

LETTER

A Tool for Selecting Plants When Restoring Habitat for Pollinators

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Conservation support tool; networks; plants; pollinators; restoration.

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Abstract

Native pollinators and, particularly bees, are a critical component of agricultural systems. Unfortunately, many factors are leading to their declines, including habitat loss. Consequently, approaches have emerged that aim to restore pollinator habitat in managed landscapes. A widely adopted technique in Europe and North America is the planting of flowering shrubs and forbs along field edges. These habitats usually include a variety of species, chosen because they are attractive to pollinators and because they flower continuously over those pollinators' flight seasons. Because there are many potential plant species with different flowering times and pollinator preferences, selecting a subset is challenging. Here, we develop a tool that identifies a plant mix that optimizes some assessment criteria (e.g., pollinator visitation, richness, or phenology). We test our tool by showing that it identifies mixes that better satisfy these criteria than ones found using conventional expert-driven methods, when applied to a plant–pollinator dataset.

Introduction

The honey bee (*Apis mellifera*) is experiencing increased colony losses (van Engelsdorp *et al.* 2009) and there is evidence that native pollinator populations are also declining (Biesmeijer *et al.* 2006; Potts *et al.* 2010; Cameron *et al.* 2011; Carvalheiro *et al.* 2013). Because pollinators are critical for plant reproduction—87% of flowering plant species (Ollerton *et al.* 2011) and 75% of agricultural crop species benefit from animal pollinators (Klein *et al.* 2007)—mitigating further declines has become a global conservation imperative (Potts *et al.* 2010; Garibaldi *et al.* 2013).

Little is known about how we can reverse pollinator declines (Winfrey 2010; Menz *et al.* 2011). However, in agricultural landscapes, where habitat loss and pesticides threaten pollinator populations (Brittain *et al.* 2010; Garibaldi *et al.* 2011; Rundlöf *et al.* 2015), multiple studies have shown that increasing vegetative diversity can boost pollinator species richness, abundance, and spa-

tial turnover (e.g., Carvell *et al.* 2007; Kohler *et al.* 2008; Haaland *et al.* 2011; Kennedy *et al.* 2013; Morandin & Kremen 2013; Scheper *et al.* 2013; Ponisio *et al.* 2016), promote specialized species (Pywell *et al.* 2012; Kremen & M'Gonigle 2015), and increase persistence (M'Gonigle *et al.* 2015). One widely used practice is the planting of flowering shrubs and/or forbs along field edges. These enhancements typically include a variety of species that flower in sequence, covering the flight seasons of many pollinator species (Garibaldi *et al.* 2014; Williams *et al.* 2015); gaps in flowering might prevent pollinators from completing their life cycles (Memmott *et al.* 2010; Burkle *et al.* 2013). Because there are many potential plant species, creating an optimal mix can be a computational and agronomic challenge. Here, we focus on the former.

Computational tools are increasingly being used for land-use planning (Meir *et al.* 2004; Sarkar *et al.* 2006; Turner & Wilcove 2006; Stralberg *et al.* 2009). For example, there are numerous tools for identifying and

optimizing acquisition of spatial land units for conservation (e.g., Turner & Wilcove 2006; Moilanen *et al.* 2009). When the goal of restoration is the assembly of a group of species, a restoration design must take into account the full needs of those species over the duration of their life cycles. For obligate mutualists, this means taking into account the interaction network between the planted species and the restoration targets (e.g., pollinators), as well as factors such as nesting or breeding resources (Menz *et al.* 2011).

Simultaneously optimizing multiple criteria is common to many conservation planning problems (Nicholson *et al.* 2006; Sarkar *et al.* 2006). Surprisingly, however, no tool exists for optimizing criteria, single or multiple, when planning restoration for pollinators. Here, we develop such a tool for identifying plant mixes that optimize a range of criteria. For example, a planner might want a phenological sequence of blooms appropriate for pollinators of a specific crop or, alternatively, a plant mix that supports the greatest pollinator species richness or visitation. We test our tool by applying it to a dataset from California's Central Valley.

