol@uvm.edu

Abstract

1. Enhancing floral resources is a widely accepted strategy for supporting wild bees and promoting crop pollination. Planning effective enhancements can be informed with pollination service models, but these models should capture the behavioural and spatial dynamics of service-providing organisms. Model predictions, and hence management recommendations, are likely to be sensitive to these dynamics.

2. We used two established models of pollinator foraging to investigate whether habitat enhancement improves crop visitation; whether this effect is influenced by pollinator foraging distance and landscape pattern; and whether behavioural detail improves model predictions.

3. The more detailed central place foraging model better predicted variation in bee visitation observed between habitat types, because it includes optimized trade-offs between patch quality and distance. Both models performed well when predicting visitation rates across broader scales.

4. Using real agricultural landscapes and simulating habitat enhancements, we show that additional floral resources can have diverging effects on predicted crop visitation. When only co-flowering resources were added, optimally foraging bees concentrated in enhancements to the detriment of crop pollination. For both models, adding nesting resources increased crop visitation. Finally, the marginal effect of enhancements was greater in simple landscapes.

5. *Synthesis and applications.* Model results help to identify the conditions under which habitat enhancements are most likely to increase pollination services in agriculture. Three design principles for pollinator habitat enhancement emerge: (a) enhancing only flowers can diminish services by distracting pollinators away from crops, (b) providing nesting resources is more likely to increase bee populations and crop visitation and (c) the benefit of enhancements will be greatest in landscapes that do not already contain abundant habitat.

KEYWORDS
agriculture, bees, central place foraging, ecosystem services, habitat enhancements, pollination, pollinator, pollinator habitat

1 | INTRODUCTION

Reproductive success for 88% of angiosperms depends on pollination by bees, birds, bats and other animals (Ollerton, Winfree, & Tarrant, 2011). Pollinators also provide a critical ecosystem service, with two-thirds of global crops benefitting from animal-mediated pollination (Klein et al., 2007), including many fruits and seeds that provide nutrients essential for balanced human diets (Eilers, Kremen, Greenleaf, Garber, & Klein, 2011). Although many taxa contribute to pollination (e.g. Ratto et al., 2018), bees are the most important crop pollinators world-wide. Increasing evidence indicates that wild bees provide pollination services that are equal or greater in value to those provided by managed bees (Garibaldi et al., 2013).

Wild bees are important for food systems and their widespread decline has prompted efforts to conserve populations in agricultural regions (Garibaldi et al., 2014). Strategies to improve wild bees focus on three key resources: floral resources, nesting sites and refugia from hazards such as pesticides or disease (Dicks et al., 2015; Roulston & Goodell, 2011). Of these three resources, floral resources are frequently identified as an important constraint of pollinator persistence in agriculture (Carvell et al., 2006; Potts, Vulliamy, Dafni, Ne'eman, & Willmer, 2003; Williams, Regetz, & Kremen, 2012). Providing floral resources can improve wild bee reproduction (Carvell, Bourke, Osborne, & Heard, 2015), abundance (Jönsson et al., 2015), species richness (Scheper et al., 2015) and population persistence (M'Gonigle, Ponisio, Cutler, & Kremen, 2015) as well as increase crop pollination (Blaauw & Isaacs, 2014).

Maintaining farm hedgerows or establishing floral strips may support biodiversity and ecosystem services, but their impacts on pollinator communities and crop visitation are varied and unclear (Scheper et al., 2015). The effectiveness of adding pollinator habitat (hence, "enhancements") depends on its size, location, bloom duration and species composition (Haaland, Naisbit, & Bersier, 2011). In particular, the "Circe principle" predicts that pollinator individuals may be attracted to resource-rich patches and remain there (Lander, Bebber, Choy, Harris, & Boshier, 2011), such that enhancements may actually distract pollinators from the crops themselves (Bartomeus & Winfree, 2011; Morandin & Kremen, 2013). Therefore, even the sign of the effect of enhancements on crop pollination services is uncertain and depends on characteristics of the strips relative to surrounding habitat.

The impact of enhancements on local resources depends on the availability of resources within the wider landscape (Scheper et al., 2015). Conservation actions are more effective in structurally simple landscapes than in structurally complex landscapes (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). In structurally complex landscapes, enhancement benefits are less pronounced because farmland populations are subsidized by the continuous colonization of species from the surrounding species-rich landscape, whereas in simple landscapes, the extent to which enhancements improve habitat conditions is greater (Kleijn, Rundlöf, Scheper, Smith, & Tscharntke, 2011). Enhancement strategies should therefore be designed and assessed within the context of landscape pattern (Carvell et al., 2011).

Exploring multiple drivers across spatial scales through field-based experimentation is difficult given the possible range of conditions and interactive effects. Ecosystem service models are one approach to overcome these experimental limitations. These models strive to link land use to altered ecosystem function and then to link these changes in function to the provision of ecosystem services that affect human well-being (Keeler et al., 2012). However, these models have two important limitations. First, they typically provide only static snapshots of current service provision or value (Naidoo et al., 2008). Approaches that instead map the marginal value – the value of a unit change in a landscape (Turner, Pearce, & Bateman, 1993) – are particularly salient because conservation decisions usually involve evaluating the outcome of incremental changes to a landscape (Ricketts & Lonsdorf, 2013). Second, ecosystem service models are typically simple, with many known dynamics excluded for tractability. The consequences of these simplifications are largely unknown because models are seldom compared to each other or validated with field data (Schulp, Burkhard, Maes, Van Vliet, & Verburg, 2014; Seppelt, Dormann, Eppink, Lautenbach, & Schmidt, 2011). It is therefore unclear to what degree findings, and hence management recommendations, are sensitive to model design and detail.

