Seasonal bee communities vary in their responses to local and landscape scales: implication for land managers

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Abstract

Context

There is great interest in land management practices for pollinators; however, a quantitative comparison of landscape and local effects on bee communities is necessary to determine if adding small habitat patches can increase bee abundance or species richness. The value of increasing floral abundance at a site is undoubtedly influenced by the phenology and magnitude of floral resources in the landscape, but due to the complexity of measuring landscape-scale resources, these factors have been understudied.

Objectives

To address this knowledge gap, we quantified the relative importance of local versus landscape scale resources for bee communities, identified the most important metrics of local and landscape quality, and evaluated how these relationships vary with season.

Methods

We studied season-specific relationships between local and landscape quality and wild-bee communities at 33 sites in the Finger Lakes region of New York, USA. We paired site surveys of wild bees, plants, and soil characteristics with a multi-dimensional assessment of landscape composition, configuration, insecticide toxic load, and a spatio-temporal evaluation of floral resources at local and landscape scales.

Results

We found that the most relevant spatial scale varied by season. Spring bees depended on landscape resources, but summer bees responded more to local quality, implying that site-level management is most likely to be successful in supporting summer bees. Semi-

natural habitats, including forests, wetlands, and other aquatic habitats, were particularly important for spring bees.

Conclusions

By considering spatial and temporal variation in resources, we developed season-specific recommendations to improve habitat quality for wild bees and offset manifold stressors threatening these essential pollinators.

Keywords: wild bees, landscape floral resources, floral phenology, soil fertility, landscape composition and configuration

1. Introduction

There is great interest in developing approaches for translational ecology (Schlesinger 2010; Enquist et al. 2017), where research is designed to provide stakeholders with information they can use to address challenges. Because of the importance of pollinators for agricultural production and resilience of ecological communities, there has been substantial investment in land management practices to increase abundance and diversity of pollinator populations. Indeed, from 2006-2016, the United States and Europe spent more than 35 billion USD on agri-environment schemes (Ansell et al. 2016), including practices targeting pollinators. While most conservation practices tend to be implemented at local scales, many recent studies of pollinator ecology focus on landscape-level phenomena, creating a disconnect with the scale at which conservation is implemented. In addition, despite documented seasonal shifts in pollinator communities and the floral resources on which they depend for nutrition, temporally resolved information on pollinator and floral communities is typically not considered. To best inform agri-environment schemes, it is necessary to understand how local and landscape quality, across seasons, co-influence pollinator communities.

Conservation practices typically ameliorate very small proportions of landscapes that pollinators experience. The spatial extent of a landscape should be 'organism-defined' (Wiens 1976), which for wild bees is typically based on the foraging distance of the bee community of interest. In the Mid-Atlantic USA, the mean foraging range of wild bees is approximately 500 m (Bartomeus et al. 2013; Kammerer et al. 2016), which, assuming equal foraging in all directions from a central nest, corresponds to a landscape of approximately 79 ha. In this region, the mean area of a habitat patch is only about 0.17 ha,

75 or 0.2% of the 79-ha landscape (M Kammerer, *unpublished analyses*) illustrating that
76 conservation practices implemented in one patch of habitat (site) improve a very small
77 proportion of the landscape that pollinators experience. Empirical data are lacking, but
78 based on common suggestions of adding habitat in roadsides, field edges, or other marginal
79 land (Hopwood 2008; Morandin and Kremen 2013), it is likely that most pollinator
80 plantings in the Mid-Atlantic USA are quite small (< 1 ha), and likely inadequate to solely
81 support whole bee communities (McCullough et al. 2021).

82 If landscape quality is a primary driver of bee communities, and conservation practices
83 improve only a small section of a landscape, how likely are conservation practices to
84 benefit wild-bee populations? A quantitative comparison of local and landscape effects is
85 necessary to decide not where, but if adding small patches of wild-bee habitat is likely to
86 realize a measurable increase in bee abundance or richness (Gonthier et al. 2014), although
87 it is challenging to evaluate on a larger scale how populations are affected (Kleijn et al.
88 2018; Scherber et al. 2019). Quantitative syntheses of agroecosystems across the globe
89 found abundance of wild bees increased with more complex landscapes and diverse local
90 plant communities or vegetation types (Kennedy et al. 2013; Shackelford et al. 2013).
91 Richness of all wild bees also increased with landscape quality, and, for solitary bees only,
92 locally diversified fields supported more species (Kennedy et al. 2013). Comparing the
93 effect of different scales, some studies have shown that local context matters more than
94 landscape quality (Coutinho et al. 2018; Rollin et al. 2019), but there are also examples
95 where landscape effects dominated (Bartholomée et al. 2020; Griffin et al. 2021; Coutinho
96 et al. 2021) or compensated for intensively managed agriculture or local contexts that are

97 otherwise challenging for wild-bee communities (Rundlöf et al. 2008; Papanikolaou et al.
98 2017).

99 Between spring and summer, composition of wild-bee communities changes
100 substantially, which could lead to seasonal variation in importance of local and landscape
101 resources. In the mid-Atlantic USA, there is substantial turnover in bee species present in
102 spring (before mid-May) versus summer and fall (Kammerer et al. 2021; Turley et al.
103 2022). With changes in composition of the bee community comes seasonal variation in
104 several important functional traits including voltinism, overwintering location, and body
105 size (Osorio-Canadas et al. 2018). Body size is strongly linked to species' typical foraging
106 distances (Greenleaf et al. 2007), likely dictating the relative importance of local and
107 landscape resources. However, to our knowledge, no studies have examined seasonal
108 variation in dependence of bees on local vs. landscape resources. Moreover, habitats vary
109 widely in the magnitude and timing of floral and nesting resources that they provide for
110 bees (Ogilvie and Forrest 2017), which can lead to temporally variable relationships
111 between wild-bee communities and land use (Cole et al. 2017; Galpern et al. 2021)

112 To facilitate translating results of landscape-scale studies to applied management and
113 conservation, pollination ecologists should quantify landscape quality based on specific,
114 seasonal resources and risks. But due to the complexity of measuring flowers, nesting, or
115 pesticide risk at the landscape-scale, these factors have been understudied (but see Guezen
116 and Forrest 2021; Smart et al. 2021; Bloom et al. 2021). Instead, most studies have
117 described landscape quality using broad landscape metrics, such as percent semi-natural
118 habitat (Ricketts et al. 2008; Kennedy et al. 2013). Broad land-use metrics are correlated
119 with many aspects of bee health and community composition (Kennedy et al. 2013;

Martínez-Núñez et al. 2020; Du Clos et al. 2020), but are less useful for applied conservation decisions, as land use is an indirect, rather than direct, driver of bee abundance and diversity (Roulston & Goodell, 2011). Land-use patterns dictate floral and nesting availability (Williams and Kremen 2007), pesticide risk, and disturbance regimes (mowing, tillage, logging), so representing landscape quality based solely on amount of semi-natural habitat cannot untangle relative importance of multiple drivers. Furthermore, different semi-natural habitat types vary in how many food resources they provide (Bartual et al. 2019), and documenting bee responses to broad land-use patterns precludes determining which habitats are most important for bees and how and when to offset resource scarcity.

To address these knowledge gaps and inform conservation practices for wild bees, we studied season-specific relationships, over a two-year period, between local and landscape quality and wild-bee communities at 33 sites in the Finger Lakes region of New York, USA. We paired field surveys of wild bees, plants, and soil characteristics at each site with a multi-dimensional assessment of landscape quality, including landscape composition, configuration, insecticide risk, and data generated from a novel, spatio-temporal evaluation of floral resources at the local and landscape scales (described in Iverson et al, in review for this issue). As part of our local-scale assessment, we measured soil characteristics because many species of wild bees nest in the soil (Harmon-Threatt 2020) and soil fertility influences floral abundance, quality and quantity of floral rewards, and resulting bee visitation (Carvalheiro et al. 2021). We included insecticide risk to wild bees in our quantification of landscape quality as myriad evidence shows insecticide exposure can

142 negatively influence bee behavior and reproduction and that insecticides used locally can
143 have far-reaching consequences (Goulson et al. 2015; Long and Krupke 2016).

144 We ask the following research questions: 1) What is the relative importance of local
145 versus landscape scale in driving bee richness and abundance? 2) Which metrics of local
146 and landscape quality best explain wild-bee abundance and richness? And 3) How do the
147 relationships in (1) and (2) vary with season? Within these broad objectives, we were also
148 able to identify which types of semi-natural habitat were the most important for spring and
149 summer bee communities and how temporal variation in floral resources at local and
150 landscape scales affects abundance and richness of wild bees. Due to a higher prevalence of
151 cavity-nesting, large-bodied social species with longer foraging ranges in summer bee
152 communities, we predicted that summer bee abundance and richness would be strongly
153 linked with landscape quality, while smaller-bodied spring bees would respond more
154 strongly to local floral resources and soil characteristics. Drawing on other studies in our
155 region documenting limited or no effect of insecticide risk on wild bees at a landscape scale
156 (McNeil et al. 2020; Kammerer et al. 2021), we expected that land use and floral area
157 metrics would be the best predictors of wild-bee communities.

158 2. Materials and methods

159 1. Study region and site selection

160 We studied wild-bee communities at 33 sites in the Finger Lakes region of New
161 York, USA (Figure 1). The Finger Lakes region is in south-central New York, and is
162 approximately 42% semi-natural land (almost all forest habitats), 8% developed, and 49%
163 agriculture, including pastureland (USDA NASS 2018). There is a regional gradient of

164 landscape composition, with high forest cover in the south, and increasing agricultural land
165 moving north and closer to the lakes. (Figure 1). In proximity to Seneca and Cayuga lakes,
166 the climate is relatively moderate, particularly well-suited for specialty crops like wine
167 grapes and tree fruit. Generally, in this region, crop diversity is quite high, especially on
168 small farms, which are common (USDA NASS 2019). Twelve percent and 42% of farms are
169 smaller than 4 ha and 20 ha, respectively (USDA NASS 2019). The small farm sizes and
170 relatively high amounts of semi-natural habitat means many agricultural areas in our study
171 region could still be considered 'complex' landscapes (Tscharntke et al. 2005). For example,
172 within 1 km, only five of our 33 study sites had less than 20% semi-natural habitat, and
173 none were below 1% semi-natural habitat (a 'cleared' landscape as defined by Tscharntke
174 et al. (2005).

175 We selected our 33 study sites from 144 locations included in a previous study
176 documenting plant community composition, local and landscape floral resources (Iverson
177 et al.) in review, see Appendix for methodology). From these sites, we selected those
178 corresponding to seven habitat types (mesic upland remnant forest (i.e., not previously
179 cleared for crops), floodplain forest, forest edge, old field, roadside ditch, mixed vegetable
180 farm, and apple orchard) that span a range of semi-natural to managed land use. Forest
181 edge plots were placed adjacent to the boundary of upland forest and neighboring habitat
182 (usually cropland), old fields were post-agricultural areas dominated by grasses and
183 goldenrod (*Solidago* spp.; *Euthamia graminifolia*), and mixed vegetable farms were
184 relatively small-scale farms that grew a diversity of fruits and vegetables. We selected the
185 33 sites from the initial 144 locations in Iverson (in review) based on attaining a sufficient
186 sample size of each of the seven selected habitat types and on maintaining a minimum

distance between sites. To ensure we were sampling independent bee communities, we chose sites that were, at minimum, one km from all other sites which, in our study region, exceeds the mean foraging range of a typical community of wild bees (Kammerer et al. 2016).

2. Wild-bee survey

At each of our 33 sites, in 2018 and 2019, we measured bee species richness and abundance using bee bowls according to the protocol of a long-term bee monitoring program in our region (Droege et al. 2016). In each year, we sampled bees in late April/early May and again in mid-July; dates were selected to correspond to peak floral abundance in forest, wetland, and successional habitats (Iverson et al. in review). We filled fluorescent blue, fluorescent yellow, and white, 355 mL Solo polystyrene plastic cups with 50:50 mix of propylene glycol and water. We placed bee bowls at the height of dominant vegetation for 7-14 d of sampling. In spring, we deployed bee bowls for 14 d, while, in summer, trap liquid evaporated more quickly, which limited our sampling to 7 d. At each site, we arranged bee bowls in 80-m transects in visible areas, alternating bowl color with 10 m between each bowl, for a total of 9 bowls per site. We placed the middle of our transects at the center of Iverson et al.'s (in review) plant survey plots, based on the recorded GPS coordinate, or, at some locations, physical flags marking the plot outline.