Methods

Data requirements and model description

We develop a genetic algorithm to find the mix (or mixes) of plants (defined as a list of k plants, $M = \{p_1, p_2, \dots, p_k\}$) that maximizes some "objective function." All code developed here is available at https://github.com/leithen/plant_selection_tool. Our tool requires three data as inputs:

1. A record of pollinator collections and corresponding plants on which they were collected.
2. An optimality criterion.
3. In some cases, trait information about the plants or pollinators (e.g., floral bloom period or timing of plant–pollinator interactions).

Details of the genetic algorithm are described in the Supplementary Materials (Section S1). In brief, the algorithm subjects an initial "population" of plant mixes to several iterations of "selection," "recombination," and "mutation," keeping track of the best mixes encountered. In any run, we require that mixes contain the same number of plants. However, by comparing across different mix sizes (i.e., different k values), we can also optimize k .

Objective functions

The objective function, f , defines the optimization criteria and allows us to compare plant mixes M_i and M_j by evaluating $f(M_i)$ and $f(M_j)$. Construction of this

function will depend on the goals. For example, one could maximize pollinator visitation (the total number of visits) or target particular pollinators. Alternatively, because pollinator flight seasons are often longer than individual plant species' bloom periods, one might want plants whose combined bloom periods span the flight seasons of the relevant pollinators. In our framework, more complex objective functions can be constructed by combining simpler ones.

In the Supplementary Materials (Section S2), we develop four simple objective functions that optimize, respectively, pollinator visitation, f_V , pollinator species richness, f_R , and phenology based on either the timing of plant–pollinator interactions, f_T , or the bloom periods of plants, f_B . The "visitation" metric, f_V , closely mimics the criterion that has been used by planners in the past, and thus we use it as a baseline against which we compare the performance of other metrics. Because we are ultimately interested in maximizing pollinator visitation and richness, while also providing coverage of the pollinators' flight seasons, we use our tool to compare the performance of plant mixes that optimize these simple criterion to mixes that optimize them in combination. Specifically, we let $f_{VRT}(M) = f_V(M) * f_R(M) * f_T(M)$ denote the objective function that optimizes pollinator visitation, pollinator species richness, and the timing of plant–pollinator interactions. Similarly, we let $f_{VRB}(M) = f_V(M) * f_R(M) * f_B(M)$ denote the objective function that optimizes visitation, species richness, and floral bloom periods.

Data collection

We test our tool using a dataset comprising ~ 8,000 wild bees netted on flowers at sixteen ~ 1.8 hectare sites in Northern California's Central Valley. Sites were situated in mixed native vegetation, vegetable farms, and orchards and were sampled eight times at regular 3-week intervals between March and August within a single season. All collections were made on days with clear skies, temperatures > 20°C and wind speeds < 2.8 m/s using timed collections (for a full description, see Forrest *et al.* 2015). Plants were identified to species and bees were identified to species or to morphospecies (~ 800 specimens to morphospecies, primarily in the genera *Lasioglossum* and *Nomada*). Records were filtered to include only collections on native plants. Additional filters could be applied here (e.g., plants could be filtered based on perceived weediness or availability/desirability).

We compare our optimized mixes to ones created using expert opinion and the same dataset described above. These mixes were created using a set of simple rules: the first three plant species were chosen by selecting the early, middle, and late blooming species that had the

largest number of occurrences of crop-visiting species, over unique combinations of sites, seasons, and bee visitors (similar to Kremen *et al.* 2002), the next three were selected in the same manner, and so on. Plant mixes based on a similar process have been used to create hedgerow enhancements at several sites in California (Kremen & M'Gonigle 2015). Comparisons to independently compiled “off the shelf” plant mixes would be helpful, but presently there are no such mixes in our study region for which we have sufficient pollinator visitation data.

