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Do the Quality and Quantity of Honey Bee-Collected Pollen Vary Across an Agricultural Land-Use Gradient?

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Abstract

Pollen is the source of protein for most bee species, yet the quality and quantity of pollen is variable across landscapes and growing seasons. Understanding the role of landscapes in providing nutritious forage to bees is important for pollinator health, particularly in areas undergoing significant land-use change such as in the Northern Great Plains (NGP) region of the United States where grasslands are being converted to row crops. We investigated how the quality and quantity of pollen collected by honey bees (*Apis mellifera* L. [Hymenoptera: Apidae]) changed with land use and across the growing season by sampling bee-collected pollen from apiaries in North Dakota, South Dakota, and Minnesota, USA, throughout the flowering season in 2015–2016. We quantified protein content and quantity of pollen to investigate how they varied temporally and across a land-use gradient of grasslands to row crops. Neither pollen weight nor crude protein content varied linearly across the land-use gradient; however, there were significant interactions between land use and sampling date across the season, particularly in grasslands. Generally, pollen protein peaked mid-July while pollen weight had two maxima in late-June and late-August. Results suggest that while land use itself may not correlate with the quality or quantity of pollen resources collected by honey bees among our study apiaries, the nutritional landscape of the NGP is seasonally dynamic, especially in certain land covers, and may impose seasonal resource limitations for both managed and native bee species. Furthermore, results indicate periods of qualitative and quantitative pollen dearth may not coincide.

Key words: mass-flowering crop, foraging, floral resource

Pollen provides protein, lipids, and other non-carbohydrate nutrition for almost all bee species (Michener 2007). Pollen quality, often measured as crude protein (e.g., Roulston et al. 2000, Hanley et al. 2008), as well as the quantity of pollen available are important for the development and health of bees (Di Pasquale et al. 2013). Limited pollen quality or quantity can negatively affect colony development and growth for both managed and native bee species (Loper and Berdel 1980, Vaudo et al. 2015, Rotheray et al. 2017). For example, low protein content in pollen negatively affects bumble bee colony survival and reproduction (Rotheray et al. 2017), and pollen quantity limits honey bee survival (Di Pasquale et al. 2016). Furthermore, nutritional deficiencies in bees can have synergistic effects with other stressors such as pesticides, disease, and land-use change (Goulson et al. 2015).

Across systems, forage limitations and poor nutrition caused by land use change are cited as primary drivers of declines in both managed and native bees (Potts et al. 2010, Vaudo et al. 2015). Thus, quantifying the value of landscapes based on the nutrition they confer to bees has been highlighted as a key area of study for countering population declines and improving the health of both native

and managed bee species (Roulston and Goodell 2011, Woodard and Jha 2017, Corby-Harris et al. 2019). Land-use change can reduce floral abundance and richness which thereby restricts the quality and quantity of floral resources available to bees (Goulson et al. 2015). Furthermore, the quality and quantity of floral resources are dynamic across the growing season (e.g., Di Pasquale et al. 2016), which makes understanding how land use interacts with seasonal variability in pollen resources important for the management of landscapes that support managed and native bees.

Honey bee (*Apis mellifera* L. [Hymenoptera: Apidae]) success is directly tied to the quality and quantity of floral resources available throughout the growing season. Colony survival and growth are negatively related to the area of row crops in the surrounding landscape (Smart et al. 2016a,b, 2018b), while the abundance and diversity of native bees and honey bees have been positively related to the availability of grasslands, bee forage crops, wooded areas, and wetlands (e.g., Riedinger et al. 2015, Danner et al. 2016, Evans et al. 2018, Vickruck et al. 2019). Similarly, the area of land enrolled in conservation programs, such as the federally administered Conservation Reserve Program (CRP), is declining in the NGP

particularly in areas that support the highest density of honey bee apiaries (Otto et al. 2018). Recent research suggests that increased CRP acreage can increase landscape suitability for supporting commercial honey bee apiaries, which likely benefits native bees as well (Otto et al. 2018). Such programs support grasslands that provide abundant floral resources targeted by beekeepers and have been demonstrated to enhance pollinator health (Otto et al. 2018).