After collection, we stored bee specimens in 70% ethyl alcohol solution until pinning and sorting. We washed, pinned, and identified bee specimens, to species when possible, with taxonomic assistance from collaborators, including Dr. David Biddinger (Penn State Center for Pollinator Research, Biglerville, PA), and Dr. Rob Jean

(Environmental Solutions & Innovations, Inc., Indianapolis, IN). We sorted specimens in the *Nomada* "bidentate" group to morphospecies, as this group is poorly resolved in existing taxonomic keys (Droege et al. 2010; Ascher and Pickering 2013). Also, some *Lasioglossum* specimens were damaged during collection or processing (n=50), so we could not reliably determine species identity. We excluded these specimens from richness analyses that required species-level identification. For all species, voucher specimens were deposited in the Frost Entomological Museum at The Pennsylvania State University in University Park, PA.

3. Local quality metrics

For each site, we measured soil characteristics and calculated plant species richness, community composition, and floral area from existing data (Iverson et al. in review).

1. *Soil collection and processing*

In May 2018, we collected soil from each of our 33 study sites. Along the bee sampling transect, we collected five soil samples with a bucket auger to a depth of 9-18 cm, depending on rock and moisture content. We took shallower soil cores (9-12cm) at sites with very rocky or wet (floodplain habitat) subsoil. Wild-bee nesting would likely be inhibited by very high rock content or completely saturated subsoils (Harmon-Threatt 2020), so we considered the shallower sampling depth representative of the most favorable zone for bee nests. To quantify bulk density, at two locations along the bee transect, we collected three undisturbed soil cores (0-3 cm, 4-6 cm, and 7-9cm deep) with a slide hammer sampler (Soilmoisture Equipment Corp, Goleta, CA). Due to high moisture or rock content at some sites, we were only able to collect two bulk density cores, but we

recorded the number of cores in each sample. For processing and analysis, we combined bulk density cores from all depths.

After collection, for all soil samples, we measured wet mass, then dried samples in an oven at 60°C for five days (or until the mass did not decrease) and measured dry mass. We calculated bulk density from dry mass and sent bucket-auger samples to the Penn State Agricultural Analytical Services Laboratory, where they measured pH, P, K, Mg, Ca, Zn, Cu, S, total nitrogen by combustion, percent organic matter, and percentage sand, silt, and clay via standard laboratory methods (Penn State Agricultural Analytical Services Lab). To summarize trends in soil characteristics, we centered and standardized soil variables and conducted a principal components analysis with the *stats* package in R (R Core Team 2021).

2. Plant species richness, abundance, community composition, and floral area

We designed our study to leverage an existing, comprehensive plant survey conducted in the greater Ithaca region, NY (Iverson et al. in review, see Appendix). In 2016 and 2017, Iverson et al. (in review) documented plant species richness and abundance at 144 sites across the most common habitat types (N=22) in the surveyed region that span across the broader classes of forest, agriculture, wetland, successional, and developed. Briefly, Iverson et al. (in review) surveyed 3-20 sites of each habitat type based on variability among sites, with a median of ~5 sites/habitat type. They used a Modified Whittaker plot design (Stohlgren et al. 1995) with halved dimensions, equating to a 10 x 25 m plot with nested subplots of varying sizes. They recorded plant cover by species in ten 0.25 m^2 quadrats and species presence in all other subplots and in the full plot. Overall

254 plant coverage was estimated based on frequency in larger subplots and coverage in the
255 0.25 m^2 quadrats. Furthermore, they recorded the species abundance of all mature, i.e.,
256 potentially flowering, angiosperm trees.

257 Using a combination of survey data and flower density and size measurements for each
258 species observed, Iverson et al. (in review) estimated floral area per species in each site. To
259 estimate flower density, for each species, they measured the number of flowers in a 0.25 m^2
260 quadrat during peak bloom and measured flower size in the field, from herbaria specimens,
261 or from published sizes in online plant databases. Then, utilizing bloom dates published in
262 a flora specific to the region, they estimated FA across the bloom window of each plant
263 species. Finally, they calculated the daily average FA per m^2 of each of the sampled habitat
264 types by averaging the sum of the FA, weighted by percent cover, of each of the flowering
265 plant species present across all plots in each habitat type (excluding apple blossoms in
266 'apple orchard' habitat, in order to capture only orchard-floor floral resources).

267 For our analysis, we summarized site-level FA curves with seven metrics: season total
268 FA, minimum FA, maximum FA, FA coefficient of variation, and total FA in spring, summer,
269 and fall. For total, maximum, and coefficient of variation, we summarized FA from April to
270 mid-November. We quantified minimum FA from a narrower timeframe associated with
271 more rapid plant growth (mid-May to mid-September) to avoid all sites receiving similarly
272 low values associated with the beginning or end of the season. We defined 'spring' as early
273 April to mid-June (day-of-year 92 to 163), 'summer' as mid-June to late August (day-of-year
274 164 to 238) and 'fall' as late August to mid-November (day-of-year 239 to 310). We
275 generated two versions of each FA metric, one that represents the FA of all plants, and the

second that only includes plant species that are known to be pollinated by insects ('IP plants', Iverson et al. in review).

From the plant survey data, we also quantified plant species richness, relative abundance, and community composition for our 33 study sites. We calculated species richness of all plants, species richness of insect-pollinated plants, and percent cover of all vegetation. We used non-metric multi-dimensional scaling (NMDS) ordination with a Bray-Curtis distance measure to quantify the main gradients in plant-community composition. Specifically, with the *vegan* package in R (Oksanen et al. 2013), we summarized the similarity between plant communities at all 144 sites surveyed by Iverson et al. (in review) and visualized the results in two dimensions. To determine the effect of varying composition of plant communities on bee abundance and richness at our 33 study sites, we included scores from the first two NMDS axes as predictor variables in our analyses.

4. Landscape quality metrics

1. Landscape composition and configuration

To describe the land cover surrounding our study sites, we used a high-resolution map of land cover available for our study region (Iverson et al. in review). This product utilized a regional 1m resolution dataset of land cover (Chesapeake Conservancy 2013) to differentiate impervious surface, trees, and low vegetation and a regional natural habitat map (Ferree and Anderson 2013) and the USDA Cropland Data Layer (USDA NASS 2018) to resolve more detailed natural and agricultural habitats, respectively. Wetland habitats were incorporated using the National Wetlands Inventory data (U.S. Fish and Wildlife

298 Service 2017) and a 'roadside ditch' habitat class was created by adding a 3m buffer on
299 either side of non-urban roads.

300 From this high-resolution land-cover map, we calculated landscape composition and
301 configuration within 1 km radius of each of our sampling sites. We selected this distance
302 because, excluding large-bodied *Bombus* sp., most wild-bee species in our region forage
303 within 1km of their nests (Kammerer et al., 2016). We grouped land-cover classes to form
304 six metrics of landscape composition: percentage of the landscape in agriculture, forest,
305 successional (old field and shrubland), wetlands, water, and developed habitats (Table S1).
306 Based on previous research examining landscape configuration effects on wild bees
307 (Kennedy et al. 2013), we also calculated six landscape configuration metrics to represent
308 the aggregation, shape, and diversity of habitat patches around our sampling sites.
309 Specifically, using the *landscapemetrics* package, version 1.4.2, in R (Hesselbarth et al.
310 2019; R Core Team 2021), we calculated edge density, Shannon diversity of land cover
311 classes, Simpson diversity of land cover classes, mean perimeter-area ratio, variation in
312 nearest neighbor distance between patches of the same class, and interspersion and
313 juxtaposition indices.

314 *2. Landscape insecticide toxic load*

315 To represent risk to wild bees from insecticide applied to agricultural crops, we
316 calculated an index of insecticide toxic load. We generated the index of insecticide toxic
317 load (Douglas et al. 2021) using our high-resolution land cover maps and insecticide data
318 from 2014, as this is the most recent year with a complete, publicly available dataset of
319 insecticide application. We estimated insecticide risk at our sampling sites in three steps.

320 First, we calculated a distance-weighted metric of landscape composition from the high-
321 resolution land cover data (see *Landscape composition and configuration*) with the
322 'distweight_lulc' function in the *beecoSp* R package (Kammerer and Douglas 2021). For
323 distance-weighting, we selected a wild-bee foraging range of 500 m, which assumes, from
324 the center of each study site, 70% and 100% of bee foraging occurs within 500-m and 1-km
325 radii, respectively. Then, for each land-cover class, we multiplied distance-weighted area by
326 the insecticide-toxic-load coefficient for a given land cover. Finally, for each study site, we
327 calculated total insecticide toxic load as the sum of insecticide load from all land cover
328 classes within a 1-km landscape. Without *a priori* knowledge of the most likely route of
329 insecticide exposure for each active ingredient, we used insecticide values corresponding
330 to the mean of oral and contact toxicity (Douglas et al. 2021).

331 *3. Floral area of landscapes*

332 We quantified the floral area of landscapes in three steps. First, we averaged floral
333 area at all sites within a land-cover class to calculate habitat-level FA per day per ha of
334 habitat. Then, for each land-cover class within 1km of our study sites, we multiplied
335 distance-weighted area (ha) in the landscape (see *Insecticide toxic load* for distance-
336 weighting details) by the habitat-level FA. Then, we summed over all land-cover classes,
337 yielding landscape-total FA per day for each of our study sites. For local and landscape
338 floral area, we calculated minimum FA, maximum FA, FA coefficient of variation, and total
339 FA in spring, summer, and fall for all plants and for insect-pollinated plant species only ('IP
340 plants', Iverson et al. in review).

341 *4. Distance to water and topography*

342 We generated distance to water and topography metrics and included these factors in our
343 analyses. To differentiate riparian sites very close to water, we calculated the minimum
344 distance from our sampling locations to water (streams, rivers, ponds, or lakes). We
345 identified water features closest to our sampling sites using the National Hydrography
346 Dataset (U.S. Geological Survey 2019a) for New York state. Lastly, we included topographic
347 information to represent the micro-climate at each of our sites. We calculated elevation,
348 slope, and aspect at each sampling site from the 1/3 arc-second (approximately 10m)
349 resolution USGS National Elevation Dataset (U.S. Geological Survey 2019b). We included
350 distance to water and topography as landscape variables because, excepting elevation, they
351 describe the relationship between the sampling site and surrounding water and
352 topographic features. However, distance to water and topography were not among the
353 most explanatory predictor variables (Figure 2), so if we had classified them as local
354 variables, our results would be largely unchanged. We used the R statistical and computing
355 language (R Core Team 2021), specifically the *sf* and *raster* packages (Pebesma 2018;
356 Hijmans 2022), for all manipulations and analyses of geospatial data.

357 **5. Statistical analyses**

358 *1. Sampling-effort adjustment*

359 Prior to analysis, we adjusted bee abundance and species-richness measures to
360 account for varying sampling effort. While we were collecting bee bowls, we recorded the
361 number of traps that were cracked, tipped over, or otherwise compromised. We present
362 abundance results as bees per successful trap per day, to adjust for varying sampling time
363 and lower sampling effort at sites where traps cracked or fell over. Unfortunately, for the

July 2019 sampling round, we lost our record of the number of compromised traps. To the best of our ability, we recreated these data from memory shortly after the sampling period by estimating the number of compromised traps per site. For wild-bee richness analyses, we adjusted for uneven effort using coverage-based rarefaction and extrapolation (Chao and Jost 2012), rather than the number of successful traps, so recreated data were not used in richness analyses. Specifically, we estimated bee richness at the mean coverage level for each season using the *iNEXT* package in R (Hsieh et al. 2016, 2018; R Core Team 2021).

2. Random forest models

We used random forest models to compare the relative importance of local vs. landscape variables, identify the most important individual predictor variables, and examine relationships between predictors and wild bee abundance and richness. Random forest models are robust to correlated predictors and can represent complex, non-linear relationships, which we expected in our dataset (Wright and Ziegler 2017). In our study region, the composition of wild-bee communities in spring is substantially different from summer and fall (Kammerer et al. 2021; Turley et al. 2022), so we analyzed our spring and summer sampling periods separately. For spring analyses, we removed floral-area metrics that represent, or were correlated with, floral resources available in summer and fall (Figure S10). Specifically, for spring analyses, we removed summer-total-floral area and fall-total-floral area of all plants and insect-pollinated ('IP') plants, maximum-floral area (IP plants) and total-floral area (IP plants).