Results

Our dataset contains 76 plant and 181 pollinator species. Assuming equal plant frequencies within mixes, there are 70,300 mixes containing three plants, 218,618,940 mixes containing six plants, and 142,466,675,900 containing nine plants. Should one wish to vary plant frequencies, these numbers would become even larger. Thus, exhaustively examining potential mixes becomes computationally intractable as the mix size and complexity increase.

We first demonstrate that our method correctly identifies the optimal plant mix for scenarios where that mix can be found exhaustively. We do this in two ways. First, for our dataset, we can do this for mixes containing up to five plants. In doing so, we found perfect congruence between these mixes and those found using our model. Second, it is possible for some criteria to find the optimal plant mix of any size. For example, the mix that maximizes pollinator visitation, f_V , can be found by ranking plants according to their total occurrence and then selecting the top k . Again, we found perfect congruence between these mixes and those found using our model. For the remaining cases, we evaluated performance by comparing tool-selected mixes to a large number of randomly generated mixes. Our tool identified mixes that outperformed all randomly generated plant mixes by a large margin (Figure 1).

We found that mixes that optimize f_{VRT} and f_{VRB} perform almost as well in maximizing their constituent components (visitation, richness, and the timing of interactions, in the case of f_{VRT} , or phenological bloom continuity, in the case of f_{VRB}) as plant mixes that optimize only those components (Figure 2). For example, a nine species mix found by maximizing pollinator visitation, species richness, and the timing of plant–pollinator interactions (f_{VRT}) provides resources to 97.7% as many pollinator species as one that maximizes only pollinator species richness, f_R . Similarly, a mix that optimizes visitation, species richness, and the floral bloom periods (f_{VRB}) provides resources to 98.4% as many species as one that

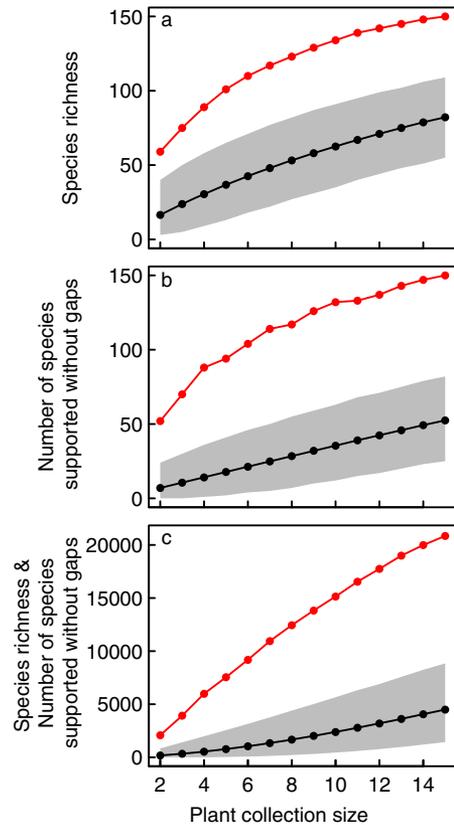


Figure 1 Performance of our tool against randomly selected plant mixes when attempting to maximize (a) pollinator richness, (b) the number of fully supported pollinators, or (c) both pollinator richness and the number of fully supported pollinators. Black curves and shaded regions show means and 95% quantiles for performance of 10^5 randomly generated models of the corresponding mix size, whereas the red curves show model scores for best models found using our tool. The algorithm was run, in each case, for 1,000 generations with a population size, N , equal to 100, probability of mutation, μ , equal to 0.01, probability of sex, ψ , equal to 1, probability of recombination, r , equal to 0.25, and strength of selection, s , equal to 5 (see Supplement S1 for descriptions of these parameters).

maximizes only pollinator richness. Analogously, mixes found by optimizing f_{VRT} and f_{VRB} support, respectively, 92.7% and 93.0% as many occurrences as one that maximizes only visitation, f_V .