However, since approximately 2007, the Northern Great Plains (NGP) has experienced significant land-use change, such as the conversion of grasslands to row crops, brought on by high commodity crop prices, bioenergy subsidies, and weakened conservation programs (Wright and Wimberly 2013, Lark et al. 2015, Otto et al. 2016). This agricultural intensification in the NGP is particularly problematic for bees, as the NGP supports ca. 38–40% of honey-producing colonies in the United States (Otto et al. 2016) and recent research has documented substantial native bee diversity across the region (e.g., Evans et al. 2018, Brendel et al. 2019, Vickruck et al. 2019). Despite this importance of the NGP to managed and native bees, research suggests loss of grasslands to agriculture in this region is negatively impacting both groups of pollinators (Smart et al. 2016a,b, 2018b; Koh et al. 2016; Otto et al. 2016). Corn and soybean production have greatly increased in the NGP in recent years, particularly in areas where registered apiaries co-occur (Otto et al. 2016). This increase in row crop production is limiting and reducing areas of bee forage historically targeted by beekeepers in the region and likely has negative effects on native bees in the region as well via reduced floral resource availability (Smart et al. 2018b).

Quantifying the quality and quantity of floral resources for native bees across landscapes is challenging due to the difficulty of conducting spatially and temporally replicated sampling across multiple land uses. In addition, sampling pollen from individual flowers or from foraging native bees to estimate pollen quality is time consuming and logistics can be cost or labor prohibitive, especially when sampling across large spatial scales. Honey bee colonies may serve as an effective model for quantifying the nutritional quality of landscapes due to their broadly polylectic foraging patterns (e.g., Leonhardt and Bluthgen 2012) and large foraging range when compared to most bee species (Gathmann and Tscharnke 2002, Zurbuchen et al. 2010). Managed honey bee colonies can be fitted with pollen traps to collect seasonally stratified samples of pollen from foraging honey bees (Smart et al. 2018a), and such sampling can be spatially and temporally replicated with minimal effort when compared to other common methods for collecting pollen samples from bees or flowers. Pollen collected from honey bees and native bees has been previously used to quantify floral resource use as well as to test how pollen quality and quantity may vary across a landscape (Beil et al. 2008, Dimou and Thrasylvoulou 2009, Di Pasquale et al. 2016, Vaudo et al. 2018, Wood et al. 2018). Using pollen samples collected from foraging honey bees could provide researchers an opportunity to quantify the abundance and nutritional quality of floral resources available to both managed and native bees over the course of the growing season as well as across land-use gradients.

We investigated how the quality and quantity of pollen collected by honey bees varied across 38 apiaries distributed along a grassland to row crop gradient in the NGP in 2015 and 2016. Specifically, we assessed whether crude protein content of honey bee-collected pollen was greater in colonies situated in apiaries surrounded by bee forage land covers such as grassland, wetlands, and bee forage crops (i.e., alfalfa, canola, and sunflower) and we investigated how those relationships may change over the growing season. We also investigated whether the quantity of pollen collected by honey bees varied across our land-use gradient and across the growing season.

We expected that pollen quality and quantity would be variable across the growing season coincident with floral blooming periods. Furthermore, we anticipated that bee-friendly land covers, particularly grasslands, would enhance the quality and quantity of pollen collected by honey bees, particularly late in the growing season when floral resources are scarce on more marginal land covers.

Methods

Study Area

Within the NGP, the Prairie Pothole Region (PPR) east of the Missouri River is typified by both perennial and annually variable wetland ‘potholes’ dotting the prairie (Euliss et al. 2004). The importance of this region to commercial beekeepers, and the rapid conversion of grassland to row crops (Otto et al. 2018) makes the PPR an ideal study system for assessing landscape-level effects of land-cover and land-use change on bee forage and health.

Site Selection

This study was part of a large-scale project to understand how land use affects honey bee colony health and productivity in the PPR. As such, details of our site selection process can be found in Smart et al. (2018b). Our goal for site selection was to select preexisting apiary locations that spanned a gradient from land covers, that we hypothesize would provide ample floral resources (grasslands, wetlands, bee forage crops) to monotypic row crops of limited pollinator value. We contacted private beekeepers who operated over multi-county areas in three states, North Dakota (ND), South Dakota (SD), and Minnesota (MN), to request permission to conduct research at their apiaries. Beekeepers provided locational information of their apiaries and we plotted these locations in a Geographic Information System (R Core Team 2018). We quantified the distribution of land covers within 4 km of each apiary based on the Cropland Data Layer (CDL, USDA National Agricultural Statistics Service Cropland Data Layer 2016). This provided us with land cover information around each potential apiary point. We binned specific CDL land covers together under three general categories following Smart et al. (2018b): grassland (grassland, conservation lands, pasture, fallow land, wildflowers, and hay land), bee forage crops (alfalfa, canola, and sunflower), and wetlands (herbaceous and woody wetlands). We then binned these points into high, medium, and low amounts of bee forage land covers (> 1 SD, ± 1 SD, and < 1 SD, respectively from the overall mean, see Smart et al. 2018b) and randomly selected 30 apiary points split evenly among each state; ensuring the land-use gradient was maintained within each state. We added six additional apiaries in ND that were part of a previous, multi-year honey bee health assessment (Smart et al. 2016a,b). To ensure adequate coverage of apiaries with low amounts of bee forage covers, we selected two additional apiaries in ND with less than 1,000 ha of grassland within 4 km. This sampling design yielded 38 research apiaries.