In preliminary analyses, we noticed that the number of predictor variables included in random forest models influenced model performance and variable importance scores

(Fox et al. 2017). To compare random forest models with the same number of predictors, we first modelled bee abundance and richness using all 72 year, landscape, and local predictors and examined the resulting variable importance scores. Then, we selected the top 35 predictors and generated a final model using only these predictors. We used 'top-35' models to compare variable importance and describe relationships between bee abundance, richness, and specific predictors (Figures 2-5). We assessed the performance of all random forest models using 10-fold cross validation repeated 15 times, and, with a grid search, selected the optimum number of trees (1000 to 5000, incremented by 1000) and variables at each tree split (15 to 30, incremented by 5). We used the random forest algorithm from the *ranger* package in R (Wright and Ziegler 2017), tuned the model with the *caret* package (Kuhn 2008, 2019), and, to examine our results (Figures 3-5), generated accumulated local effects (ALE) plots with the *iml* package (Molnar et al. 2018). ALE plots depict the relative effect of changing one predictor variable and are centered at zero so each value on the curve is the difference from the mean prediction of the random forest model. For each season, we present local effect plots for year (Figure 5) and the top four variables predicting bee abundance and richness (Figures 3-4).

3. Results

1. Wild-bee communities

In spring and summer, we documented diverse wild-bee communities. Our survey yielded 3108 specimens, 1666 in 2018 and 1442 in 2019. We collected more bees in spring (n=2130) compared with summer (n=987), particularly in the second year when our summer sampling generated only 282 individuals. We documented 127 species of wild

408 bees of 21 genera, with 94 species present in spring and 78 in summer. *Andrena,*
409 *Lasioglossum,* and *Ceratina* were the most abundant spring genera, representing 78% of the
410 individuals we observed (Figure 6). At the species-level, the most abundant spring bees (>
411 5% spring abundance) were *Andrena carlini* Cockerell, *Ceratina calcarata* Robertson, *Osmia*
412 *cornifrons* Radoszkowski, *Ceratina dupla* Say, and *Andrena hippotes* Robertson. In summer,
413 *Lasioglossum* was the most abundant genus, followed by several other genera in the family
414 Halictidae (*Agapostemon, Augochlora, and Halictus*). *Lasioglossum leucozonium* Schrank,
415 *Agapostemon virescens* Fabricius, *Lasioglossum versatum* Robertson, *Peponapis pruinosa*
416 Say, and *Augochlora pura* Say were the most abundant summer species (> 5% of summer
417 abundance).

418 **2. Local quality**

419 *1. Characterizing local quality*

420 We characterized several dimensions of local quality for wild bees, including floral
421 area, plant richness and community composition, and soil characteristics. Of the seven
422 habitats included in our study (mesic upland remnant forest, floodplain forest, forest edge,
423 old field, roadside ditch, mixed vegetable farm, and apple orchard), mesic upland remnant
424 forest and forest edge had highest floral area, peaking in early spring (Figure 7). In summer
425 and fall, floral resources in all habitats were generally much lower, excepting an early-fall
426 peak in flowers in old fields associated with goldenrod (*Solidago* spp. and *Euthamia*
427 *graminifolia*) bloom period (Figure 7, Figure S3).

428 Our analysis of plant community composition revealed clear differentiation between
429 plant communities in different habitats. We analyzed the full set of habitat types (n=22,

Iverson et al. (in review) to capture broad gradients in composition of plant communities that were not evident when including only our focal habitats (n =7, M Kammerer, *unpublished analyses*). Considering all 22 habitats, the first ordination axis ('NMDS1') differentiated habitat types according to the intensity of human management (Figure S1, stress = 0.153), with unmanaged forest and wetland habitat separating from managed agricultural and developed habitats (lawn, row crops, orchards, vegetable farms, pasture, and hay fields). Old fields, roadside ditches, tree rows, and forest edge habitats were intermediate, containing plants associated with managed and unmanaged habitats. In subsequent random forest models, we included site values on NMDS axis one as a proxy for intensity of management. The second axis was less clear, but seemed to represent a gradient of moisture content, separating wetlands from forest and managed habitats, with floodplain forests in the middle (Figure S1).

We found significant variation in soil characteristics between the seven habitat types we sampled. There were two main gradients in our soil dataset revealed by the principal components analysis (Figure S2). Explaining 26.4% of the variation in our soil data, the first principal component was associated with pH, soil texture (percent sand, silt, and clay), water content, organic matter, and total nitrogen. Roadside ditches had more basic, sandier soil than any of the other habitat types, except some floodplain forest samples. All other habitat types had loam to silt-loam soil. Interestingly, soil texture was highly variable between floodplain forests, with soil texture in this habitat encompassing the full range of texture classes represented at all other sites. The second principal component explained 20.0% of variation in soil characteristics and correlated with soil clay content, potassium, copper, phosphorus, zinc, clay content, and cation exchange capacity.

Specifically, some vegetable farm and orchard samples had much higher potassium, phosphorus, copper, and zinc content than the other habitats, likely due to fertilizer or manure application to support crop growth. Soils at forested sites were characterized by higher organic matter and total nitrogen, possibly from leaf litter accumulation.

2. *Local quality effects on wild bees*

Comparing spring to summer, we documented substantially different relationships between local quality and bee abundance (Figure 2). In spring, we observed moderate effects of local characteristics on wild bees, with three local variables (soil potassium, soil phosphorus, and management intensity as reflected in plant community composition) among the top predictors of abundance or richness. Abundance of spring bees increased with higher levels of soil potassium and lower soil phosphorus measured at the site, with the greatest increase between approximately 75 and 125 ppm potassium (Figure S9 B-C). Abundance of spring bees was lower in more-managed sites (Figure S9 A). In summer, abundance of wild bees was influenced by the level of management (plant community composition) and presence of fall-flowering plants (Figure 2). At the less-managed sites (remnant forests and floodplain forests, NMDS axis one loading less than approximately -0.1), we observed lower abundance of summer bees (Figure 4A). Bee abundance was intermediate in forest edge, old field, and ditch habitats (NMDS1 =-0.1 to 0.4), and highest in orchards and mixed vegetable farms (NMDS1 > 0.4). Sites with very low or no fall-flowering plants also had notably lower abundance of summer bees, but, when floral area

was greater than approximately 10,000 m^2/ha of habitat, bee abundance did not increase with additional fall flowers (Figure 4C).

For richness of wild bees, local quality had weak effects on spring and summer bees (Figure 2). In spring, we observed approximately one additional bee species at sites with more than 25 plant species. In summer, soil fertility, bulk density, and water content were the most important local predictors. We documented slightly more species of bees at sites with intermediate total soil nitrogen, bulk density, and water content, peaking at approximately 30%, 1.18 g/cm^3, and 0.31 g/g, respectively (Figure 4F-H).

3. Landscape quality

1. Characterizing landscape quality

We noted substantial variation in the composition and configuration of landscapes surrounding our study sites (1 km radius), while topography was more consistent (Figures S5-S7). In our study landscapes, amount of developed land ranged from zero to approximately 50%, while forest and natural habitats ranged from zero to more than 70%. All landscapes surrounding our study sites were at least 18% agriculture, up to a maximum of 91% agricultural land. Distance to the nearest water source was generally low, with a maximum of 580 m. Most of our study sites had relatively low insecticide toxic load values, but insecticide toxicity was substantially higher in landscapes with significant apple and grape production (Figure S5). Edge density was the most variable configuration metric, while the interspersion and juxtaposition index and perimeter-area ratio were more consistent. Both Shannon and Simpson diversity indices were left-skewed, capturing the diverse agricultural, natural, and developed land cover types present in our study region (Figure S6).

2. Landscape quality effects on wild bees

In spring, we documented higher abundance of wild bees at locations with more wetland, surface water, natural habitat, and flowers in the surrounding landscape (Figure 3A-D). In our study region, wetlands and surface water are a relatively small percentage of most landscapes (3.42% ± 3.54%, mean ± standard deviation of wetland area), but we found substantially higher abundance of spring bees at sites with 4-5% wetland in the landscape compared with those that had 0-2% wetland (Figure 3A). Between approximately 20 and 60% natural land in the landscape, abundance of spring bees increased, likely due to additional floral resources and nesting sites (Figure 3C). Lastly, we observed higher abundance of spring bees with more variable (higher CV) landscape-level floral area (FA, Figure 3D). In our study region, high variability in FA comes from multiple, high peaks in spring FA from flowering trees in forested habitats (Figure 7).

For species richness of spring bees, the amount of developed land, elevation, and distance to water in the landscape were among the best predictors. We found more species at low elevation sites and locations with some developed land in the landscape, although most of our study landscapes had a relatively small amount of developed land (less than 10%) (Figure 3E-F). At sites less than 100 m from water, we observed approximately two more species of spring bees than sites that were 400 m or more from the nearest stream, lake, river, or pond (Figure 3H).

Compared with spring, in summer, landscape effects on wild bees were moderated. We did not detect any relationship between landscape quality and abundance of summer bees, but three landscape variables (percent agriculture, percent natural, and north-south aspect) were among the most important predictors of richness of summer bees (Figure 2).

We observed a threshold of approximately 55% of the landscape in agriculture, above which richness of summer bees dropped substantially (Figure 4E). Insecticide toxic load, slope, and landscape configuration metrics were not among the most important predictors of spring or summer bee communities.

4. Relative importance of year, local, and landscape quality for wild bees

Generally, with our 72 local and landscape-quality metrics, we were able to explain a substantial amount of the variation in wild-bee abundance and richness. Modeling abundance of bees in both seasons, we explained more than 38% of the variation in our data using year, local, and landscape variables (Table 1). We had more unexplained variation for species richness, with mean r-squared values of 20% and 28% for the best random forest models in spring and summer, respectively (Table 1). Across all models, however, our prediction error was very high (72%-108% of mean abundance or richness, Table 1), indicating we are unable to reliably predict bee communities in additional locations or years. As a result, we focused on presenting relationships among landscape and local quality and bee abundance and richness, rather than prediction.

Comparing landscape, year, and local predictors, we found generally that landscape variables and year explained more of the variation in bee abundance and richness than local quality. However, the importance of local versus landscape scale was different for abundance and richness models and varied by season (Figure 2). For abundance of spring bees and richness of summer bees, landscape variables were the most important predictors (Figure 2). In spring, year was, by far, the most important predictor of species richness, with more species of spring bees in 2019 than 2018 (Figure 5). In addition to year, for

richness of spring bees, we observed weak effects of landscape composition, but only one local variable was among the best predictors (Figure 2). Year was also the most important predictor of abundance of summer bees, but, unlike spring richness, local quality was almost as important (Figure 2).

4. Discussion

In this study, we found that bee abundance and richness responded to an interplay of landscape, local quality, and year with significant differences between spring and summer bee communities. Though we predicted spring bees would be more dependent on local quality than summer bees, we instead found that spring abundance and spring and summer richness were mostly associated with landscape quality, specifically landscape floral resources in the springtime and percentage of landscapes occupied by wetlands, water, natural, and agricultural habitats. Summer abundance was significantly affected by local conditions, including soil fertility, plant-community composition, and local-scale floral resources in the fall. Consistent with our previous studies, predicted insecticide risk in the landscape was not a significant factor for the wild bee communities in our study. Here, we discuss wild-bee responses to landscape, then local quality, with recommendations for designing conservation practices and suggestions for future research.

Wetlands and surface water were very important landscape features for supporting spring bees; therefore, we expect that restoring or conserving relatively small patches of these habitats could substantially improve landscape quality in spring. We observed more species of spring bees closer to water, indicating that terrestrial-aquatic interfaces likely

support specialist bees or plant species important for spring bees (Stewart et al. 2017). This pattern underscores the short foraging distance of many wild-bee species in our study region, as bee richness decreased substantially only 200m removed from water. In our study region, wetland habitats, especially shrub and emergent wetlands, host a unique community of plants, including some herbaceous flowering plants not found in other habitats (Figure S1). Several of the plant species associated with floodplain and emergent wetland habitats are recommended for pollinator plantings (e.g. *Eutrochium purpureum, Helianthus decapetalus*; Byers et al., n.d.), or are closely related to known pollinator-attractive species (e.g. *Bidens cernua, Hydrophyllum canadense, Stachys hispida*), suggesting they might also provide pollen or nectar resources for wild bees (Tuell et al. 2008). There are relatively few studies documenting wild-bee communities in wetlands, although most report rich bee communities in and around water and wetland habitats (Stewart et al. 2017; Vickruck et al. 2019), including presence of some threatened species (Moroń et al. 2008). In our study, relatively small areas of wetlands in a landscape correlated with higher bee abundance and richness, so we conclude that surface water and wetland habitats would be feasible targets of conservation programs seeking to improve landscape quality for wild bees. Also, wetlands host many other insect, birds, and amphibian taxa (Riffell et al. 2003; Gibbons et al. 2006; O'Neill and O'Neill 2010), and thus wetland restoration and conservation could contribute more broadly to biodiversity goals. These findings also confirm the importance of existing programs that protect wetland habitat from agricultural and urban development.