Importantly, these mixes provide better phenological coverage than ones that only maximize visitation (compare blue and red curves to black curve in Figures 2b and 2c). For example, the nine species mix that maximizes visitation, species richness, and the timing of plant–pollinator interactions (f_{VRT}) or, respectively, phenological bloom continuity, f_{VRB} , can support 17.5% (respectively, 14.2%) more species across their life cycles than one that maximizes only visitation, f_V . Furthermore, in our dataset, these gains are largest for collections of smaller sizes. Thus, our tool effectively

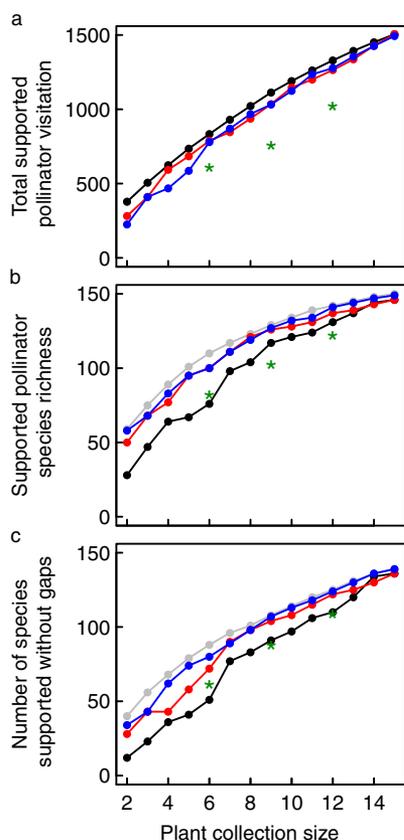


Figure 2 Performance of optimal models of varying plant size, as measured by the total supported pollinator visitation (a), the total supported pollinator richness (b), and the total number of pollinators supported for the complete duration of their flight seasons (c). Each curve corresponds to plant mixes that were selected using a different optimality criterion. In each panel, the gray curve shows the performance of plant mixes optimized for only the criteria of interest in that panel, and thus provides an upper limit. We also consider three additional criteria. The black curve denotes plant mixes optimized for only visitation, f_V , whereas the blue and red curves denote, respectively, plant mixes optimized for the more complex composite functions $f_{VRT} = f_V * f_R * f_T$ and $f_{VRB} = f_V * f_R * f_B$. Green asterisks denote plant mixes that have been created by experts using this same dataset in the past. In panel (a), the black curve obscures the gray curve because they correspond to the same objective function.

finds mixes that, in theory, support a greater number of pollinators more evenly across the duration of their flight seasons and, further, the efficiency gains are greater when only a smaller number of plants can be included, which is frequently the case due to cost and availability.

Lastly, we found that our tool identified mixes that performed noticeably better than ones created using expert opinion for this same dataset (compare asterisks to blue and red curves in Figure 2). For example, the nine species mix that maximizes visitation, richness, and the timing of plant–pollinator interactions (f_{VRT}) or, respectively, phenological bloom continuity, f_{VRB} , could, in

theory, support 18.1% (respectively, 21.5%) more species across their life cycles than an expert-derived mix of the same size.

Discussion

Selecting the optimal mix of plants when restoring habitat for pollinators is a computational and logistical challenge (Menz *et al.* 2011). Here, we have developed a tool to help identify mixes of plants that, in theory, will provide floral resources capable of supporting pollinator communities. We applied our tool to a plant–pollinator dataset and showed that it identified mixes that, if established, could sustain diverse pollinator communities over the duration of those pollinators’ flight seasons.

There are numerous conservation support tools for solving similar problems, such as selecting spatial land units for habitat conservation or restoration (Sarkar *et al.* 2006). These tools can be structurally similar to ours, using algorithmic methods to select an optimal subset from a larger set (e.g., see Possingham *et al.* 2000; Moilanen *et al.* 2005). However, when the targets of restoration are interaction networks, it is necessary to develop methods that explicitly incorporate species interactions. For example, here, selected plants need to flower such that their bloom periods will combine to cover the pollinator’s flight seasons.