Pollen Collection and Crude Protein Analysis

Honey bee colonies used in this research were owned and operated by collaborating commercial beekeepers who each employed standard practices for maintaining their honey bee colonies. Our pollen sampling began when the honey bee colonies were transported to our research apiaries from out of state each spring in late May. We fitted each of two colonies per apiary with a 10-frame Superior Pollen Trap (Mann Lake, Hackensack, MN). We ensured each colony fitted with a pollen trap was queenright and free from symptoms associated with observable diseases (e.g., fungal and bacterial infections,

common viral symptoms). Pollen traps were activated for 72 h every 2 wk beginning in early June and ending in mid-September. Pollen was collected from pollen traps into sealed plastic bags and kept on ice during transportation. All pollen was stored at -20°C prior to analysis. We sorted all pollen samples in the lab to remove non-pollen material (e.g., wax debris, bee carcasses). From each sample, we obtained a 5 g sub-sample of pollen, which was homogenized with a mortar and pestle, dried at 60°C for 60 h, and then sent to Midwest Labs in Omaha, NE for protein analysis (AOAC 990.03). Crude protein was reported as the percent dry weight of protein within each sample (5 g pollen from a single pollen trap on a single date).

Statistical Analysis

Prior to analysis, we re-quantified the land cover of each apiary for 2015 and 2016 when annual CDL data became available (USDA National Agricultural Statistics Service Cropland Data Layer 2016). To assess how pollen protein varied by land cover and across the growing season, we used generalized additive mixed-effects models (GAMM) comparing pollen crude protein across sampling date, hectares of grassland, bee forage crops, and wetland as well as between years (2015 or 2016). We included sampling date nested within colony nested within apiary as a random effect to account for repeated measures. We also included interactive terms for each land cover (grassland, bee forage crops, and wetland) with sampling week to investigate seasonal variation in pollen protein across each land cover. This same model structure was used for assessing whether honey bees collected different quantities of pollen across bee forage land covers. GAMMs were selected over more commonly used linear regression techniques due to typical patterns in floral phenology and the quantity of floral resources across a growing season most often presenting nonlinear trends (e.g., Di Pasquale et al. 2016, Requier et al. 2017). This type of model tests for overall effects of continuous variables without assuming a linear relationship. As we expected non-linear trends through time, we modeled sampling week and interactive sampling week \times land cover terms as smoothed cubic regression splines with shrinkage, which penalizes overfitting based on the number of observations. While we provide summary data on an additional land-cover type surrounding our 38 apiaries (i.e., corn and soybeans, Fig. 1), we did not include it in our statistical models as they are inversely colinear with our land covers of interest. Land covers were initially log-transformed because the range of grassland area is an order of magnitude larger than other land covers (e.g., Fig. 1); however, transforming did not alter results so we report results from models with unscaled land-use area. In the models reported below, we tested the variance inflation factor (VIF) for land cover

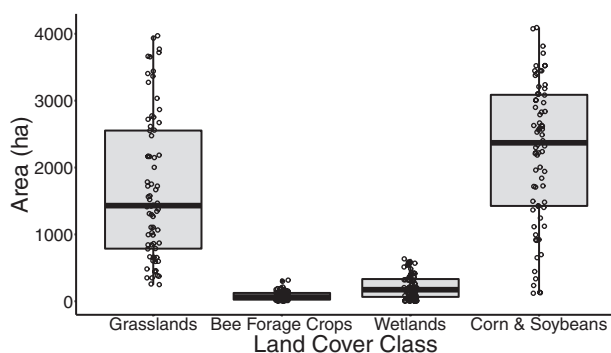


Fig. 1. Area in hectares of land cover classes within 4 km of each apiary within our study design. Each point is an individual apiary in 2015 or 2016.

parameters to ensure that possible collinearity between land-use parameters did not exceed the recommended VIF thresholds for removal (James et al. 2013). All analyses were performed in R version 3.5.1 (R Core Team 2018) using the packages *bbmle* (Bolker and R Core Team 2017), *car* (Fox and Weisburg 2011), *gamm4* (Wood and Scheipl 2017), *ggplot2* (Wickam 2016), *lme4* (Bates et al. 2015), *lmerTest* (Kuznetsova et al. 2017), and *mgcv* (Wood 2011).