Bees are central place foragers (Olsson, Brown, & Helf, 2008; Schoener, 1979) that vary in their flight range (Greenleaf, Williams, Winfree, & Kremen, 2007), yet ecosystem service models for crop-pollinating bees typically include simplifying assumptions regarding dispersal ability and behaviour. The model by Lonsdorf et al. (2009) assumes that bees diffuse out from the nest and use habitats indiscriminately with respect to foraging returns. By contrast, the more recent model by Olsson, Bolin, Smith, and Lonsdorf (2015) assumes that bees optimize habitat use to maximize fitness. These models differ in their treatment of foraging behaviour; whether this detail affects agreement between predicted and observed crop visitation remain untested.

Here, we use two established models of pollinator foraging to investigate whether habitat enhancement improves crop visitation. Our objectives are to (a) validate and compare these pollination service models, (b) apply the models to test the effects of habitat enhancement on crop visitation and (c) ask whether effects depend on the species' foraging ability and landscape context. We use field observations of bee visitors to compare predictions of both models. We then apply the models to predict the marginal change in visitation following simulated additions of pollinator habitat. We compare predictions from different sizes, resource composition and for bees with different foraging ranges. Finally, we evaluate the degree to which effectiveness of enhancements depends on broader landscape pattern.

2 | MATERIALS AND METHODS

2.1 | Models

We use two habitat-use models: the Lonsdorf et al. model (LEM) (Lonsdorf et al., 2009) and the central place foraging model (CPF) (Olsson & Bolin, 2014). Solitary and social bees are central place
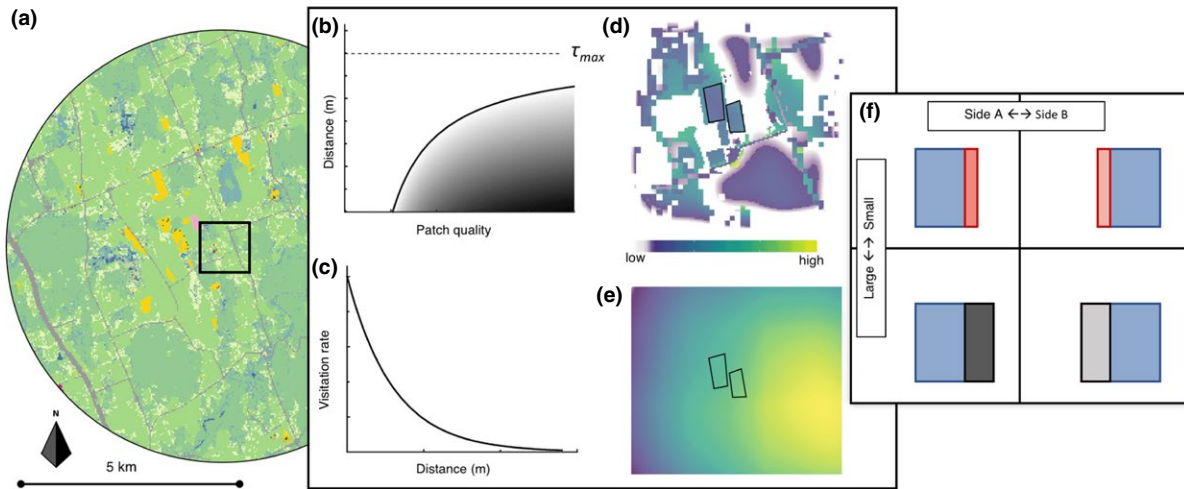
FIGURE 1 Modelling crop pollination. Given (a) land cover information, two pollinator foraging models, (b) the central place foraging model (CPF) and (c) the Lonsdorf et al. model (LEM) make spatially explicit predictions of pollinator visitation (d, e). We simulate the addition of pollinator habitat enhancements (f) next to blueberry fields (blue squares) that vary in patch size (*small*, red; *large*, black) and resource composition (F; F + N; N; not depicted)

foragers that provision brood with resources collected within a home range around a nest (Cresswell, Osborne, & Goulson, 2000). In both models, bees require places to nest, and fitness at a nest site depends on the amount and proximity of foraging resources. Therefore, the input data for both models are maps of nesting and foraging suitability. Both models assume that number of bees produced (i.e. fitness) is entirely dependent on nesting quality and floral resources, and that each nesting site (pixel) can only have a single nest. The models produce indices of habitat quality and bee visitation rates from the available nests during a single time period and therefore do not include population dynamics or competition.

The difference between the models lies in their treatment of foraging behaviour. The LEM predicts that pollinator foraging, and therefore patch visitation, decreases with increasing distance to patches and bees therefore diffuse into the landscape from nest site (Figure 1c,e). The CPF describes optimal patch selection by a pollinator which is determined by distance to a given patch from the nest and the quality of the patch (Figure 1b). Within the CPF framework, pollinator travel distances are dynamic with respect to the habitat quality of the entire landscape, such that they will be shorter in areas with more patches of high floral quality. Pollinators therefore concentrate on nearby, high quality patches (Figure 1d). The models' different treatment of foraging behaviour results in distinct predictions of the rate that pollinators visit patches. The theory of both models has been previously described, but we present basic necessary theory in Supplementary Methods (see Supporting Information).

2.2 | Model comparison

For ecosystem services provided by organisms, behavioural assumptions may fundamentally change model predictions. However, the models' predictions have yet to be comparatively validated. We, therefore, first compare how well model predictions fit observed visitation levels across different landscapes. We then use observations of bee visitors in patches of different forage quality to validate and compare predictions of both models.

2.2.1 | Field observations

We observed bees during the flowering season (May–June) of high bush blueberry (*Vaccinium corymbosum* L.) over three summers (2013–2015) in an agricultural region of Vermont, USA (for more information on field observations, see Supplementary Methods in Supporting Information). We standardize pollinator activity observations to between 09:30 and 14:00 hr, clear to hazy skies, temperature above 15°C and wind speeds less than 3 m/s. Within a 1-m^2 area observers recorded all flower visitors during 10-min observation periods.