In spring, wild bees are heavily dependent on resources provided by the surrounding landscape, most likely from mass flowering of trees in forest habitats. We found more

588 spring bees at sites with multiple, high peaks in spring floral resources from flowering
589 trees in forests. Past research has documented a diverse wild-bee community in tree
590 canopies (Urban-Mead et al. 2021) and demonstrated that solitary bees consume spring
591 pollen from wind-pollinated trees (Kraemer and Favi 2010). In our study, spring bee
592 abundance was positively associated with floral resources provided by the entire plant
593 community (wind and insect pollinated plants) reinforcing the finding that these bees use
594 trees not traditionally thought to be 'insect pollinated', such as oaks (*Quercus* spp.),
595 hickories (*Carya* spp.), birches (*Betula* spp.), American beech (*Fagus grandifolia*), and
596 maples (*Acer* spp.). The pattern we observed suggests that spring bees were able to take
597 advantage of very large pulses of floral resources such that short periods of mass flowering
598 may be equally beneficial as consistently high levels of flowering (Hemberger et al. 2020).

599 In summer, diversified vegetable farms and apple orchards hosted high abundance
600 of bees, but not all species persisted in highly managed landscapes. In mid-summer, old
601 fields had more floral resources than agricultural habitats (Figure 7), but plant
602 communities in orchards and mixed vegetable farms hosted higher bee abundance. We
603 speculate that, in these agricultural habitats, flowers of crop plants and weeds in
604 fencerows, fallow, or between-row sections of fields are particularly important floral
605 resources for bees. Indeed, many studies have documented the importance of weeds in
606 providing forage for bees in both agricultural and urban areas (Norris and Kogan 2005;
607 Bretagnolle and Gaba 2015; Requier et al. 2015; Rollin et al. 2016). Also, most of the farms
608 and orchards we sampled were not intensively tilled or have substantial untilled area in
609 proximity, which likely benefits species of ground-nesting bees (Ullmann et al. 2016).
610 While some agricultural habitats can support relatively high bee abundance, like many

611 other studies (Kennedy et al. 2013; Grab et al. 2018), we documented fewer species of
612 summer bees in landscapes with a high proportion of agricultural land. In contrast to our
613 sampled vegetable and orchard crop farms, most of the agricultural land in our study was
614 intensively managed row crop agriculture. Similar to simplified bee communities in urban
615 areas, crops and weedy plants in intensively managed agricultural habitats host a subset of
616 all bee species, likely generalist, disturbance-tolerant species (Harrison et al. 2018).

617 We found that soil fertility was an important component of local habitat quality for
618 wild bees, potentially due to fertility effects on floral resources. Intermediate soil fertility
619 was associated with higher richness of wild bees in summer. We posit that soil fertility
620 primarily affected wild-bee communities at our study sites by mediating plant vigor and
621 flowering. Soil-nutrient levels influence richness and composition of plant communities
622 (Tilman 1987; DiTommaso and Aarssen 1989; Wilson and Tilman 1991), but, we found
623 little evidence that plant community shifts drove fertility effects on bees because plant
624 richness was a poor predictor of bee abundance and richness, and plant community
625 composition and soil fertility were weakly correlated (Pearson's r = -0.6, -0.52, and 0.4
626 between NMDS axis 1 and soil organic matter, total nitrogen, and potassium, respectively).
627 Other studies have shown that soil-nutrient levels influence size and number of flowers
628 and quality and quantity of nectar and pollen produced, with measurable effects on bee
629 visitation (Burkle & Irwin, 2010; Burkle & Irwin, 2009; Cardoza et al., 2012). Based on our
630 results, manipulating soil nutrients within restoration and conservation plantings may
631 increase floral resources and associated bee communities, but we need targeted
632 experimental research to verify that patterns we documented are consistent and strong

633 enough to be a successful management strategy without accompanying unintended
634 consequences.

635 For both seasons, soil texture was notably absent from our list of important local
636 variables. If, at the local level, wild-bee communities were limited by the availability of
637 nests, we expected that soil texture would have been an important soil characteristic, as
638 many wild bees nest in the ground or use soil for cavity partitions (Pinilla-Gallego et al.
639 2018; Harmon-Threatt 2020). In our study, soil texture within each study site was not a
640 strong predictor of bee abundance or richness, suggesting that numbers of suitable nest
641 sites may be governed by soil characteristics within the larger landscape (Hellwig et al.
642 2022) , which we could not capture. Few studies have quantified landscape-scale nesting
643 resources (Ariza et al. 2022), likely in part due to poor characterization of preferred
644 nesting conditions of wild bees (Harmon-Threatt 2020) and challenges associated with
645 existing soil maps (Cambardella et al. 1994; Moral et al. 2010). In the future, it would be
646 extremely valuable to quantify, at the landscape-scale, availability of soil, wood, stem, and
647 cavity nest sites for wild bees based on empirical data, mirroring the Iverson et al. (in
648 review) effort to estimate landscape floral resources.

649 We observed notable differences between the two years of our study, with more species
650 of spring bees and fewer summer bees in 2019 compared with 2018. In 2019, early spring
651 was warmer than 2018 and we delayed our sampling time due to logistical constraints
652 which likely altered the composition of the bee community we sampled. We attribute the
653 higher richness of spring bees in 2019 to a better match between our sampling time and
654 flight period of most spring bees (Kammerer et al. 2021). The differences in the summer
655 collections was likely also due to weather conditions in the previous year, as the summer of

656 2018 was extremely rainy, with near-record high precipitation (DiLiberto 2018), which
657 may have reduced foraging opportunities and negatively affected bee populations (Tuell
658 and Isaacs 2010; Vitale et al. 2020). Evaluating the effect of weather conditions on bee
659 communities requires multiple years of sampling, and thus we did not formally include
660 these variables in this study, but such analyses have been conducted in other studies
661 (Kammerer et al. 2021; Filazzola et al. 2021).

662 Though we were able to provide important insights about how local and landscape
663 variable influence bee communities, our study has several limitations. First, we sampled
664 wild bees using pan traps, which perform poorly in areas with abundant floral resources
665 and have some taxonomic biases, including under-sampling large bodied bees (Roulston et
666 al. 2007; Baum and Wallen 2011). By using pan traps, we were not able to determine if the
667 bees we sampled were nesting or foraging within our study site, or en route to a different
668 patch. We minimized, but could not completely exclude, the latter outcome by not using
669 extremely attractive blue vane traps (Gibbs et al. 2017). Second, our estimates of local and
670 landscape floral area assumed flower production is solely a function of the composition of
671 plant communities of a given locale. In quantifying landscape floral area, we assumed plant
672 communities of the same habitat type had equal numbers of flowers. In reality, the number,
673 size, and quality of floral resources is influenced by many factors, including temperature,
674 moisture availability, and soil fertility (Cardoza et al. 2012; Mu et al. 2015). For each site,
675 we estimated local floral area based on relative abundance of plants present at the site but
676 did not measure realized flowering in each year of our study. We suspect that soil fertility
677 influenced bee abundance and richness at our study sites by changing flower production
678 per unit vegetative cover, but lacking surveys of realized floral area at every site, we could

679 not test this hypothesis. Third, we conducted bee surveys 1-3 years after Iverson et al plant
680 surveys. Comparing habitat types, we expect the major trends in plant community
681 composition, floral area, and richness (Figures S2-S4) would be robust to this 1-3 year time
682 lag. In mesic upland remnant forests, floodplain forests, and forest edges, most species are
683 long-lived trees and shrubs, so we expect little change in plant composition and floral area.
684 In old fields, roadside ditches, mixed vegetable farms, and apple orchards, mowing,
685 spraying, or crop rotation may have shifted plant communities in the time between plant
686 and bee sampling. From our field observations, none of our sites experienced major
687 disturbances like fire or pest outbreak. Fourth, by choosing to analyze our data with
688 random forest models, we could not assess interactions between local and landscape
689 quality. Local and landscape quality metrics were only weakly correlated across scales
690 (minimum, mean, and maximum Pearson's r = -0.6, 0.01, and 0.56, respectively, Figure
691 S10), potentially suggesting independent effects of local and landscape quality, but we
692 could not examine these questions. Finally, while assessing conservation plantings for
693 pollinators, it has been a persistent challenge to assess whether adding flowers for bees
694 increases wild-bee populations, or just concentrates individuals in high-quality patches.
695 Our multi-dimensional characterization of local quality cannot definitively show that high-
696 quality sites improved bee fitness, compared with drawing in more individuals that were
697 already present in the landscape. In the future, to provide a measure of wild-bee
698 reproductive output, we recommend researchers use passive traps or visual observation in
699 tandem with nest boxes or colonies of managed bees (see Martínez-Núñez et al. 2020;
700 Centrella et al. 2020). Two recent studies also presented promising methods to detect
701 landscape-scale changes in wild-bee abundance or richness (Kleijn et al. 2018; Scherber et

al. 2019), and it would be valuable to test these methods in more complex landscapes, such as in our study region.

5. Conclusion

In this study, we identified key components of landscape and local quality for wild bees, generating essential targets for bee conservation programs. Building on previous research showing that bees respond to both landscape and local resources, we found that the most relevant spatial scale varies by season and can differ when considering bee abundance or richness. Spring bees were heavily dependent on landscape resources, but abundance of summer bees responded to local, rather than landscape quality, implying that site-level management is most likely to be successful in supporting (or at least attracting) summer bees. In highly agricultural landscapes, however, improving local quality for summer bees will likely primarily benefit disturbance-tolerant, generalist species because rare bees are typically absent from these landscapes (Harrison et al. 2019). By quantifying landscape-scale floral resources, we found that semi-natural habitats, specifically forests, provision spring bees, likely by providing large pulses of resources from flowering trees. Many areas in our study region already have large patches of forest habitat, suggesting that adding more trees or shrubs represents a small marginal gain when compared with existing resources. Rather, to support spring bees in landscapes with relatively high forest cover, we recommend targeted additions or restorations of wetlands and surface-water features, habitats that should also provide conservation benefits for other plant and animal taxa. By considering spatial and temporal variation in resources, we developed context and season-

724 specific recommendations to improve habitat quality for wild bees, a critical component of

725 conservation efforts to offset the manifold stressors threatening these taxa.