Results

Corn and soybean crops were the dominant land cover around study apiaries (mean \pm SE: 2235.07 ± 123.57 ha) while the land-use area of bee-friendly land covers around study apiaries was mostly grassland (mean \pm SE: 1683.60 ± 127.02 ha, Fig. 1). VIF values testing for collinearity among land uses in pollen protein and weight models were well below the removal thresholds of 5 and 10 for both models testing pollen protein (grasslands: 1.49 bee forage crops: 1.05, wetlands: 1.51, sampling date: 1.00) as well as pollen weight (grasslands: 1.44, bee forage crops: 1.05, wetlands: 1.50, sampling date: 1.00), suggesting that the variance among parameters, and thus results, in the models reported below are not inflated by collinearity.

When accounting for repeated measures at colonies nested within apiaries, we observed no linear relationship between honey bee-collected pollen protein and hectares grassland, bee forage crops, or wetland (Table 1, Fig. 2). Likewise, we observed no linear trend in pollen weight collected by honey bees across variable amounts of grassland, bee forage crops, or wetland (Table 2, Fig. 3). Pollen protein and pollen weight were both significantly different between the years 2015 and 2016, with pollen protein being slightly greater in 2016 and the weight of pollen collected being greater in 2015 (Tables 1 and 2, Fig. 4).

Pollen protein varied nonlinearly across the growing season with a peak in mid-July in both years (Table 1, Fig. 4A). Furthermore, pollen protein responded differently to sampling date dependent on land cover class (Table 1). Area of grassland positively trended with pollen protein late in the growing season, yet pollen protein declined with greater grassland cover when pollen protein was greatest (Table 1, Fig. 5A). Pollen protein increased with greater area of bee forage crops during the mid-July peak (Table 1, Fig. 5C). Pollen protein was also greatest at intermediate wetland acreage at the mid-July peak (Table 1, Fig. 5E).

Pollen weight, the quantity of pollen collected by honey bees, also varied nonlinearly across the growing season, with peaks in mid-June and mid-August, although these trends were less pronounced in 2016 compared to 2015 (Table 2, Fig. 4B). Land cover and sampling date also showed significant interactions with pollen quantity, presenting relatively uniform responses across land cover classes. Hectares of grassland, bee forage crops, and wetland, all demonstrated generally positive influence on pollen weight across the growing season (Table 2, Fig. 5B, D, and F), except for bee forage crops showing a slight decline in pollen weight early in the growing season (Table 2, Fig. 5D).

Discussion

We assessed how the protein content and quantity of honey bee-collected pollen varied across a gradient of land use from grassland to row crop and observed pollen crude protein content and pollen weight to vary across the sampling season interactively with land use. Generally, we observed that pollen crude protein was variable across the growing season, with honey bee-collected pollen protein peaking in mid-July, while the quantity of pollen collected by honey

Table 1. Pollen protein generalized additive mixed-effects model compared across hectares grasslands, bee forage crops, wetlands, year, sampling date, and smoothed interactive terms

Parametric coefficients	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	20.34	1.71	11.91	<0.01
Grassland	<0.01	<0.01	-0.08	0.94
Bee forage crops	<0.01	<0.01	-0.78	0.44
Wetland	<0.01	<0.01	0.01	1.00
Year	0.50	0.24	2.10	0.04
Smoothed terms	edf	<i>F</i>	<i>P</i>	
Date	2.78	16.41	<0.01	
Date × grassland	1.71	0.26	<0.01	
Date × bee forage crops	1.36	0.11	0.02	
Date × wetland	1.57	0.29	<0.01	

Parametric coefficients refer to the terms being included as linear parameters, while smoothed terms are modeled as cubic regression splines with shrinkage. 'edf' is the effective degrees of freedom.

P values bolded at ≤ 0.05 .