To compare model performance within landscapes, we observed pollinators in two patch types over 2 years (2016–2017): open scrub (OS) and blueberry (BLU), respectively, representing patches with low and high average floral density. Open scrub patches were present within 300 m of all farms (N = 8) and are characterized as open areas dominated by early successional grasses and forbs. We paired sampling such that pollinator observations at patches occurred synchronously or within 1 hr of each other. In each 1-m^2 observation plot, we recorded the total number of floral units (Rundlöf, Persson, Smith, & Bommarco, 2014).

2.2.2 | Model parameters

We predict pollinator visitation and fitness across a range of parameter values. The CPF's two parameters (τ_x and ω) determine a bee's maximum foraging distance and the trade-off between energy gains and travel costs respectively. We present three CPF bee types along a gradient of habitat selection strategies that balance
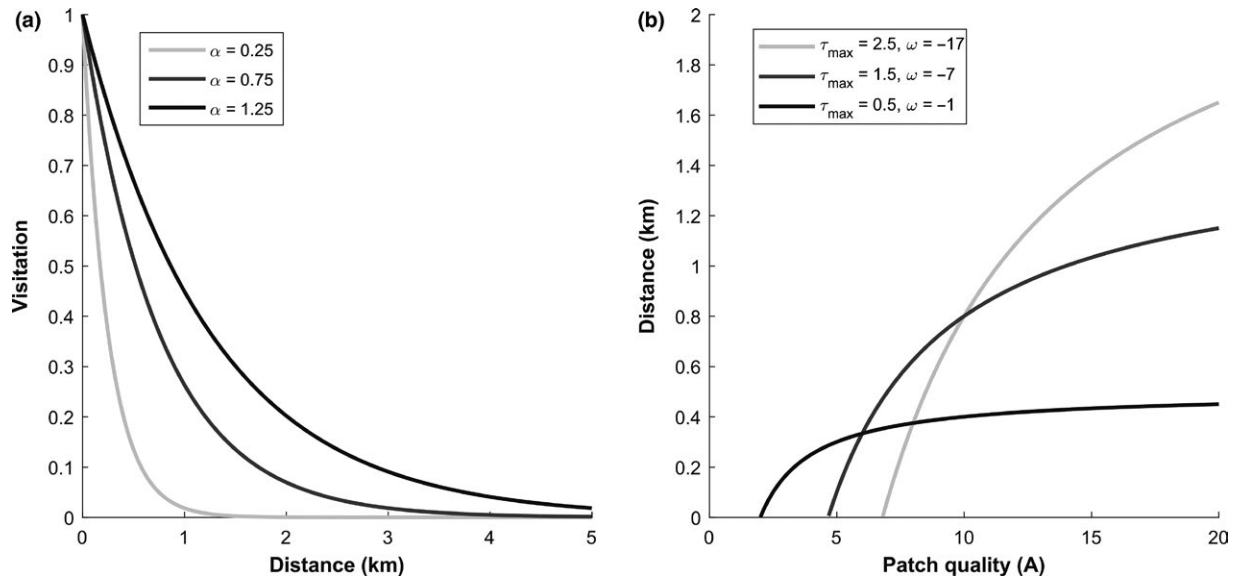
FIGURE 2 Model parameters determining foraging range used in analysis for the (a) LEM and (b) CPF

foraging ability and patch acceptability. For example, the bee type with the largest τ_x (2.5 km) has a correspondingly low ω_x value (−17), and thus, the minimum patch quality (A) it can use is relatively high (Figure 2). These parameter combinations represent realistic metabolic trade-offs between flexibility in patch acceptance and foraging distance (Westphal, Steffan-Dewenter, & Tscharntke, 2006). The LEM's parameter (α) determines the average distance in kilometres a bee would fly. We present three LEM bee types with average flight distances ranging from 0.25 to 1.25 km (Figure 2). With these parameters, both models investigate bees with similar flight ranges.

2.3 | Model application

We simulate habitat enhancement across different strategies of size, location and resource composition. We then test whether the effect of enhancements on crop visitation is moderated by larger scale landscape quality.

2.3.1 | Baseline landscapes

We focus on agricultural landscapes in Vermont, USA, characterized by heterogeneously distributed pastureland and cultivated farmland combined with intact natural areas, predominately deciduous hardwood forests. We use the national Crop Data Layer (CDL, NASS 2008) to provide maps of surrounding landcover centred on focal blueberry fields studied in Nicholson, Koh, Richardson, Beauchemin, and Ricketts (2017). These baseline maps were resampled from 30 m to 9 m resolution, in order to enable more fine-grain addition of habitat patches (see below). Based on similarity in crop characteristics, we reduced 173 agricultural land use categories to 32 representative crop types and retained 13 non-crop categories. We attribute relative floral and nesting values (ranging from 0 to 20) to these 45 landcover types based on expert opinion (see Supplementary Methods

or Koh et al., 2016 for full description of methods). These maps provide our baseline data of floral and nesting availability.

2.3.2 | Landscapes with simulated pollinator habitat

We generated "enhancement" scenarios by virtually adding a pollinator habitat to each farm landscape. For each farm, we centred habitat enhancements along the opposing longer edges of each crop field. Because focal crop fields vary in size, we developed two size classes of pollinator enhancements that were proportionally equivalent to the focal field. Small enhancements were approximately 18% of focal field size and large enhancements were approximately 36% of focal field size (Figure 1f), these result in areas that are within the range of enhancements sizes in empirical studies (Blaauw & Isaacs, 2014; Haaland et al., 2011). Finally, we generated three pollinator habitat resource composition scenarios: patches provide only floral resources (F), only nesting resources (N) or both (F + N). For F scenarios, we reclassified pollinator habitat patches to have a maximum floral value (1.0), while keeping nesting values equal to baseline nesting values. For N scenarios, we did the same for nesting values, while keeping floral values equal to baseline. For F + N scenarios, we set both values to the maximum. This results in 12 possible enhancement scenarios (i.e. two size classes, two sites and three resource compositions).

