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Gabriela M. Quinlan

Rufus Isaacs

Clint R. V. Otto

Autumn H. Smart

Meghan O. Milbrath

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Association of excessive precipitation and agricultural land use with honey bee colony performance

Gabriela M. Quinlan · Rufus Isaacs ·
Clint R. V. Otto · Autumn H. Smart ·
Meghan O. Milbrath

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Abstract

Context From landscape variables to weather, multiple environmental factors affect honey bees and other pollinators. Detailed honey bee colony assessments in a variety of landscape and weather conditions offer the opportunity to develop a mechanistic understanding of how landscape composition, configuration, and weather are associated with colony nutrition, demography, and productivity.

Objectives Our objective was to test if weather and landscape characteristics (e.g., agricultural versus

forested land use) are associated with different honey bee colony outcomes (foraged nectar mass, foraged pollen mass, pupal population size, and adult population size change).

Methods We collected detailed colony measurements on over 450 honey bee colonies over four years across an agricultural-to-forested land use gradient in Michigan, USA.

Results We found that higher than normal precipitation in the preceding spring and fall was negatively correlated with colony size change and with foraged nectar mass, respectively. Sites surrounded by less agricultural land and more forested land also had fewer pupae by the end of summer.

Conclusions These inter-dependent colony metrics offer insights into environmental-plant-pollinator dynamics. Our finding that extreme weather events, associated with climate change, are negatively correlated with colony performance point to likely lagged effects of weather on pollinator floral resources. Landscapes managed with climate-resilient, temporally continuous floral resources are likely to support pollinators. Capturing extreme weather phenomena in field studies is a valuable way to investigate the associations between land use, climate change and biological systems. However, caution should be taken in overinterpreting observational studies, so further research is needed.

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G. M. Quinlan (✉) · R. Isaacs · M. O. Milbrath
Department of Entomology, Michigan State University,
East Lansing, MI 48824, USA
e-mail: gmq5021@psu.edu

R. Isaacs
e-mail: isaacsr@msu.edu

M. O. Milbrath
e-mail: mpi@msu.edu

C. R. V. Otto
U.S. Geological Survey Northern Prairie Wildlife Research
Center, Jamestown, ND 58410, USA
e-mail: cotto@usgs.gov

A. H. Smart
Department of Entomology, University of Nebraska-
Lincoln, Lincoln, NE 68583, USA
e-mail: asmart8@unl.edu

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Introduction

Almost all bee species rely exclusively on flowering plants to fulfill their nutritional requirements through pollen and nectar, and mutualisms between plants and pollinators is integral to ecosystem functioning across the world (Bascompte and Jordano 2007; Soares et al. 2017). Bees' reliance on flowering plants makes them sensitive to environmental impacts on plant communities (Hegland et al. 2009; Winfree et al. 2009; Soares et al. 2017). Since the early twenty-first century, there has been recognition of bee declines linked to environmental stressors, including lack of sufficient floral resources, exposure to pesticides, and parasites and disease (Potts et al. 2010; Goulson et al. 2015). The role of climate change and its association with floral communities and plant-pollinator interactions has also been recognized (Hegland et al. 2009; Ziska et al. 2016). These stressors interact, further imperiling pollinator communities and individual species (Alaux et al. 2010; DeGrandi-Hoffman et al. 2010; Doublet et al. 2015).

Honey bee colony survival data indicate that environmental factors that constrain the availability and quality of flowering resources (e.g., landscape composition and configuration, weather), are significantly associated with honey bee colony overwintering survival (Switanek et al. 2017; Kuchling et al. 2018; Van Esch et al. 2020; Calovi et al. 2021). Using a model selection approach, Van Esch et al. (2020) found that weather (the number of frost days and flying hours, which are related to bees' ability to forage for resources) and landscape connectivity were among the best variables for describing colony overwintering survival. In Pennsylvania, USA, Calovi et al. (2021) found that weather variables over three years were the most important predictors of colony overwintering survival, whereas landscape metrics (land use and topography) were of little importance. Analysis of a six-year beekeeper survey dataset from Austria revealed that warmer, drier weather (Switanek et al. 2017), as well as more developed land and forests (Kuchling et al. 2018) were each associated with reduced overwintering survival.

Other honey bee studies have gathered more in-depth colony data, but often only assess these outcomes in the context of either land use or weather. Smart et al. (2018) studied colonies extensively in two apiaries (i.e., sites where colonies are kept) that

differed in the proportion of agricultural land in the surrounding forage landscape, finding more protein-rich pollen, greater mass gain, and lower pesticide exposure in a less agriculturally intensive apiary. Similarly, Smart et al. (2016) assessed both colony survival and honey production and found a positive correlation with proportion of uncultivated forage land in the surrounding landscape. Conversely, Sponsler and Johnson (2015) found that foraged nectar and pollen as well as wax production were higher in landscapes with more agriculture. Likewise, Alburaki et al. (2017) found higher brood production and colony mass (a proxy for honey production) in agriculturally intensive areas. Holmes (2002) also assessed honey yields and found temperature and precipitation were correlated with honey yield, suggesting weather is related to both bees' ability to forage and flowering plants' ability to produce nectar. Given the variable associations of landscape and weather with end-of-season colony health metrics in honey bees, it is important to explore these interactions throughout the summer activity period to understand the relative importance of different drivers on colony productivity.