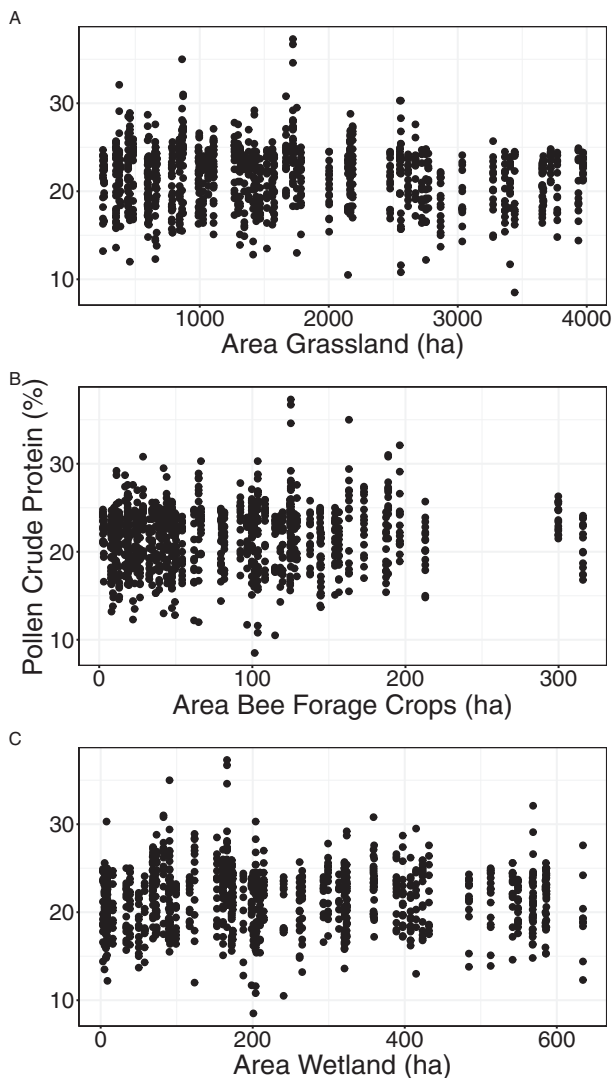


Fig. 2. Percent crude protein for pollen samples plotted across area of (A) grassland, (B) bee forage crops, and (C) wetland. See Table 1 for model output. Each point represents a pollen sample at an individual colony.

bees had two maxima in mid-June and mid-August. These results suggest that the floral resources available to bees in our study region are seasonally dynamic and that the provisioning of pollen resources

in different land covers varies across the growing season. While this comes as little surprise when considering floral phenology, there is yet limited work investigating the variability in quality of floral resources at a landscape scale and even less research that relates land cover to the phenology of floral resources (Woodard and Jha 2017, Vaudo et al. 2018). Furthermore, similar quantity of floral resources as well as similar quality resources were likely available for honey bees across the range of semi-natural to agricultural land uses in our study, albeit at different times. Area of grasslands promoted late-season pollen protein while the area of bee forage crops increased early-season pollen protein. These analyses together suggest that phenological changes in floral community composition likely have larger effects than the gradient of land use on the quality and quantity of pollen resources available to honey bees, yet land use can influence the timing of pollen resource availability and quality.

Pollen quality was highly variable across the growing season and demonstrated interactive effects with different land covers. Previous work in Europe quantified pollen quality across a growing season in an agricultural landscape and observed peaks in early and late season with a mid-season slump (Di Pasquale et al. 2016), which is a similar trend to ours. While the exact timing between this European semi-natural system and the PPR is slightly different, with our maximum protein content being observed in mid-July, the general trendline of the patterns are relatively close, possibly reflecting the availability of different quality resources or shifting nutritional needs. Indeed, pollen species diversity, as well as nutritional content, of honey bee-collected pollen has been found to vary seasonally, which may relate to differential seasonal nutritional requirements in honey bees (DeGrandi-Hoffman et al. 2018). Pollen quality was different between years as well; however, the seasonal pattern was relatively similar between years, with the peaks and troughs being more pronounced in 2015 versus 2016 (Fig. 4A). This variance in pollen quality between years could be driven by variable environmental conditions supporting different floral community composition and thus different pollen suites.

When considering land cover alongside seasonal variation, pollen protein responded most strongly to grassland cover, yet did so differently across the season. Early in the growing season, when overall pollen quality was at its maximum, pollen protein declined with increasing grassland cover. Late in the season, grassland cover promoted pollen protein, and we hypothesize this was driven by late-season floral resources remaining among grassland covers at a time when marginal bee forage land covers have lower floral resources. Hectares of bee forage crops also trended positively with

Table 2. Pollen quantity generalized additive mixed-effects model compared across hectares grasslands, bee forage crops, wetlands, year, sampling date, and smoothed interactive terms

Parametric coefficients	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	62.72	49.08	1.28	0.20
Grassland	0.01	0.01	0.59	0.55
Bee forage crops	0.04	0.09	0.49	0.62
Wetland	0.03	0.04	0.62	0.53
Year	-24.22	6.74	-3.60	<0.01
Smoothed terms	edf	<i>F</i>	<i>P</i>	
Date	2.48	5.24	<0.01	
Date × grassland	2.11	0.16	<0.01	
Date × bee forage crops	1.29	0.06	0.04	
Date × wetland	1.54	0.16	<0.01	

Parametric coefficients refer to the terms being included as linear parameters, while smoothed terms are modeled as cubic regression splines with shrinkage. 'edf' is the effective degrees of freedom.

P values bolded at ≤0.05.