2.3.3 | Landscape quality index

To characterize broader landscape composition, we follow Kennedy et al. (2013) and use an index of landscape quality (LQI) that links the number of bees produced at a nest site to the surrounding habitat. The LEM and CPF both code land-cover classes in terms of their contributions to pollinator floral and nesting resources – with landscapes containing more high resource quality patches resulting in greater landscape-wide fitness. The scale of the landscape characterized
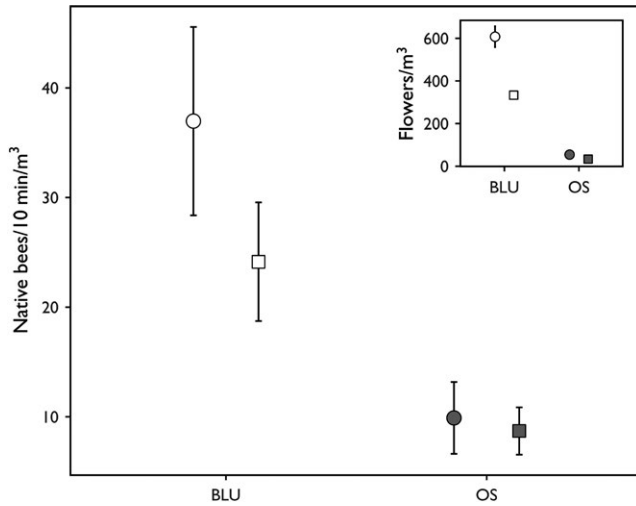
FIGURE 3 Observed native bee visitation rates between blueberry (BLU: white) and open scrub (OS: grey) habitat patches for 2016 (circles) and 2017 (squares). Inset depicts floral unit density at the same patches

was dynamic with respect to pollinator foraging distance. To calculate LQI, we average fitness values within an area equal to three times α for the LEM and two times τ_x for the CPF. These scales ensured that we measured the landscape available for bees visiting our focal crop pixels. Consistent with Olsson et al. (2015), the models' assessments of landscape quality are strongly correlated (Pearson's $r = 0.93$; Supporting Information Figure S1).

2.4 | Analyses

2.4.1 | Model comparison analysis

Our aim is to compare both models' predicted visitation with field observations. We compared observed and predicted data for each foraging model with linear mixed-effects regression using the LME4 package in R (v. 3.3.2) (Bates, Mächler, Bolker, & Walker, 2015). For each statistical test, we looked at the main effect of predicted visitation as well as a model prediction by year interaction. We included year and farm as random effects to account for differences in observed visitation values associated with these variables. We analysed data at the farm by year level and log-transformed ($\ln(x + 1)$) native bee visitation rate (visits/bee/1 m^3/10 minutes) to ensure normally distributed residuals. To compare model performance between landscapes, we average visitation at the eight farms for each year and compared observed and predicted visitation (log-transformed) with linear mixed-effects models with year as a random effect.

2.4.2 | Model application analysis

Our aim is to quantify the marginal change in pollination services to blueberry resulting from pollinator habitat enhancement. We applied the LEM and CPF to both enhanced and baseline maps and calculated the difference in visitation (V) across all i blueberry pixels:

$$\Delta_V = \sum_{i=1}^{i} V_{i,\text{enhanced}} - \sum_{i=1}^{i} V_{i,\text{baseline}}$$

where Δ_V is the change in visitation resulting from the addition of pollinator habitat patches in the landscape. We used these results to determine to what extent enhancement is modified by broader landscape composition and pollinator habitat strategy using mixed-effect models. We included fixed effects for pollinator habitat patch size (small or large) and resource composition (N, F and N + F) and their interaction with each other and landscape quality. We treated the different locations of pollinator habitat as sites and included them as a random factor nested within farm. We performed backward model selection eliminating terms based on model AIC. To compare effects across bee foraging ranges, we performed the model selection procedure for each value but retained the model with most terms. We then analysed the predicted change in visitation for each bee type with this largest model. We present type II Wald F tests with Kenward–Roger degrees of freedom approximation (Kuznetsova, Brockhoff, & Christensen, 2017). We validated all statistical models for normality and homogeneity of variances.

3 | RESULTS

3.1 | Model validation and comparison

Model predictions diverge considerably when comparing visitation at different patches within landscapes. Our field observations showed that blueberry patches (BLU) had greater floral density and more native bee visits than open scrub (OS) patches (Figure 3; floral density: $F_{1,22} = 378.4$, $p < 0.0001$; visitation: $F_{1,22} = 19.25$, $p = 0.0002$). The CPF predictions fit those field observations, whereas the LEM predictions did not (Figure 4). For the LEM, there was a poor fit to observed visitation (Figure 4a; $R^2 = 0.04$; $F_{1,6.007} = 1.321$; $p = 0.29$). For the CPF, there was a positive fit to observed visitation (Figure 4b; $R^2 = 0.42$; $F_{1,27.64} = 25.51$; $p < 0.001$). For simplicity, we report results for only the far-foraging bees (i.e. α = 1.25 and $\tau_x = 2.5$); however, results do not qualitatively differ across parameter values for either model (Supporting Information Table S1). Comparing model results between landscapes show that both models predicted landscape level visitation for a far-foraging bee, albeit marginally for the LEM (Supporting Information Figure S2; LEM: $R^2 = 0.21$; $F_{1,13} = 3.896$; $p = 0.07$; CPF: $R^2 = 0.24$; $F_{1,13} = 4.788$; $p = 0.048$), and LEM fit decreases with foraging range (Supporting Information Table S2).