726

727

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References

Ansell D, Freudenberger D, Munro N, Gibbons P (2016) The cost-effectiveness of agri-environment schemes for biodiversity conservation: A quantitative review. Agric Ecosyst Environ 225:184–191. https://doi.org/10.1016/j.agee.2016.04.008

Ariza D, Meeus I, Eeraerts M, et al (2022) Linking remote sensing data to the estimation of pollination services in agroecosystems. Ecol Appl. https://doi.org/10.1002/eap.2605

Ascher JS, Pickering J (2013) Discover Life bee species guide and world checklist (Hymenoptera:Apoidea:Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species

Bartholomée O, Aullo A, Becquet J, et al (2020) Pollinator presence in orchards depends on landscape-scale habitats more than in-field flower resources. Agric Ecosyst Environ 293:106806. https://doi.org/10.1016/j.agee.2019.106806

Bartomeus I, Ascher JS, Gibbs J, et al (2013) Data from: Historical changes in northeastern US bee pollinators related to shared ecological traits. Dryad Digit Repos. https://doi.org/10.5061/dryad.0nj49

Bartual AM, Sutter L, Bocci G, et al (2019) The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. Agric Ecosyst Environ 279:43–52. https://doi.org/10.1016/j.agee.2019.04.009

Baum KA, Wallen KE (2011) Potential Bias in Pan Trapping as a Function of Floral Abundance. J Kans Entomol Soc 84:155–159. https://doi.org/10.2317/JKES100629.1

Bloom EH, Wood TJ, Hung K-LJ, et al (2021) Synergism between local- and landscape-level pesticides reduces wild bee floral visitation in pollinator-dependent crops. J Appl Ecol 58:1187–1198. https://doi.org/10.1111/1365-2664.13871

Bretagnolle V, Gaba S (2015) Weeds for bees? A review. Agron Sustain Dev 35:891–909. https://doi.org/10.1007/s13593-015-0302-5

Burkle L, Irwin R (2009) The importance of interannual variation and bottom–up nitrogen enrichment for plant–pollinator networks. Oikos 118:1816–1829. https://doi.org/10.1111/j.1600-0706.2009.17740.x

Burkle LA, Irwin RE (2010) Beyond biomass: measuring the effects of community-level nitrogen enrichment on floral traits, pollinator visitation and plant reproduction. J Ecol 98:705–717. https://doi.org/10.1111/j.1365-2745.2010.01648.x

Byers E, Godwin HW, Kordek W, et al West Virginia Pollinator Handbook. USDA NRCS, West Virginia Division of Natural Resources, The Xerces Society for Invertebrate Conservation

Cambardella CA, Moorman TB, Novak JM, et al (1994) Field-Scale Variability of Soil Properties in Central Iowa Soils. Agron J 58:1501–1511. https://doi.org/10.2136/sssaj1994.03615995005800050033x

Cardoza YJ, Harris GK, Grozinger CM (2012) Effects of Soil Quality Enhancement on Pollinator-Plant Interactions. Psyche J Entomol 2012:. https://doi.org/10.1155/2012/581458

Carvalheiro LG, Bartomeus I, Rollin O, et al (2021) The role of soils on pollination and seed dispersal. Philos Trans R Soc B Biol Sci 376:20200171. https://doi.org/10.1098/rstb.2020.0171

Centrella M, Russo L, Moreno Ramírez N, et al (2020) Diet diversity and pesticide risk mediate the negative effects of land use change on solitary bee offspring production. J Appl Ecol 57:1031–1042. https://doi.org/10.1111/1365-2664.13600

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547. https://doi.org/10.1890/11-1952.1

Chesapeake Conservancy (2013) Land Cover Data Project. https://chesapeakeconservancy.org/conservation-innovation-center-2/high-resolution-data/land-cover-data-project/. Accessed 11 May 2020

Cole LJ, Brocklehurst S, Robertson D, et al (2017) Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. Agric Ecosyst Environ 246:157–167. https://doi.org/10.1016/j.agee.2017.05.007

Coutinho JG da E, Garibaldi LA, Viana BF (2018) The influence of local and landscape scale on single response traits in bees: A meta-analysis. Agric Ecosyst Environ 256:61–73. https://doi.org/10.1016/j.agee.2017.12.025

Coutinho JGE, Hipólito J, Santos RLS, et al (2021) Landscape Structure Is a Major Driver of Bee Functional Diversity in Crops. Front Ecol Evol 9:624835. https://doi.org/10.3389/fevo.2021.624835

DiLiberto T (2018) A soggy summer for the Mid-Atlantic in 2018. In: Natl. Ocean. Atmospheric Adm. https://www.climate.gov/news-features/event-tracker/soggy-summer-mid-atlantic-2018

DiTommaso A, Aarssen LW (1989) Resource manipulations in natural vegetation: a review. Vegetatio 84:9–29. https://doi.org/10.1007/BF00054662

Douglas MR, Baisley P, Soba S, et al (2021) Putting pesticides on the map for pollinator research and conservation. bioRxiv. https://doi.org/10.1101/2021.10.18.464808

Droege S, Engler JD, Sellers EA, O'Brien L (2016) National protocol framework for the inventory and monitoring of bees. U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center

Droege S, Rightmyer MG, Sheffield CS, Brady SG (2010) New synonymies in the bee genus Nomada from North America (Hymenoptera: Apidae). Zootaxa 2661:1. https://doi.org/10.11646/zootaxa.2661.1.1

Du Clos B, Drummond FA, Loftin CS (2020) Noncrop Habitat Use by Wild Bees (Hymenoptera: Apoidea) in a Mixed-Use Agricultural Landscape. Environ Entomol 49:502–515. https://doi.org/10.1093/ee/nvaa001

Enquist CA, Jackson ST, Garfin GM, et al (2017) Foundations of translational ecology. Front Ecol Environ 15:541–550. https://doi.org/10.1002/fee.1733

Ferree C, Anderson MG (2013) A Map of Terrestrial Habitats of the Northeastern United States: Methods and Approach. https://www.conservationgateway.org/ConservationByGeography/NorthAmerica/UnitedStates/edc/reportsdata/terrestrial/habitatmap/Pages/default.aspx. Accessed 12 Jul 2022

Filazzola A, Matter SF, MacIvor JS (2021) The direct and indirect effects of extreme climate events on insects. Sci Total Environ 769:145161. https://doi.org/10.1016/j.scitotenv.2021.145161

Fox EW, Hill RA, Leibowitz SG, et al (2017) Assessing the accuracy and stability of variable selection methods for random forest modeling in ecology. Environ Monit Assess 189:316. https://doi.org/10.1007/s10661-017-6025-0

Galpern P, Best LR, Devries JH, Johnson SA (2021) Wild bee responses to cropland landscape complexity are temporally-variable and taxon-specific: Evidence from a highly replicated pseudo-experiment. Agric Ecosyst Environ 322:107652. https://doi.org/10.1016/j.agee.2021.107652

Gibbons JW, Winne CT, Scott DE, et al (2006) Remarkable Amphibian Biomass and Abundance in an Isolated Wetland: Implications for Wetland Conservation. Conserv Biol 20:1457–1465. https://doi.org/10.1111/j.1523-1739.2006.00443.x

Gibbs J, Joshi NK, Wilson JK, et al (2017) Does Passive Sampling Accurately Reflect the Bee (Apoidea: Anthophila) Communities Pollinating Apple and Sour Cherry Orchards? Environ Entomol 46:579–588. https://doi.org/10.1093/ee/nvx069

Gonthier DJ, Ennis KK, Farinas S, et al (2014) Biodiversity conservation in agriculture requires a multi-scale approach. Proc R Soc B Biol Sci 281:20141358–20141358. https://doi.org/10.1098/rspb.2014.1358

Goulson D, Nicholls E, Botías C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347:1255957. https://doi.org/10.1126/science.1255957

Grab H, Poveda K, Danforth B, Loeb G (2018) Landscape context shifts the balance of costs and benefits from wildflower borders on multiple ecosystem services. Proc R Soc B Biol Sci 285:20181102. https://doi.org/10.1098/rspb.2018.1102

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596. https://doi.org/10.1007/S00442-007-0752-9

Griffin SR, Bruninga-Socolar B, Gibbs J (2021) Bee communities in restored prairies are structured by landscape and management, not local floral resources. Basic Appl Ecol 50:144–154. https://doi.org/10.1016/j.baae.2020.12.004

Guezen JM, Forrest JRK (2021) Seasonality of floral resources in relation to bee activity in agroecosystems. Ecol Evol 11:3130–3147. https://doi.org/10.1002/ece3.7260

Harmon-Threatt A (2020) Influence of Nesting Characteristics on Health of Wild Bee Communities. Annu Rev Entomol 65:39–56. https://doi.org/10.1146/annurev-ento-011019-024955

Harrison T, Gibbs J, Winfree R (2018) Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. Glob Change Biol 24:287–296. https://doi.org/10.1111/gcb.13921

Harrison T, Gibbs J, Winfree R (2019) Anthropogenic landscapes support fewer rare bee species. Landsc Ecol 34:967–978. https://doi.org/10.1007/s10980-017-0592-x

Hellwig N, Schubert LF, Kirmer A, et al (2022) Effects of wildflower strips, landscape structure and agricultural practices on wild bee assemblages – A matter of data resolution and spatial scale? Agric Ecosyst Environ 326:107764. https://doi.org/10.1016/j.agee.2021.107764

Hemberger J, Frappa A, Witynski G, Gratton C (2020) Saved by the pulse? Separating the effects of total and temporal food abundance on the growth and reproduction of bumble bee microcolonies. Basic Appl Ecol 45:1–11. https://doi.org/10.1016/j.baae.2020.04.004

Hesselbarth MHK, Sciaini M, With KA, et al (2019) landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42:1648–1657. https://doi.org/10.1111/ecog.04617

Hijmans RJ (2022) raster: Geographic Data Analysis and Modeling. Version R package version 3.5-15URL https://CRAN.R-project.org/package=raster

Hopwood JL (2008) The contribution of roadside grassland restorations to native bee conservation. Biol Conserv 141:2632–2640. https://doi.org/10.1016/j.biocon.2008.07.026

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7:1451–1456. https://doi.org/10.1111/2041-210X.12613

Hsieh TC, Ma KH, Chao A (2018) iNEXT: Interpolation and Extrapolation for Species Diversity. Version 2.1.17URL http://chao.stat.nthu.edu.tw/blog/software-download/

Iverson A, Evans A, Li K, et al Identifying gaps in landscape-level floral resources: A potential constraint for pollinator communities? Landsc Ecol in review, see Appendix for methodology:

Kammerer M, Douglas MR (2021) land-4-bees/beecoSp: beecoSp R package (v1.0.0). Zenodo. https://doi.org/10.5281/zenodo.5586224

Kammerer M, Goslee SC, Douglas MR, et al (2021) Wild bees as winners and losers: Relative impacts of landscape composition, quality, and climate. Glob Change Biol 27:1250–1265. https://doi.org/10.1111/gcb.15485

Kammerer MA, Biddinger DJ, Joshi NK, et al (2016) Modeling Local Spatial Patterns of Wild Bee Diversity in Pennsylvania Apple Orchards. Landsc Ecol 31:2459–2469. https://doi.org/10.1007/s10980-016-0416-4

Kennedy CM, Lonsdorf E, Neel MC, et al (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol Lett 16:584–599. https://doi.org/10.1111/ele.12082

Kleijn D, Linders TEW, Stip A, et al (2018) Scaling up effects of measures mitigating pollinator loss from local- to landscape-level population responses. Methods Ecol Evol 9:1727–1738. https://doi.org/10.1111/2041-210X.13017

Kraemer ME, Favi FD (2010) Emergence Phenology of Osmia lignaria subsp. lignaria (Hymenoptera: Megachilidae), Its Parasitoid Chrysura kyrae (Hymenoptera: Chrysididae), and Bloom of Cercis canadensis. Environ Entomol 39:351–358. https://doi.org/10.1603/en09242

Kuhn M (2008) Building Predictive Models in R Using the caret Package. J Stat Softw 28:. https://doi.org/10.18637/jss.v028.i05

Kuhn M (2019) caret: Classification and Regression Training. Version R package version 6.0-84URL https://CRAN.R-project.org/package=caret

Long EY, Krupke CH (2016) Non-cultivated plants present a season-long route of pesticide exposure for honey bees. Nat Commun 7:11629. https://doi.org/10.1038/ncomms11629

Martínez-Núñez C, Manzaneda AJ, Isla J, et al (2020) Low-intensity management benefits solitary bees in olive groves. J Appl Ecol 57:111–120. https://doi.org/10.1111/1365-2664.13511

McCullough CT, Angelella GM, O'Rourke ME (2021) Landscape Context Influences the Bee Conservation Value of Wildflower Plantings. Environ Entomol 50:821–831. https://doi.org/10.1093/ee/nvab036

McNeil DJ, McCormick E, Heimann AC, et al (2020) Bumble bees in landscapes with abundant floral resources have lower pathogen loads. Sci Rep 10:22306. https://doi.org/10.1038/s41598-020-78119-2

Molnar C, Casalicchio C, Bischl B (2018) iml: An R package for Interpretable Machine Learning. J Open Source Softw 3:786. https://doi.org/10.21105/joss.00786

Moral FJ, Terrón JM, Silva JRM da (2010) Delineation of management zones using mobile measurements of soil apparent electrical conductivity and multivariate geostatistical techniques. Soil Tillage Res 106:335–343. https://doi.org/10.1016/j.still.2009.12.002

Morandin LA, Kremen C (2013) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. Ecol Appl 23:829–839. https://doi.org/10.1890/12-1051.1

Moroń D, Szentgyörgyi H, Wantuch M, et al (2008) Diversity of wild bees in wet meadows: Implications for conservation. Wetlands 28:975–983. https://doi.org/10.1672/08-83.1

Mu J, Peng Y, Xi X, et al (2015) Artificial asymmetric warming reduces nectar yield in a Tibetan alpine species of Asteraceae. Ann Bot 116:899–906. https://doi.org/10.1093/aob/mcv042

Norris RF, Kogan M (2005) Ecology of Interactions Between Weeds and Arthropods. Annu Rev Entomol 50:479–503. https://doi.org/10.1146/annurev.ento.49.061802.123218