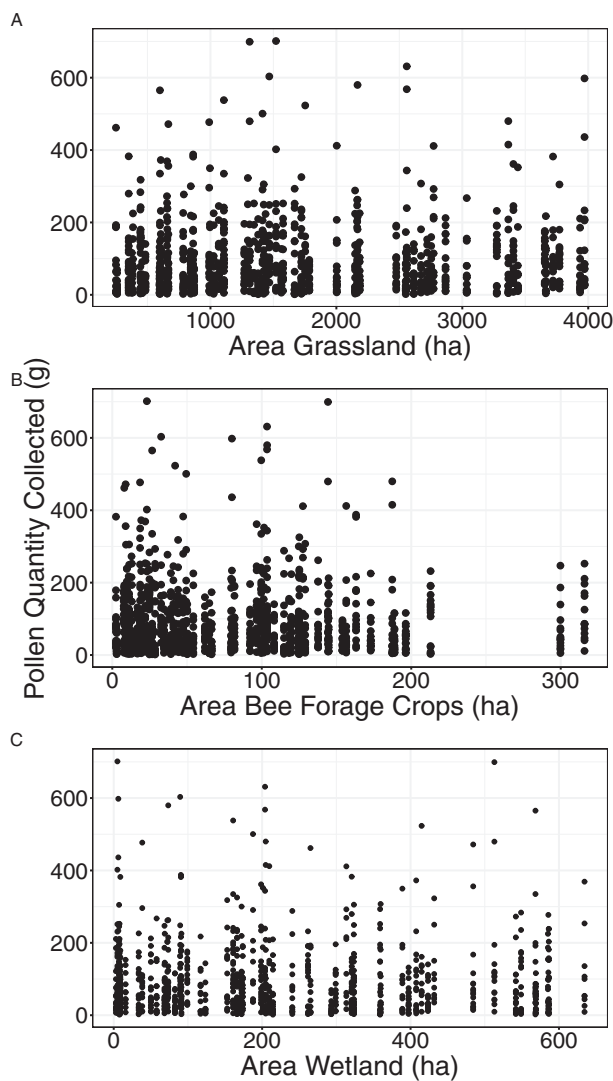


Fig. 3. Pollen quantity samples plotted across area of (A) grassland, (B) bee forage crops, and (C) wetland. See Table 2 for model output. Each point represents a pollen sample at an individual colony.

pollen protein, particularly early in the growing season (Fig. 5C), although the relatively low area of these crops in our study, coupled with the low variance (Fig. 1), suggests caution when comparing

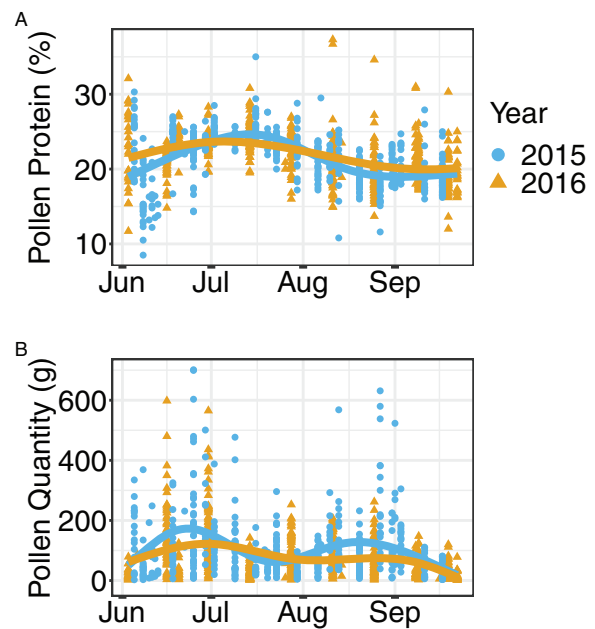


Fig. 4. (A) Percent crude protein by sampling date and (B) pollen quantity in grams by sampling date. Lines are generalized additive mixed model best fits for each year with shaded 95% confidence intervals. Circles are pollen samples collected from individual colonies in 2015, triangles are samples from 2016. See Tables 1 and 2 for model outputs.

bee forage crop trends to grassland cover. Were a positive trend between area bee forage crops and pollen protein early in the season to persist across a greater spatial area, it could suggest that pulsed blooms of mass-flowering crops provide floral resources when other land covers have limited forage (e.g., Holzschuh et al. 2013). Wetlands, the other land cover of interest in this study, tended to provide their peak in pollen protein at intermediate areas. Wetlands in this region are highly variable, and the floral resources they provide to pollinators may vary with the landscape context of each specific wetland; e.g., wetlands in row crops agriculture are often farmed up to their boundaries, providing limited floral resources, whereas with terrestrial buffers may provide areas for flowers to grow. Thus, what qualifies as a wetland under the CDL may cover a wide range of possibilities for floral resource abundance and quality, leading to an unclear response in our analyses. Grassland was the focal land cover in our study and wetlands were included secondarily in the analysis because of their ecological importance