3.1.1 | Effects of enhancement strategy

The CPF better captures differences in patch quality (see above); we therefore focus on CPF model results henceforth (LEM results are reported in Supporting Information). The marginal effect of habitat enhancements depended on resource composition ($\tau_x = 2.5$: $F_{2,145} = 128.7$; $p < 0.001$; Figure 5). Adding only floral (F) resources resulted in non-positive (i.e. decrease or no change) visitation change. Adding only nesting resources (N) caused non-negative visitation
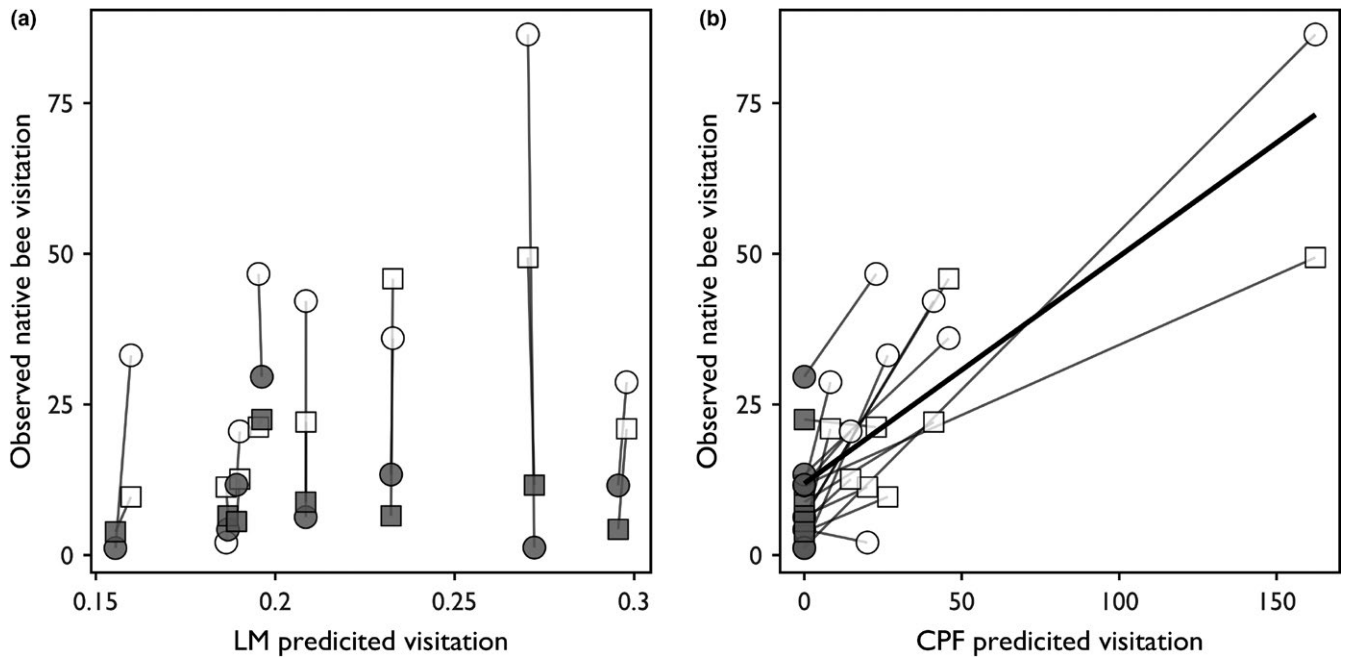
FIGURE 4 Model agreement with field data, using predicted visitation rates from LEM (a) and CPF (b). Symbols depict visitation at blueberry (white) and open scrub (grey) habitat patches for 2016 (circles) and 2017 (squares) for far-foraging bees. Thin grey lines connect co-occurring patches. Black line depicts linear fit between model-predicted and observed visitation

change, and when added with floral resources (F + N) could rescue negative pollination change. These results do not qualitatively differ across bee foraging ranges for either model (Figure 5). Patch size also influenced CPF-predicted visitation change, but the effect was dependent on resource composition (τ_x = 2.5: $F_{2,145}$ = 9.14; p < 0.001; Figure 5). Specifically, when patches only add floral resources, crop visitation decreases less for small patches (Figure 5). Conversely, visitation change from adding nesting resources was greater with larger patches.

3.1.2 | Effects of landscape quality

Landscape quality modified the marginal effect of additional pollinator habitat (Table 1; Figure 6). Because this relationship did not qualitatively differ between patch size (Supporting Information Figure S4), we focus on results from large enhancements. For the CPF, if pollinator habitat patches added only floral resources (F, dashed line), change in visitation was independent of landscape quality (Figure 6). If pollinator habitat added nesting resources (N, dotted line) or floral and nesting resources (F + N, solid line), change in visitation decreased with increasing landscape quality; however, this effect depended on bee foraging range (see below).

3.1.3 | Effects of bee foraging range

For short foraging (τ_x = 0.5) and medium foraging bees (τ_x = 1.5), the effect of added pollinator habitat decreased with increasing landscape quality, except when only floral resources were added (Table 1; Figure 7). For the far-foraging bee (τ_x = 2.5), there was no

significant interaction between resource composition and landscape quality (Table 1).

4 | DISCUSSION

Our model comparisons reveal that behavioural assumptions result in diverging predictions of pollinator response to local land use change. Our model application shows that the benefits of establishing pollinator habitat depend strongly on enhancement strategy and landscape context. Additional floral resources may concentrate pollinators away from crop patches, while adding nesting resources increases pollination. Taken together, our results demonstrate that (a) accounting for organism behaviour enhances predictive power, (b) promoting crop pollination through habitat enhancement depends on whether floral or nesting resources are added, (c) enhancement effectiveness depends on landscape context and (d) bees with different foraging strategies vary in their response to habitat enhancements.