In developing our tool, we have created several simple objective functions with a focus on improving phenological coverage via bloom periods (f_B) or the timing of plant–pollinator interactions (f_T). These functions could be refined in the presence of more comprehensive datasets or more specific restoration goals. For example, the frequency of each plant species within a mix is not considered here but is likely an important factor. In order to incorporate this, a planner would need to articulate how to score different compositions of the same mix; a difficult task. A planner may also want a mix that targets pollinators of a specific crop (e.g., Kremen *et al.* 2002) or one that does not bloom while their crop is flowering (in order to promote movement of pollinators into the field). She/he might also require particular plants or pollinators be included/supported. In this case, the remaining plants would be selected to optimize the objective function, constrained by the initial choice of required species. In the reserve design literature, this is analogous to forcing the algorithm to include existing protected areas (Possingham *et al.* 2000). Such modifications could be easily accommodated in our framework.

All of our metrics are based on visitation data. This is potentially problematic for three related reasons. First, plant or pollinator species that are rarely detected will often be incorrectly inferred to have short bloom

periods or flight seasons. Second, restoration may subsequently favor common species (Kleijn *et al.* 2015). Third, the list of eligible plants will not contain those on which specimens were never collected, potentially omitting interactions that are rare or have low detectability (e.g., nocturnal visitors). Additionally, visitation data do not indicate whether pollinators were foraging for pollen or nectar on a given plant species. To overcome these problems, planners would ideally begin with a list of all potential plant species across the landscape and their bloom periods and resources provided, all pollinator species and their flight periods, and an interaction matrix. While floral bloom periods could potentially be estimated, obtaining an interaction matrix is only possible using collections, as we have done here. Thus, the approach we have taken (sampling in nearby pristine and agricultural habitats) is a practical and economic option, with the acknowledgment that additional sampling might improve the end result.

In a recent paper, Russo *et al.* (2013) proposed a heuristic for restoring pollinator habitat using attributes of interaction networks to select plants. They assess the value of each plant species by considering network attributes such as “node duration,” which they define as “the number of times out of the total number of samples that a species participates in the network.” Such an approach, where one ranks individual species provides valuable insight into the roles played by different plant species. Our tool extends their approach by developing a formal, reproducible method for selecting mixes that optimize network metrics. With sufficient data, it would be straightforward to extend our optimization functions to use pollinator preference strengths instead of visitation rates. This might alleviate some of the problems discussed in the previous paragraph.

There are other important considerations and constraints to consider when designing a restoration such as economic costs, plant availability, compatibility of seed mixtures, local soil conditions, land-use type, perceived weediness, pest control, and the availability of preexisting foraging and nesting resources (Balzan *et al.* 2014). While incorporating such constraints is beyond our scope here, these factors could certainly be included within the algorithm. For example, one could obtain nursery prices and construct an objective function that calculates the cost of a mix. This cost function could then be built into an objective function or added as a constraint.

In practice, expert opinion is critical in planning any restoration and this tool is not intended to replace it, but to support it, by providing a formal and transparent structure to a process that typically uses informal application of the logic described here. Furthermore, we found that our model-selected plant mixes performed substantially

better than expert-derived ones. Thus, as the complexity of the problem grows, so does the helpfulness of conservation support tools such as this one.

The method we present marks a first step in the development of computational tools to aid in selection of plant mixes for use in the restoration of pollinator communities. Beyond the potential extensions of this method described above, it will be important to test these mixes empirically. Otherwise, it is difficult to know whether the subsets of plants identified by our tool will actually support the establishment and persistence of the target pollinator communities (M'Gonigle *et al.* 2015). Such next steps are the focus of ongoing work; we are incorporating a broader array of criteria into the development of actual plant mixes and testing these on the ground with plantings (Williams & Lonsdorf, *in prep.*)

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Supplementary Materials S1. Genetic Algorithm

Supplementary Materials S2. Objective functions

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