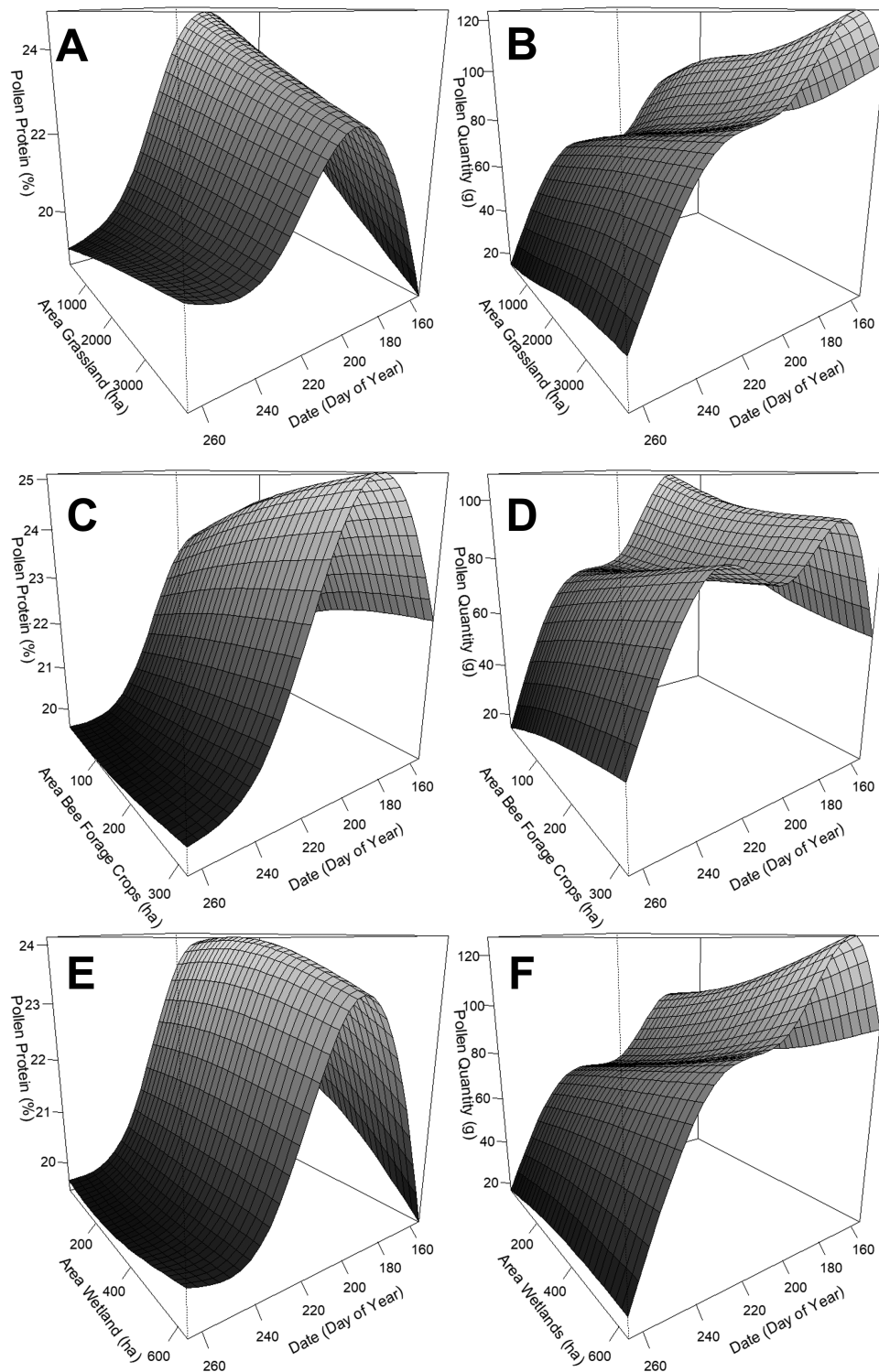


Fig. 5. Generalized additive mixed model (GAMM) fits for interactive terms of land cover class \times sampling date. Surface represents GAMM fitted values for parameters. (A): Percent pollen protein over area of grassland \times sampling date, (B): pollen quantity over area grassland \times sampling date, (C): percent pollen protein over area bee forage crops \times sampling date, (D): pollen quantity over area bee forage crops \times sampling date, (E): percent pollen protein over area wetland \times sampling date, and (F): pollen quantity over area wetland \times sampling date. See [Tables 1](#) and [2](#) for model outputs.

in the PPR (Euliss et al. 2004) and their potential value for pollinators (Evans et al. 2018, Vickruck et al. 2019). Wetlands have recently become a focal point in pollination ecology as potential habitat refugia for native bee species in the NGP (Evans et al. 2018, Vickruck et al. 2019) and quantifying the floral resource

availability of wetlands in different landscapes could be a useful direction of future research, particularly in the PPR.