Side by side validation of ecosystem service models reveals the conditions under which models do or do not perform well. In this case, we see that accurately capturing foraging behaviour improves model performance. Our comparison showed that the central place foraging model, because it accounts for trade-offs between patch quality and distance, better captured variation in bee visitation between habitat types. Both models can predict the relative abundance of bees at landscape scales, particularly for far-foraging bees. Previous work across multiple regions shows that the LEM captures substantial variance in observed bee abundance among farms (Lonsdorf et al., 2009) and this model is useful for predicting the landscape scale supply of pollination
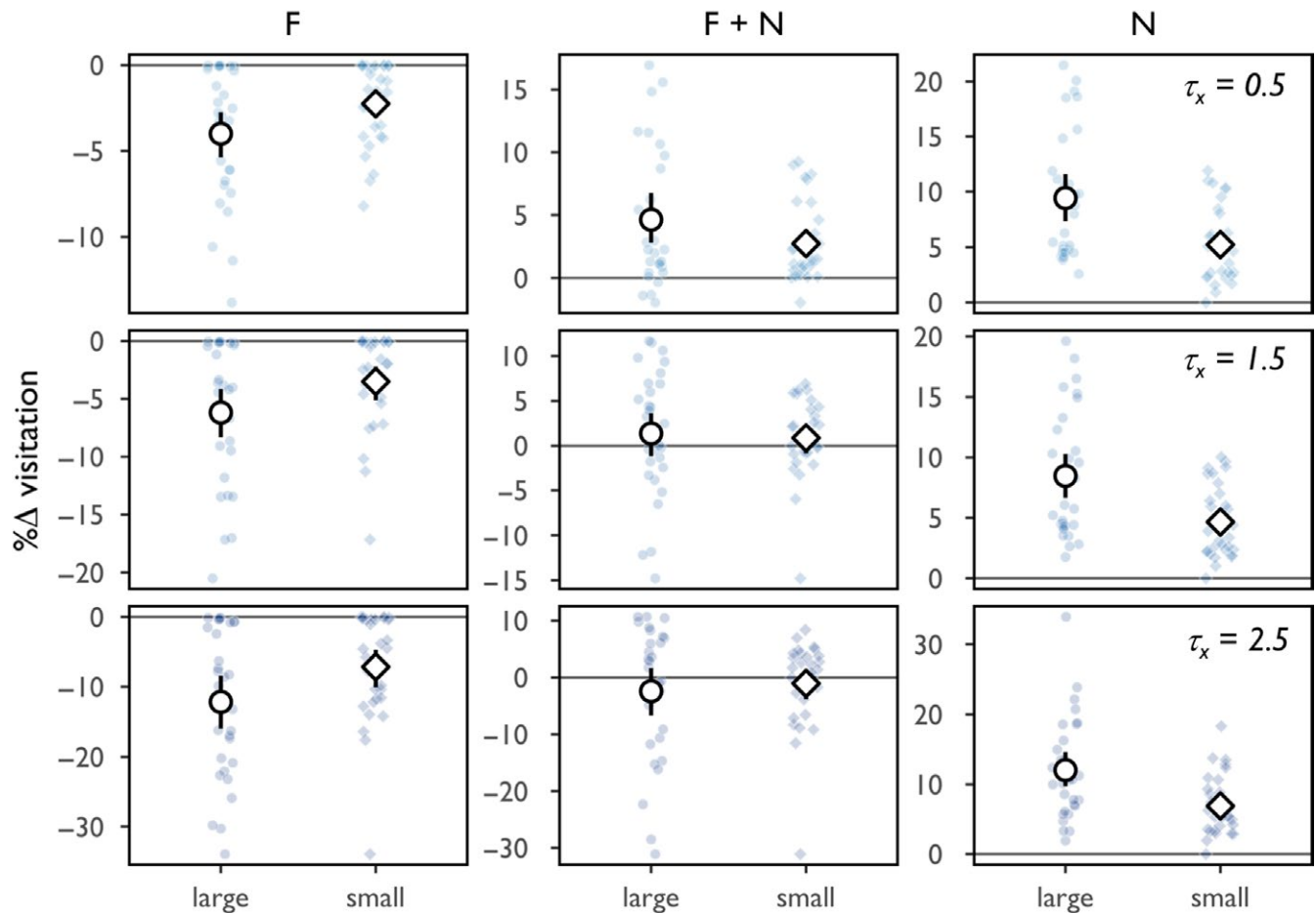
FIGURE 5 Pollinator habitat enhancement strategy affects crop visitation. The predicted percent change in crop visitation for the CPF varies both in sign and magnitude. Symbols depict average visitation change with 95% confidence intervals resulting from habitat enhancements that differed in size (*large*, circles; *small*, diamonds), resource composition (columns: F, only floral; F + N, floral and nesting; N, only nesting) and bee foraging distance (rows: $\tau_x = 0.5$, light blue; $\tau_x = 1.5$, blue; $\tau_x = 2.5$, dark blue)

TABLE 1 Effects of pollinator habitat enhancement strategy and landscape quality on the marginal change in crop pollination predicted by the CPF for bees with three foraging ranges

CPF	$\tau_x = 0.5$			$\tau_x = 1.5$			$\tau_x = 2.5$		
	F	*df*	*p*	*F*	*df*	*p*	*F*	*df*	*p*
HE size	10.67	1,143	0.001	0.964	1,143	0.328	0.179	1,143	0.673
Resource composition	190.6	2,143	<0.001	141.2	2,143	<0.001	131.7	2,143	<0.001
Landscape quality	3.578	1,13	0.081	2.158	1,13	0.166	0.672	1,13	0.427
HE size × Rsrsc composition	15.14	2,143	<0.001	11.40	2,143	<0.001	9.365	2,143	<0.001
Landscape quality × Rsrsc composition	15.19	2,143	<0.001	8.188	2,143	<0.001	2.694	2,143	0.071

services (Koh et al., 2016). However, a known limitation of the LEM is that it does not perform well in fine-grain heterogeneous landscapes (Kennedy et al., 2013), perhaps because bees do not forage optimally (Olsson et al., 2015). We validate both models with observational data to demonstrate that, while both models predict landscape-scale patterns of abundance, the CPF captures patch differences and therefore excels at predicting field visitation change resulting from habitat addition.