Ogilvie JE, Forrest JR (2017) Interactions between bee foraging and floral resource phenology shape bee populations and communities. Curr Opin Insect Sci 21:75–82. https://doi.org/10.1016/j.cois.2017.05.015

Oksanen J, Blanchet FG, Kindt R, et al (2013) vegan: Community Ecology Package. Version R package version 2.0-7URL http://CRAN.R-project.org/package=vegan

O'Neill KM, O'Neill JF (2010) Cavity-Nesting Wasps and Bees of Central New York State: The Montezuma Wetlands Complex. Northeast Nat 17:455–472. https://doi.org/10.1656/045.017.0307

Osorio-Canadas S, Arnan X, Bassols E, et al (2018) Seasonal dynamics in a cavity-nesting bee-wasp community: Shifts in composition, functional diversity and host-parasitoid network structure. PLOS ONE 13:e0205854. https://doi.org/10.1371/journal.pone.0205854

Papanikolaou AD, Kühn I, Frenzel M, et al (2017) Semi-natural habitats mitigate the effects of temperature rise on wild bees. J Appl Ecol 54:527–536. https://doi.org/10.1111/1365-2664.12763

Pebesma E (2018) Simple Features for R: Standardized Support for Spatial Vector Data. R J 10:439. https://doi.org/10.32614/RJ-2018-009

Penn State Agricultural Analytical Services Lab Soil Testing Methods. https://agsci.psu.edu/aasl/soil-testing/methods

Pinilla-Gallego MS, Crum J, Schaetzl R, Isaacs R (2018) Soil textures of nest partitions made by the mason bees Osmia lignaria and O. cornifrons (Hymenoptera: Megachilidae). Apidologie 49:464–472. https://doi.org/10.1007/s13592-018-0574-2

R Core Team (2021) R: A Language and Environment for Statistical Computing. Version 4.1.2. Vienna, Austria. URL http://www.R-project.org

Requier F, Odoux J-F, Tamic T, et al (2015) Floral Resources Used by Honey Bees in Agricultural Landscapes. Bull Ecol Soc Am 96:487–491. https://doi.org/10.1890/0012-9623-96.3.487

Ricketts TH, Regetz J, Steffan-Dewenter I, et al (2008) Landscape effects on crop pollination services: are there general patterns? Ecol Lett 11:499–515. https://doi.org/10.1111/j.1461-0248.2008.01157.x

Riffell SK, Keas BE, Burton TM (2003) Birds in North American Great Lakes coastal wet meadows: is landscape context important? Landsc Ecol 18:95–111

Rollin O, Benelli G, Benvenuti S, et al (2016) Weed-insect pollinator networks as bio-indicators of ecological sustainability in agriculture. A review. Agron Sustain Dev 36:. https://doi.org/10.1007/s13593-015-0342-x

Rollin O, Pérez-Méndez N, Bretagnolle V, Henry M (2019) Preserving habitat quality at local and landscape scales increases wild bee diversity in intensive farming systems. Agric Ecosyst Environ 275:73–80. https://doi.org/10.1016/j.agee.2019.01.012

Roulston T, Goodell K (2011) The role of resources and risks in regulating wild bee populations. Annu Rev Entomol 56:293–312. https://doi.org/10.1146/annurev-ento-120709-144802

Roulston TH, Smith SA, Brewster AL (2007) A Comparison of Pan Trap and Intensive Net Sampling Techniques for Documenting a Bee (Hymenoptera: Apiformes) Fauna. J Kans Entomol Soc 80:179–181. https://doi.org/10.2317/0022-8567(2007)80[179:ACOPTA]2.0.CO;2

Rundlöf M, Nilsson H, Smith HG (2008) Interacting effects of farming practice and landscape context on bumble bees. Biol Conserv 141:417–426. https://doi.org/10.1016/j.biocon.2007.10.011

Scherber C, Beduschi T, Tscharntke T (2019) Novel approaches to sampling pollinators in whole landscapes: a lesson for landscape-wide biodiversity monitoring. Landsc Ecol 34:1057–1067. https://doi.org/10.1007/s10980-018-0757-2

Schlesinger WH (2010) Translational Ecology. Science 329:609–609. https://doi.org/10.1126/science.1195624

Shackelford G, Steward PR, Benton TG, et al (2013) Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. Biol Rev 88:1002–1021. https://doi.org/10.1111/brv.12040

Smart AH, Otto CRV, Gallant AL, Simanonok MP (2021) Landscape characterization of floral resources for pollinators in the Prairie Pothole Region of the United States. Biodivers Conserv 30:1991–2015. https://doi.org/10.1007/s10531-021-02177-9

Stewart RIA, Andersson GKS, Brönmark C, et al (2017) Ecosystem services across the aquatic–terrestrial boundary: Linking ponds to pollination. Basic Appl Ecol 18:13–20. https://doi.org/10.1016/j.baae.2016.09.006

Stohlgren TJ, Falkner MB, Schell LD (1995) A Modified-Whittaker nested vegetation sampling method. Vegetatio 117:113–121. https://doi.org/10.1007/BF00045503

Tilman D (1987) Secondary Succession and the Pattern of Plant Dominance Along Experimental Nitrogen Gradients. Ecol Monogr 57:189–214. https://doi.org/10.2307/2937080

Tscharntke T, Klein AM, Kruess A, et al (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecol Lett 8:857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tuell JK, Fiedler AK, Landis D, Isaacs R (2008) Visitation by Wild and Managed Bees (Hymenoptera: Apoidea) to Eastern U.S. Native Plants for Use in Conservation Programs. Environ Entomol 37:707–718. https://doi.org/10.1603/0046-225X(2008)37[707:VBWAMB]2.0.CO;2

Tuell JK, Isaacs R (2010) Weather During Bloom Affects Pollination and Yield of Highbush Blueberry. J Econ Entomol 103:557–562. https://doi.org/10.1603/EC09387

Turley N, Joshi N, Biddinger D, López-Uribe M (2022) Six years of wild bee monitoring shows dramatic seasonal shifts in biodiversity and species declines. Preprints

Ullmann KS, Meisner MH, Williams NM (2016) Impact of tillage on the crop pollinating, ground-nesting bee, Peponapis pruinosa in California. Agric Ecosyst Environ 232:240–246. https://doi.org/10.1016/j.agee.2016.08.002

Urban-Mead KR, Paige Muñiz, Jessica Gillung, et al (2021) Bees in the trees: Diverse spring fauna in temperate forest edge canopies. For Ecol Manag 10. https://doi.org/10.1016/j.foreco.2020.118903

U.S. Fish and Wildlife Service (2017) National Wetland Inventory. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC

U.S. Geological Survey (2019a) National Hydrography Dataset. U.S. Geological Survey

U.S. Geological Survey (2019b) 3D Elevation Program (3DEP), 1/3 arc-second

USDA NASS (2018) USDA National Agricultural Statistics Service Cropland Data Layer. USDA-NASS, Washington, DC

USDA NASS (2019) 2017 Census of Agriculture: New York State and County Data

Vickruck JL, Best LR, Gavin MP, et al (2019) Pothole wetlands provide reservoir habitat for native bees in prairie croplands. Biol Conserv 232:43–50. https://doi.org/10.1016/j.biocon.2019.01.015

Vitale N, Torretta JP, Durante S, et al (2020) Similarities and differences in the realized niche of two allopatric populations of a solitary bee under environmental variability. Apidologie. https://doi.org/10.1007/s13592-020-00731-y

Wiens JA (1976) Population Responses to Patchy Environments. Annu Rev Ecol Syst 7:81–120. https://doi.org/10.1146/annurev.es.07.110176.000501

Williams NM, Kremen C (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. Ecol Appl 17:910–921

Wilson SD, Tilman D (1991) Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. Oecologia 88:61–71. https://doi.org/10.1007/BF00328404

Wright MN, Ziegler A (2017) ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. J Stat Softw 77:. https://doi.org/10.18637/jss.v077.i01

Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contributions

MK, JFT, and CMG conceived and designed the study. KL and ALI created high-resolution land-use data, ALI collected plant community composition, floral density, and flower size datasets, and MK conducted soil and wild-bee sampling. MK analyzed the data and led manuscript writing. All authors contributed critically to the drafts and gave final approval for publication.

Data Availability

All data required for the analyses presented here will be permanently archived in the Dryad Digital Repository. Code necessary to complete the analyses described here are archived on Zenodo (Kammerer 2021).

Tables and Figures

Table 1: Performance of random forest models predicting wild-bee abundance and richness at 33 sites in the Finger Lakes region of New York, USA. We show mean abundance or

richness, root mean-squared error (RMSE), r-squared (variance explained), and mean absolute error (MAE) as mean ± standard deviation from 10-fold cross validation, repeated 15 times. We tuned the number of variables at each tree split (mtry) and the number of trees (ntrees) with a grid search and present optimal values for each random forest model.

Season	Response Variable	Mean Abundance or Richness	Variables Included in RF Model	RMSE	R-squared	MAE	mtry	ntrees
spring	Abundance Day^{-1} $Trap^{-1}$	0.28 ± 0.27	Landscape, Year, Site	0.20 ± 0.10	0.46 ± 0.32	0.15 ± 0.06	25	5000
	Richness	11.79 ± 8.60	Landscape, Year, Site	8.07 ± 3.33	0.20 ± 0.23	5.97 ± 2.20	25	5000
summer	Abundance Day^{-1} $Trap^{-1}$	0.25 ± 0.27	Landscape, Year, Site	0.21 ± 0.11	0.38 ± 0.24	0.16 ± 0.06	30	1000
	Richness	7.13 ± 7.24	Landscape, Year, Site	6.09 ± 2.76	0.28 ± 0.25	4.74 ± 1.76	15	5000

Figure 1: Map of study sites in the Finger Lakes region of New York, USA. Bees were sampled in spring and summer 2018- 2019 at 33 sites in seven habitats defined by Iverson et al (in review; mesic upland remnant forests, floodplain forests, forest edges, old fields, roadside ditches, mixed vegetable farms, and apple orchards).

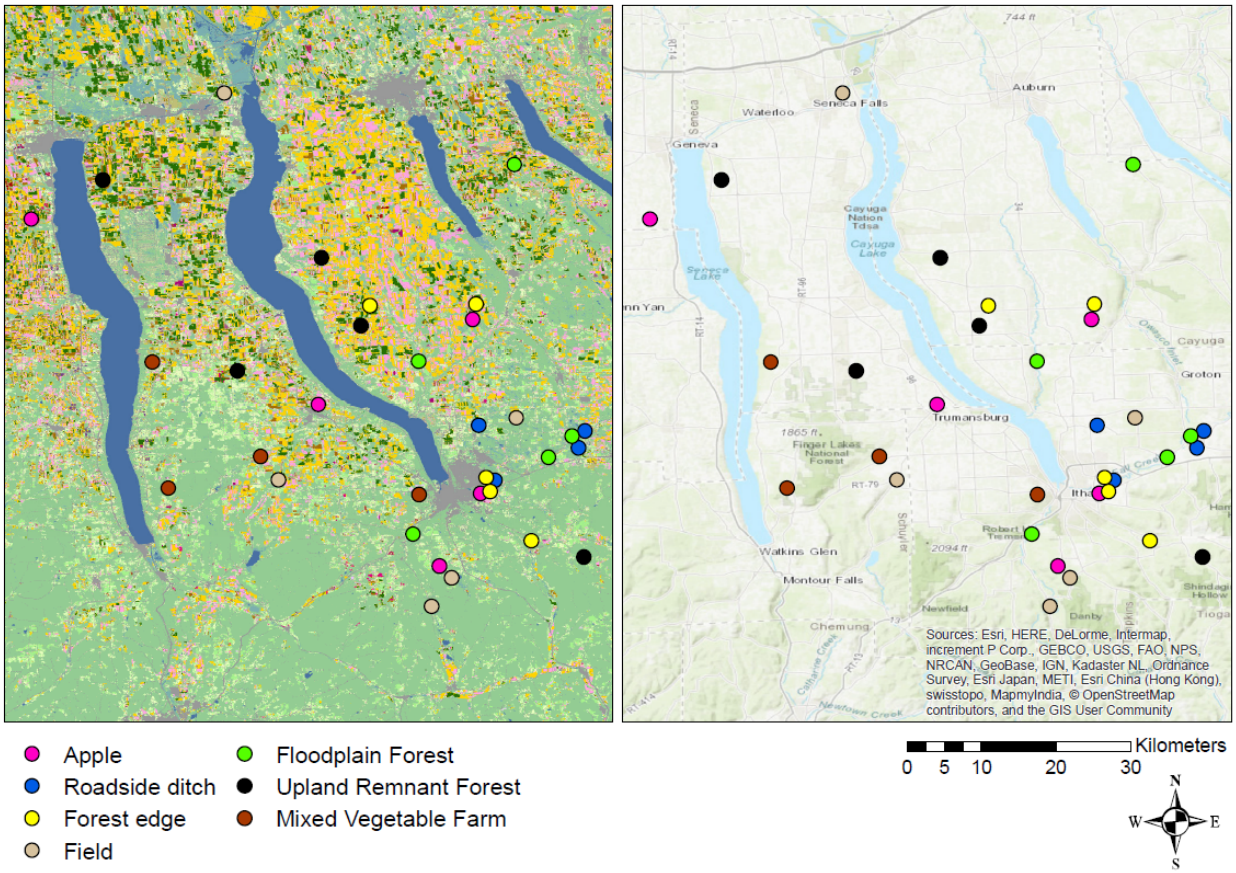

Figure 2: Variable-importance scores of the top 21 variables from random forest models predicting wild-bee abundance and richness. Bees were sampled in 2018 and 2019 at 33 sites in the Finger Lakes region of New York, USA. We calculated landscape variables for area within 1km of our study sites. For the most important variables, symbols denote directionality of the relationship ('++' = moderate/highly positive, '+' = slightly positive, '-' = slightly negative, and '--' = moderate/highly negative). Variable abbreviations are as follows: 'CV floral area' = coefficient of variation of floral area, 'Plant composition, mmt intensity' = composition of plant community associated with a gradient in management intensity (Figure S1) .