Pollen collection was generally greater as the area of land covers predicted to provide more pollen resources increased, particularly with grasslands (Fig. 5B), suggesting that such land covers

may enhance the availability of pollen for honey bees on the landscape. The quantity of pollen collected by honey bees is regulated by the amount of brood being reared in the colony and the quantity of pollen currently stored in the hive (e.g., Free 1967, Fewell and Winston 1992). Therefore, the timing in the quantity of pollen collected across these combinations of land cover and date likely correlate to either periods of colony buildup in the number of workers or suggest that pollen could be less abundant at other points in the season. When comparing the timing of maxima for pollen quality and quantity in different land covers, our findings suggest that the quality of pollen collected across the landscape is temporally variable throughout the growing season, and therefore there may be periods of *qualitative* pollen dearth which may not necessarily coincide with *quantitative* dearth in pollen resources. Additional research comparing pollen quality and quantity against floral community data across growing seasons will be necessary to address this unexpected result.

Considering our results in the context of previous work, our observed patterns of high temporal variability in the quality and quantity of pollen collected by honey bees with some evidence of a land use signal suggests that native bees could also face pollen limitations due to land use. Evidence is mixed as to whether honey bees can even detect or discriminate between pollens based on quality (e.g., Pernal and Currie 2001, Cook et al. 2003, Corby-Harris et al. 2019), as individual foragers are more likely to target, and recruit nestmates to, large patches of abundant flowers where they may collect greater quantities of pollen regardless of resource quality (Leonhardt and Bluthgen 2012, Vaudo et al. 2016). However, there is some recent evidence that honey bees diversify the species of pollens collected at a colony-level (Nürnberger et al. 2019). Overall, pollen collected by honey bees is representative of their generalist foraging patterns (e.g., Wood et al. 2018) and our pollen sampling likely, at least coarsely, reflects the pollen available on the landscape. In contrast, many species of native bees do preferentially forage for pollen based on quality, follow oligolectic foraging patterns, or target specific floral families at different times of the season (e.g., Leonhardt and Bluthgen 2012, Wood et al. 2018); therefore, it's possible that some native bee species may be limited by pollen quality, or quantity of specific flora, across our study area in the NGP. An added complication for native bee species is that their flight distances are relatively limited compared to honey bees (Gathmann and Tscharnke 2002, Zurbuchen et al. 2010). Honey bees have been observed to have a wide range of maximum foraging distances (1.2 to 14.0 km, Zurbuchen et al. 2010); however, known foraging distances of native bees are well within the 4 km radius of our study design (<2.8 km, Zurbuchen et al. 2010). Thus, where honey bees may overcome local resource limitations, native bee species with short foraging ranges may be more likely to show strong negative effects of land use on the quality and/or quantity of pollen they are able to collect. In future studies, it would be useful to stratify the distance of land cover analyses to address the massive distances at which honey bees have the potential to forage, as in our study, it is likely that our honey bees at least had access to floral resources outside our 4 km distance.

Following previous correlations between land use and honey bee health in the NGP (e.g., Otto et al. 2016, Smart et al. 2016a,b) we observed effects of land use on honey bee-collected pollen crude protein content as well as the quantity of pollen collected. The NGP supports the highest density of honey bee colonies in the United States (Otto et al. 2016) and our study used active, commercial apiaries as our research sites. Thus, our land-use gradient is most representative of areas where beekeepers choose to keep commercial honey bee colonies. By partnering with beekeepers and utilizing

their existing apiary locations, we did not conduct sampling in areas where beekeepers do not keep honey bee colonies due to poor land-use conditions with limited bee forage. We have previously demonstrated that beekeepers across the study region target and self-select high-quality apiaries and avoid those dominated by crops providing little to no resources (Otto et al. 2016). Extending our study into areas that are avoided by beekeepers would provide a more complete depiction of how pollen quality and quantity might vary as a function of land use across the region.

In sampling honey bee collected pollen we observed differences in pollen protein content and the quantity of pollen collected across multiple growing seasons and observed these trends to differ slightly between different bee-friendly land covers. Future research could focus on testing which floral species contribute to this seasonal variability in pollen resources, as this could provide a relatively unexplored mechanistic explanation for how land use influences the nutritional landscape for pollinators.

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