We find that the net effect of pollinator habitat enhancement depends critically on what resources that new habitat offers. We consistently saw large differences in crop visitation depending on whether pollinator enhancements added floral or nesting resources. When only flowering resources were added, the CPF predicted large negative change in crop visitation because bees were selectively foraging in the enhancement instead of crops. Our simulations provide support for the Circe principle; when presented with a wealth of concurrently
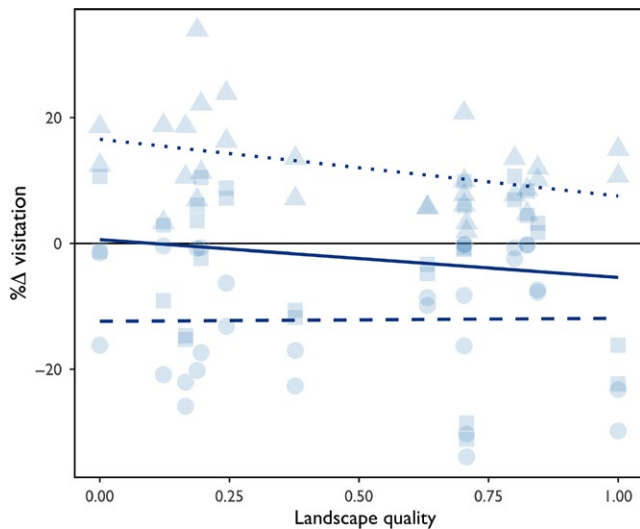
FIGURE 6 Landscape moderates the effect of pollinator habitat enhancement on crop visitation change. The effect of landscape quality (*x*-axis) and resource composition (F, dashed line and circles; F + N, solid line and squares; N, dotted line and diamonds) on crop visitation resulting from pollinator habitat enhancement as predicted by the CPF ($\tau_x = 2.5$)

flowering resources, pollinators remain in resource-rich patches. While numerous studies have demonstrated a conservation benefit of adding flower strips (i.e. increased species richness and greater population abundance), fewer studies have shown a corresponding increase in pollination services to crops (but see Blaauw & Isaacs, 2014; Feltham, Park, Minderman, & Goulson, 2015). Other studies have found little or no effect of habitat enhancement on pollinator communities (Sardiñas, Ponisio, & Kremen, 2016). Jönsson et al. (2015) found that bumblebees were more abundant in sown flower strips than in adjacent habitat, a response that agrees with our simulations.

Adding nesting resources increased crop visitation for both models. Our model results suggest that inconsistent observations from field experiments could be driven by whether or not additional pollinator habitat augmented nesting availability. We observed the greatest CPF-predicted increase in visitation when pollinator habitat added only nesting resources. Adding nesting resources effectively increases the number of bees that a given landscape is able to support. Previous work has demonstrated that pollinator populations are constrained by the availability of nesting resources (Potts et al., 2005; Steffan-Dewenter & Schiele, 2008) and nest location can be a key determinant of the distribution of pollination in a landscape (Dainese et al., 2018; Lonsdorf et al., 2009; Sardiñas & Kremen, 2014). In addition to demonstrating unintended consequences of adding floral resources, our simulations highlight the importance of creating nesting habitat for promoting bee populations and crop pollination.

We observed that landscape quality moderated the effect of establishing pollinator habitat. We found the effect of habitat addition tended to be greatest in simple landscapes, lending support to theories of landscape-moderated conservation effectiveness (Kleijn et al., 2011; Tscharntke et al., 2005). The conservation benefits of local management should be highest in structurally simple rather than in cleared or in complex landscapes. Complex landscapes with abundant natural areas have high levels of immigration (Bianchi, Booij, & Tscharntke, 2006; Ricketts et al., 2008) and offer spatio-temporal stability of resources (Rundlöf et al., 2014; Schellhorn, Gagic, & Bommarco, 2015). Local interventions such as additional habitat may not result in meaningful pollination change in complex landscapes because a mosaic of different habitats already exists and the "ecological contrast" of enhancements is small (Kleijn et al., 2011). For the CPF, we observed the strongest landscape moderation when pollinator habitat enhanced local populations through additional nesting resources. When only floral resources were added,
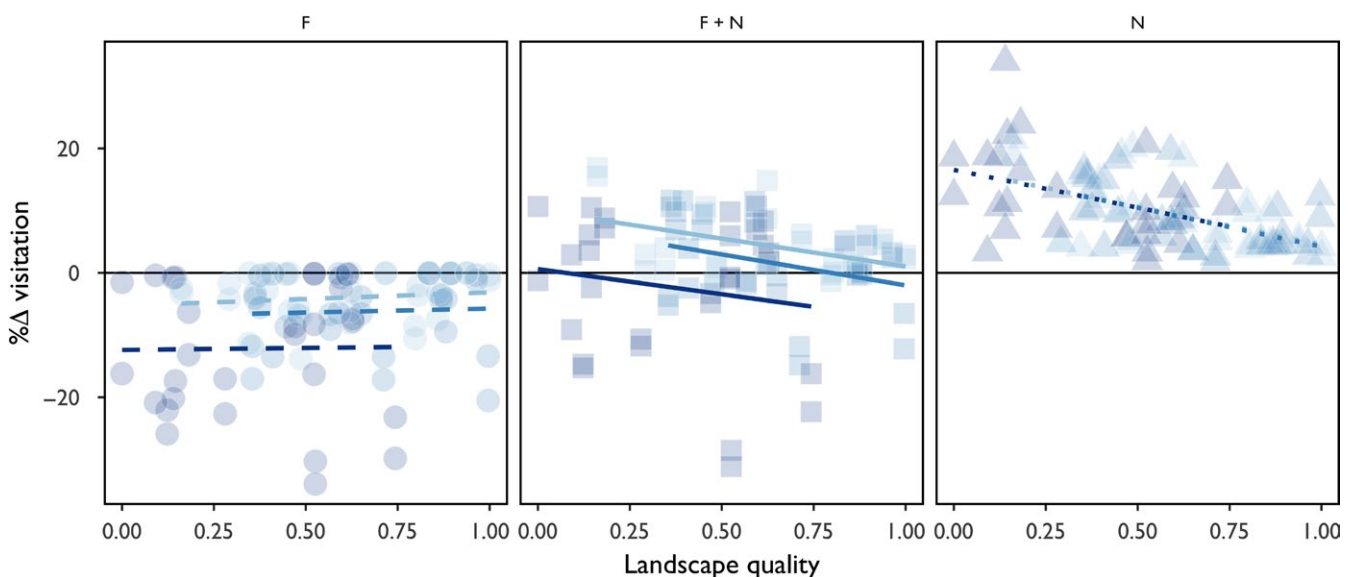