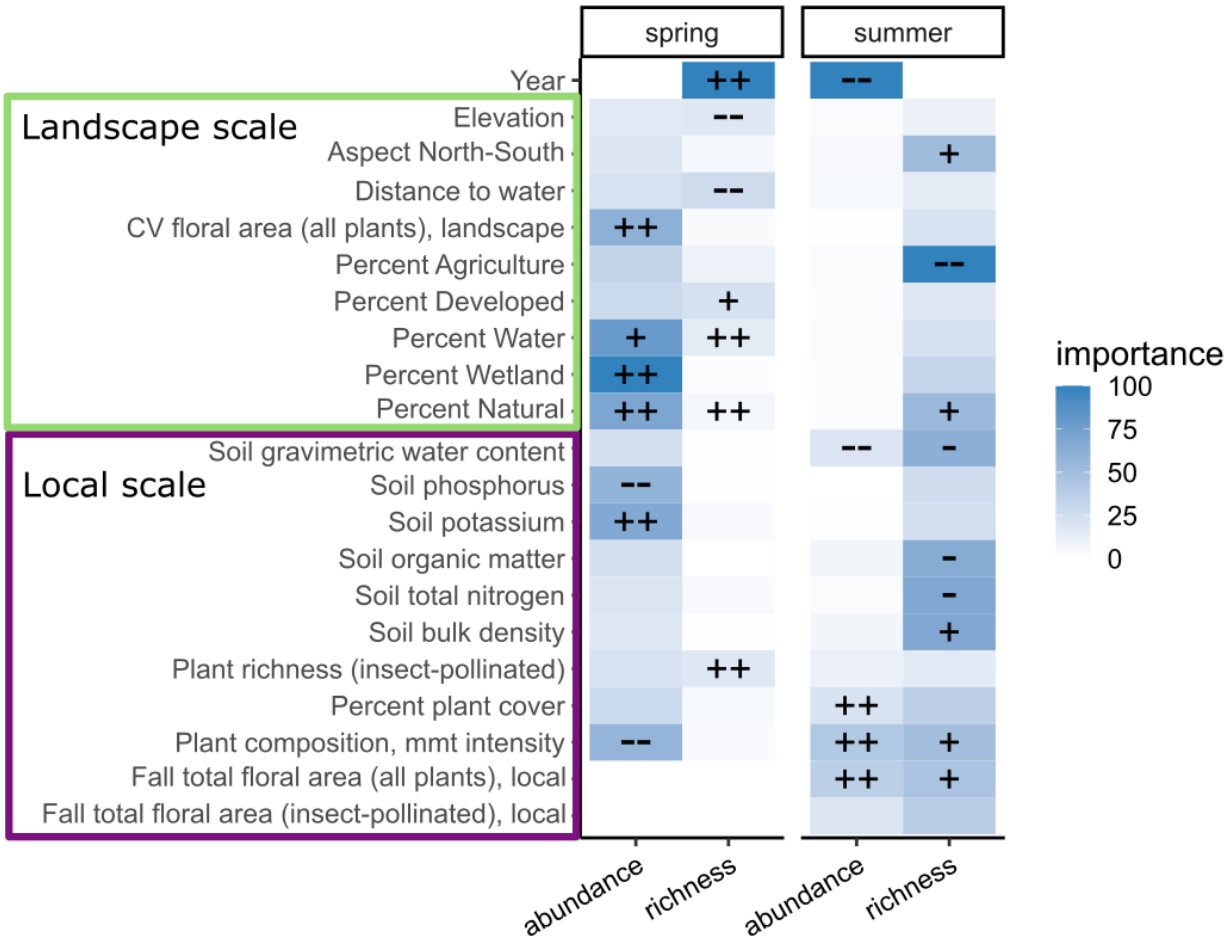

Figure 3: Relationship between landscape and local predictors and wild-bee abundance and richness in the spring. For both abundance and richness models, we show the top four predictors (excluding year, shown in Figure 5), with x-axis truncated to 10-90% quantiles (n=29 sites). 'IP' indicates insect-pollinated plants. To enable comparing relative effects across seasons with varying mean abundance or richness (Table 1), we depict values on the y-axis as difference from the predicted mean.

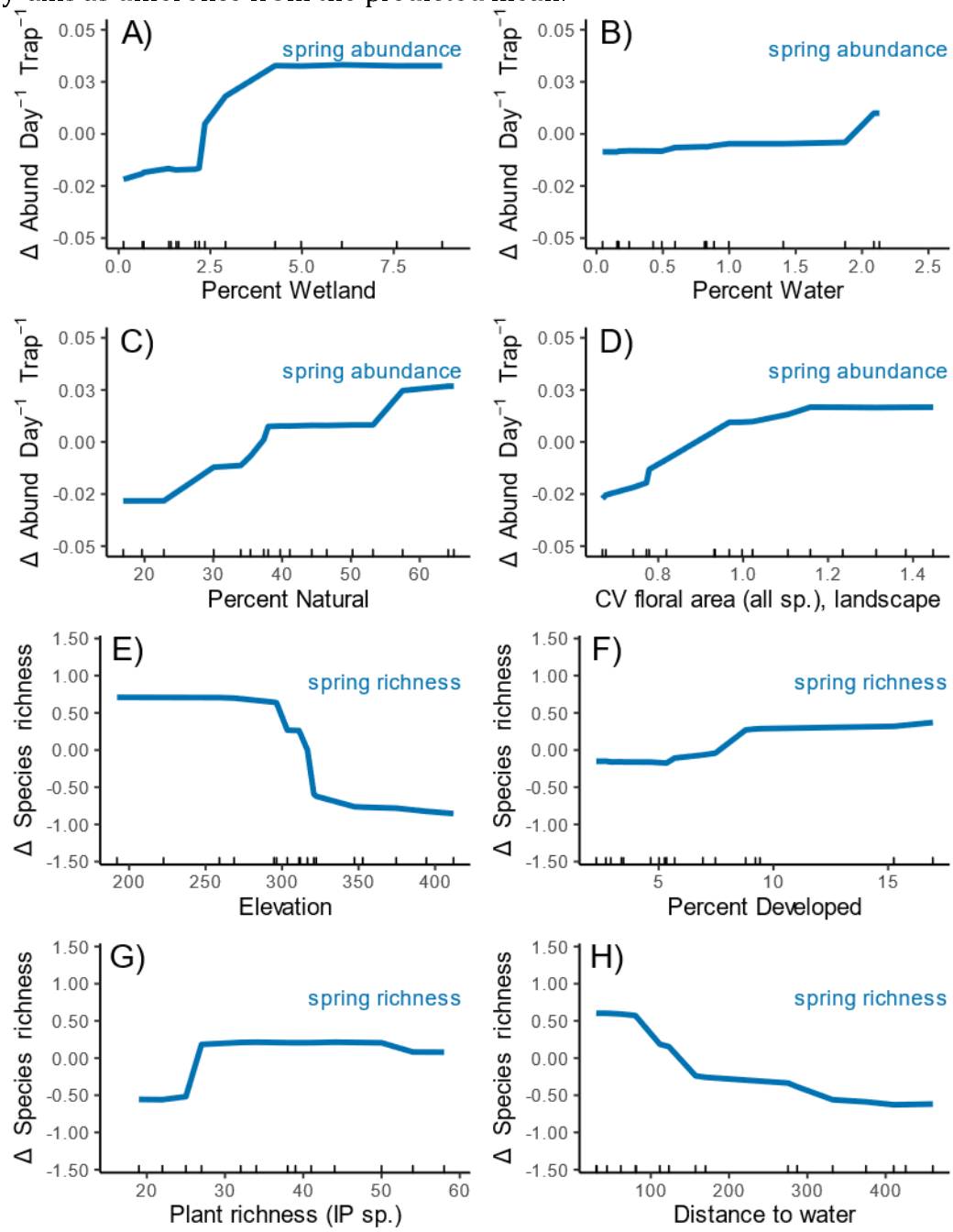

Figure 4: Relationship between landscape and local predictors and wild-bee abundance and richness in the summer. For both abundance and richness models, we show the top four predictors (excluding year, shown in Figure 5), with x-axis truncated to 10-90% quantiles (n=29 sites). To enable comparing relative effects across seasons with varying mean abundance or richness (Table 1), we depict values on the y-axis as difference from the predicted mean.

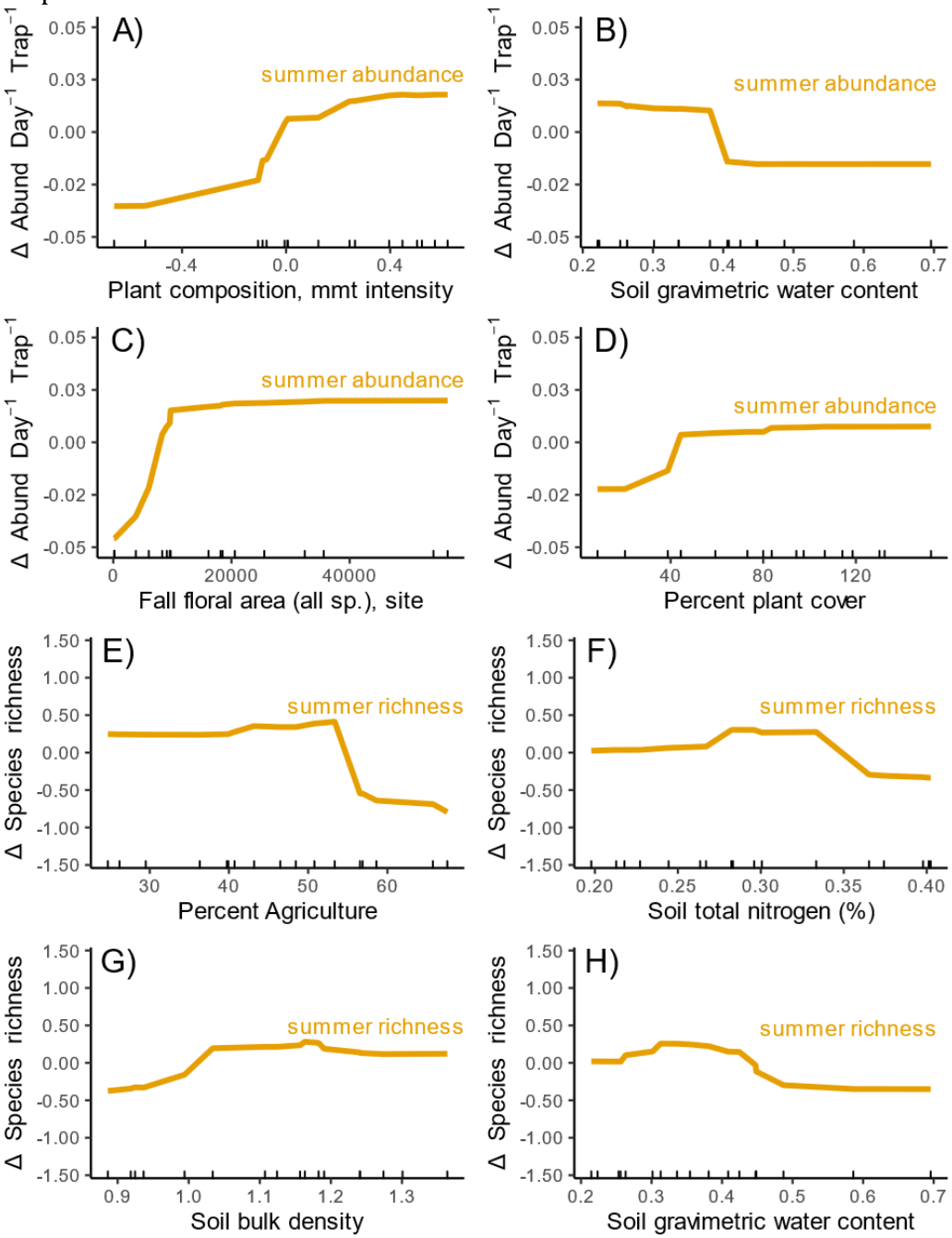

Figure 5: Difference between 2018 and 2019 for abundance (top) and richness (bottom) of wild bees in spring and summer estimated using a random forest model. To enable comparing relative effects across seasons with varying mean abundance or richness (Table 1), we depict values on the y-axis as difference from the predicted mean.