FIGURE 7 Landscape-moderated effect of habitat enhancement depends on bee foraging range. Lines depict the interaction between landscape quality and resource composition predicted by the CPF for bees with increasing foraging range (as in Figure 2: $\tau_x = 0.5$, light blue; $\tau_x = 1.5$, blue; $\tau_x = 2.5$, dark blue)

landscape context did not matter. We propose that this difference is because landscape moderation affects population-level processes rather than behaviour (Rundlöf & Smith, 2006).

We also observed that bee foraging range influenced how strongly landscape quality moderated the effect of additional pollinator habitat. Specifically, within the CPF framework, we did not observe a significant interaction between landscape quality and resource composition for far-foraging bees (i.e. τ_x = 2.5). These results suggest that, because these bees are able to utilize resources across a larger range, they are less responsive to small scale land use change. In the context of wild bee biodiversity conservation, these results indicate that enhancements most impact bees with shorter foraging ranges, which are often locally rare and small bees (Bommarco et al., 2010).

A few caveats deserve mention regarding predictions derived from applying models to real landscapes. First, we analyse changes in visitation that would occur only during the period of crop bloom. Additional floral resources are most likely to benefit pollinators during periods of low availability, within and across years (Häussler, Sahlin, Baey, Smith, & Clough, 2017; Rundlöf et al., 2014). While we focus on responses of pollinator communities to enhancement at a single point in time, other models have considered temporal dynamics. Häussler et al. (2017) found that, in simulated landscapes, flower strips resulted in population growth over time. Taken together, our results suggest that providing additional floral resources may benefit wild bee populations in the long term, while impacting pollination services by distracting bees during crop bloom. Second, the present versions of the CPF and LEM do not allow for inter- or intraspecific competition. Incorporating competition would permit investigation of how different foraging behaviours may result in species coexistence, and this work is underway (Bolin, Smith, Lonsdorf, & Olsson, 2018). Third, although the size of enhancements we introduced matches dimensions of enhancements introduced in empirical studies (Blaauw & Isaacs, 2014; Haaland et al., 2011), they are still quite large. We recognize that creating pollinator habitat may create opportunity costs if arable land is taken out of production. This research is ongoing and field trials are currently investigating the cost-effectiveness of pollinator habitat enhancement for crop pollination (Isaacs et al., 2017). Programmes to support pollinator conservation management can help offset some of these costs. Finally, although we validate both models with observational data, our model application is predictive and more work is needed to determine how generalizable our findings are. Here, we focus on a single biogeographic region and our models were validated with two crop types. Our results could be different in other contexts, where site-specific aspects of farm management or pollinator habitat design could influence how crop pollination changes (Williams & Lonsdorf, 2018).

5 | CONCLUSIONS

Our findings demonstrate that spatially explicit ecosystem service models are useful for predicting the effects of land use change.

Determining the marginal value of local land use change, such as pollinator habitat enhancement, requires a model that captures foraging decisions based on patch quality and distance. Our CPF simulations show that if bees forage optimally, then the Circe principle can occur, whereby crop pollinators concentrate in co-flowering enhancements. Pollinator conservation research largely focuses on floral resources, but here we show the importance of providing nesting substrate as well. The effectiveness of pollinator habitat not only depends on resources provided but also larger landscape quality. Enhancing biodiversity and ecosystem services are frequently shaped by land use interactions across spatial scales, and our results show that pollinator habitat enhancement is no exception. Managing ecosystem services in agriculture is best supported by models that accurately capture the behaviour and landscape dynamics of the organisms underpinning service provision.

AUTHORS' CONTRIBUTIONS

All authors contributed to the conception and design of the study; C.C.N. collected the data; C.C.N. and O.O. performed the analyses; C.C.N. wrote the manuscript; all authors provided feedback on analyses, interpretation of results and edited the manuscript.

DATA ACCESSIBILITY

Data available via the Ricketts Lab Figshare https://doi.org/10.6084/m9.figshare.7443431.v1 (Nicholson et al., 2018).

ORCID

Charlie C. Nicholson (iD) https://orcid.org/0000-0002-7164-0529

Taylor H. Ricketts (iD) https://orcid.org/0000-0001-9688-7977

Ola Olsson (iD) https://orcid.org/0000-0003-0789-1064

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