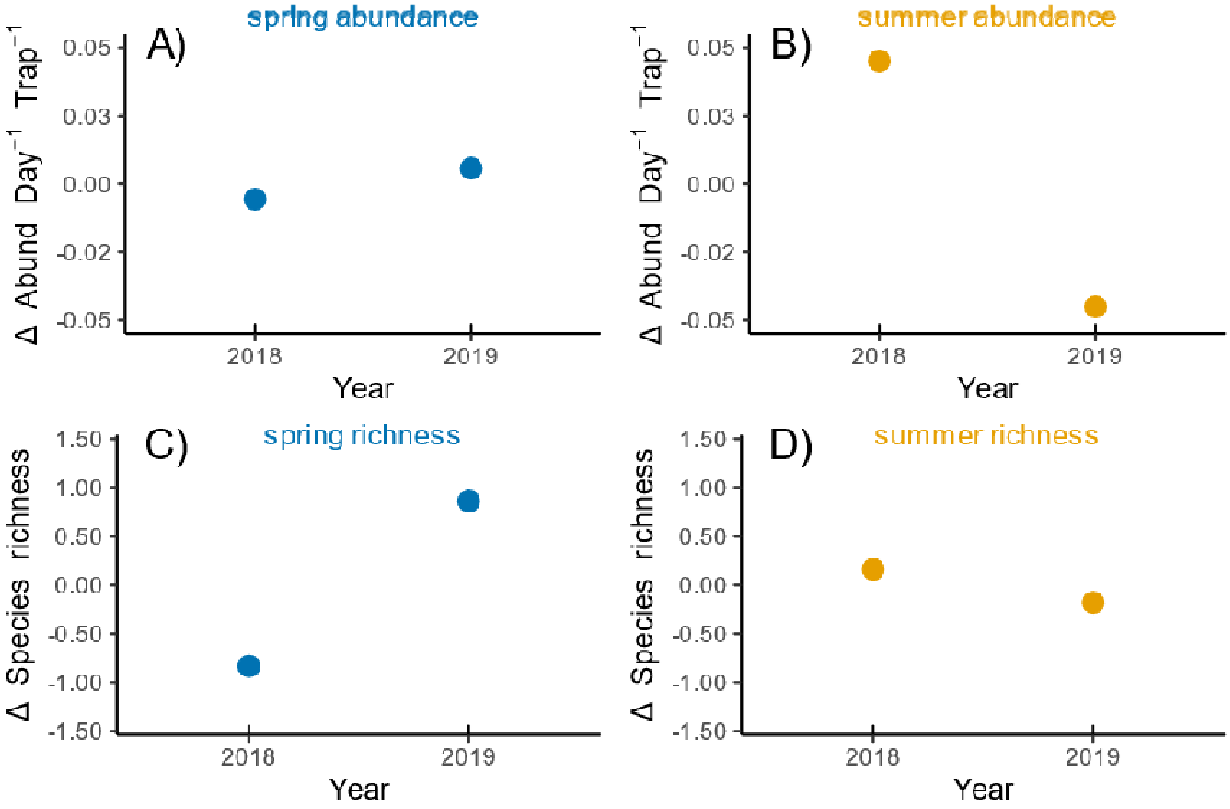

Figure 6: Abundance of wild-bee genera by season (panel A) and year (panel B) at 33 sites in the Finger Lakes region of New York, USA.

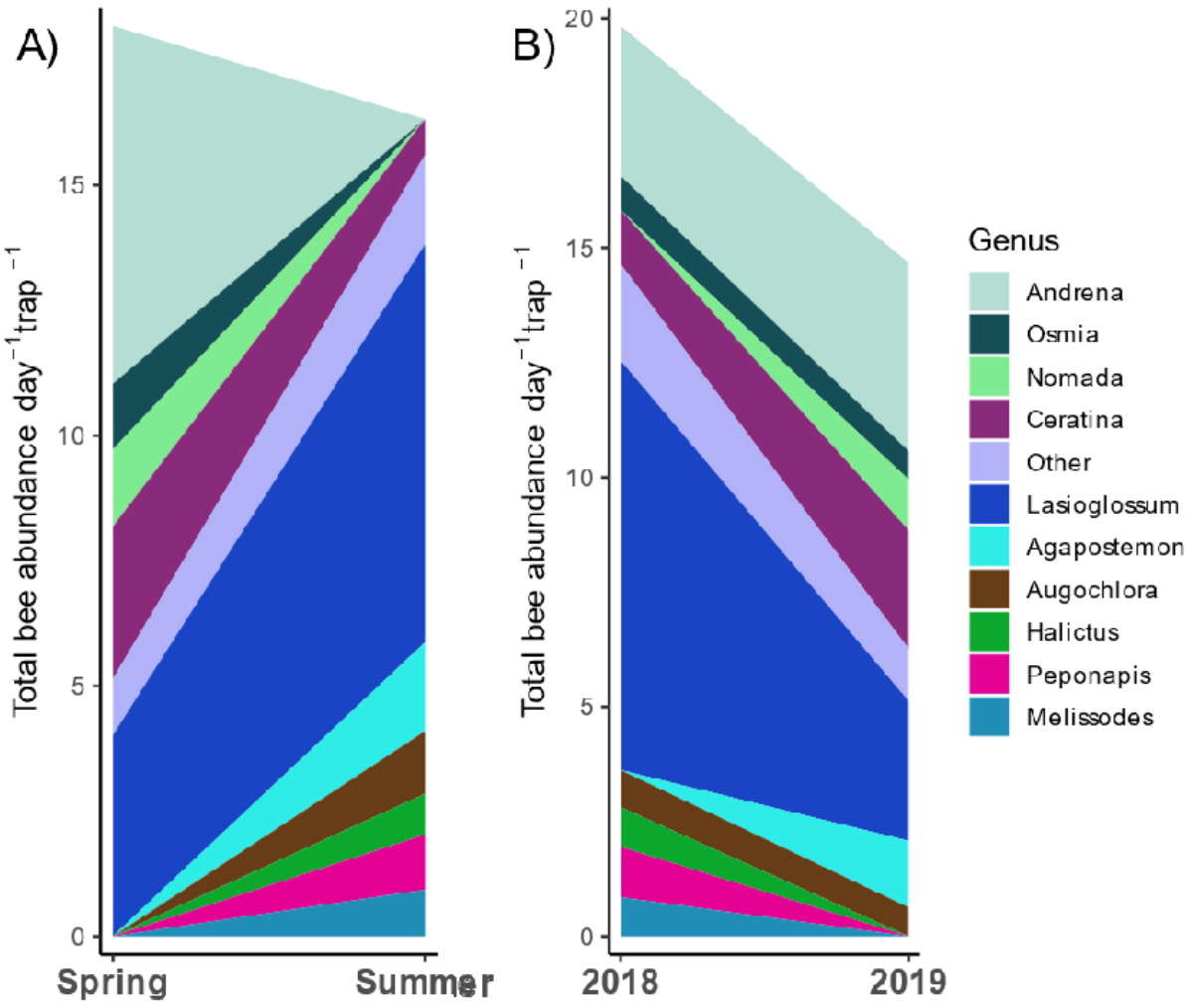
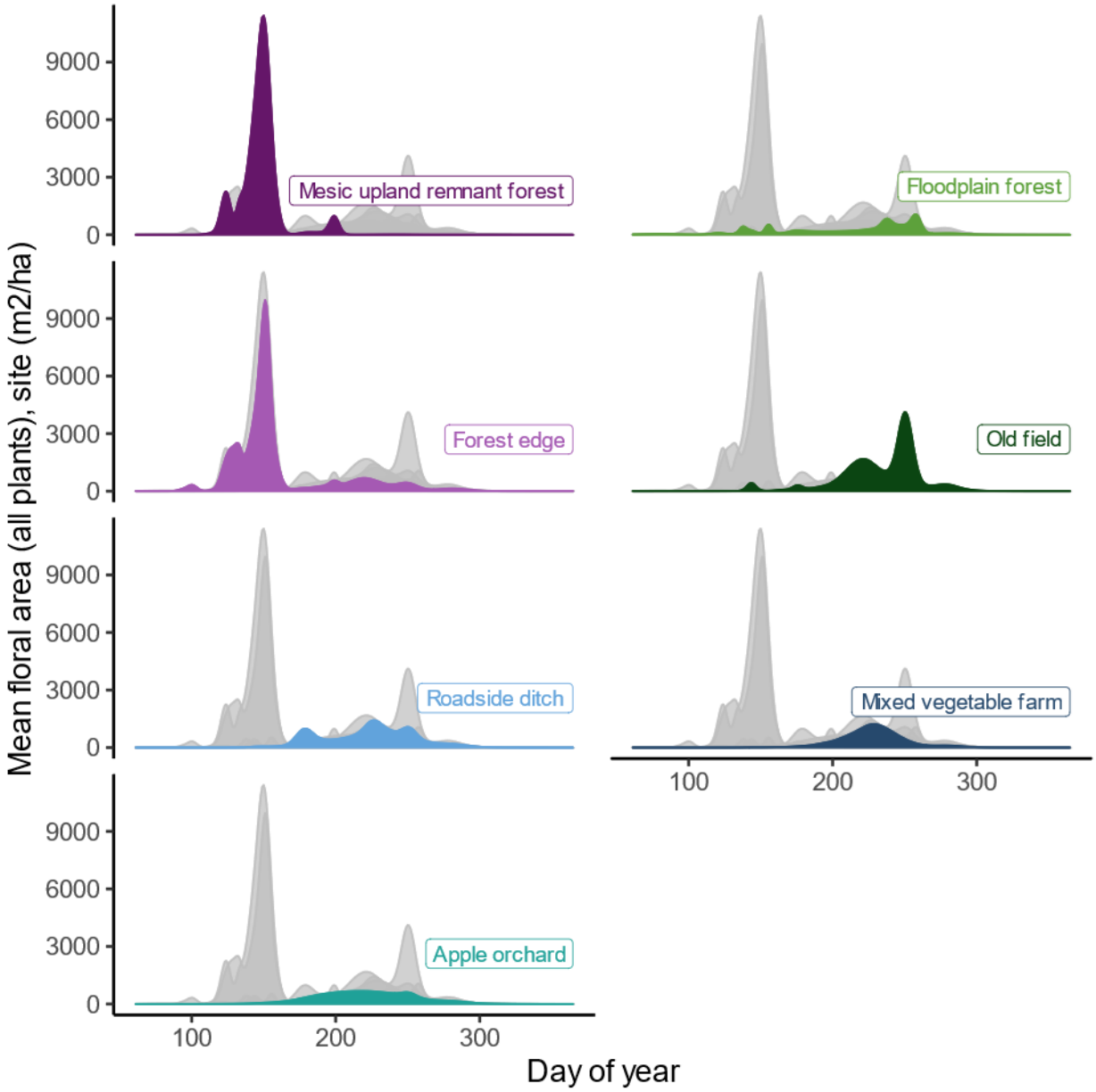
Figure 7: Floral area over time available in seven habitats in the Finger Lakes region of New York, USA. Floral area values represent all flowering plants. Floral area of the labelled habitat is represented with a colored polygon, while all other habitats are indicated with the grey polygons.