We expect that detailed honey bee colony data will support more effective management decisions by revealing inconspicuous or indirect environmental associations with colony productivity. Honey bee colony assessments can provide information on current colony productivity, future colony condition, and potential sources of stress such as poor nutrition or pest infestation rates. Honey bees store resources in the colony: carbohydrates in the form of nectar and honey and protein in the form of pollen and bee bread. The abundance of stored resources provides information on the ability of the surrounding forage landscape to provide resources (Sponsler et al. 2020). Because these resources are nutritionally important to adult bee productivity as well as brood rearing, stored resources can predict future colony success (Brodschneider and Crailsheim 2010). During summer, honey bees rear brood (worker bee pupae) continuously, commensurate with nutritional resources (Khoury et al. 2013) and hive space. The abundance of developing brood in a colony (eggs, larvae, and pupae) provides demographic information. Worker bee pupae are capped for nine days before emergence (Bertholf 1925), so the area of capped brood (pupae) provides an estimate of colony size in the

near future. Additionally, while colonies may cannibalize open brood (larvae and eggs) when resources become scarce, capped brood has already received all necessary nutrients for development, and is therefore not cannibalized (Schmickl and Crailsheim 2001). So even if resource conditions change, capped brood is a reliable estimate of future colony size as well as recent resource conditions.

In this study we sought a better understanding of the relative association between landscape composition, configuration, and weather with colony productivity outcomes. These colony productivity outcomes included foraged nectar mass, foraged pollen mass, area of capped brood, and change in adult population size.

Methods

Site selection and colony enrollment

From 2015 to 2018 we inspected 456 commercially managed, migratory honey bee colonies distributed across 18 apiaries (12 colonies inspected per apiary) (Fig. S1). In 2015, colonies in four apiaries were inspected, in 2016 six additional apiaries were added for a total of ten apiaries, and in 2017 two additional apiaries were added for a total of 12 apiaries. In 2018, six of the 2017 apiaries were inspected along with six new sites for a total of 12 apiary locations (Table S1).

Colonies were inspected once in July (initial inspection) and once in September (final inspection) of each year. During each inspection we assessed colonies for cluster size, presence of a laying queen, and varroa mite (*Varroa destructor*) infestation (Rosenkranz et al. 2010). Presence of a laying queen was confirmed by finding the queen and/or freshly laid eggs. Varroa mite infestation levels were assessed using the sugar roll method on approximately 300 bees (Macedo et al. 2002). We enrolled only colonies that had a laying queen in July. We also excluded a colony from analysis if it died or experienced a queen event (queen loss or replacement) by the final inspection. This left 367 of the 456 colonies, with an average of ~10 colonies per apiary and a minimum of 7 colonies per apiary (Table S2).

Landscape metrics

Proportion of area within 4 km of each apiary in various land use classes was determined using the 2017 Cropland Data Layer (CDL) (USDA NASS 2017) in R with packages *sp* (Pebesma et al. 2020), *rgdal* (Bivand et al. 2020), *raster* (Hijmans et al. 2020), and *sf* (Pebesma 2018). There were 66 different land use classifications identified by the CDL across our 18 sites (within each 4 km buffer). We used these data to calculate three honey bee-relevant landscape metrics: land use Shannon diversity, mean patch area, and an agricultural versus forested land use variable.

Shannon diversity is a measure of richness and evenness. Landscapes with multiple different land use covers (high land use richness), present at even proportions in the landscape (high land use evenness) have the highest Shannon diversity score (O'Neill et al. 1988). We chose this metric because Michigan is one of the most agriculturally diverse states in the country (Bertone 2017), which is effectively captured by the high thematic resolution of agricultural crops in the CDL. The diversity of land use types may increase resource availability and accessibility by increasing the diversity and complementarity of floral resources for honey bees at a landscape scale (Benton et al. 2003; Mandelik et al. 2012; St. Clair et al. 2020). Alternatively, less diverse landscapes with a single, abundant high-quality land cover can provide a boon of resources and are easy for foragers to locate in the landscape (Beekman and Lew 2008; Dolezal et al. 2019). Land use Shannon diversity within each buffer was calculated in R using the *vegan* package (Legendre et al. 2018).

Mean patch size, the average size of contiguous patches of land within a landscape, was also calculated. Michigan has one of the smallest average farm sizes of the Midwestern U.S. (USDA NASS 2019). Smaller patch size is often associated with more natural, extensive landscapes, which are theoretically beneficial to pollinators (Tscharntke and Brandl 2004). Landscapes made up of smaller patches also have greater edge area, which often contain abundant flowering weeds that support honey bee foraging (Bretagnolle and Gaba 2015; Quinlan et al. 2021a, b). However, it may be more difficult for honey bees to find high-quality resources in extremely patchy landscapes (Beekman and Lew 2008). Mean patch area within each

buffer was calculated in R using the landscapemetrics package (Hesselbarth et al. 2019), specifying queen's case for connectivity of patches.

We also created a landscape composition metric to summarize the agricultural to forested land use gradient of our sites, using similar methods to Sponsler and Johnson (2015). First, the 66 land use classifications were binned into the following categories: staple crops (corn, soy, small grains), non-staple crops (all other crops), grassy-herbaceous land (hay, wildflower, switchgrass, fallow, and pasture), forests, urban, wetland, and NA (undefined, barren, and water). The resulting six land use classifications (excluding NA) were then summarized using principal components analysis (Sponsler and Johnson 2015). We determined that the first principal component (PC1) alone was sufficient for describing variation in our land use data based on the broken stick criteria (Jackson 1993) (Fig. S2). Furthermore, using only the first component is a supported statistical practice for honey bee research (Pirk et al. 2013).

Weather

For each of our sites, we obtained seasonal weather data for the preceding year and 30-year normal climate data. Data on monthly mean temperature and precipitation within a year's time preceding our inspections were obtained from Oregon State's PRISM project (2004) using the prism package in R by averaging pixel values (4 km-resolution) within 4 km of each apiary. September through December weather from the preceding calendar year (T_{-1}) and January through August weather from each colony inspection year (T_0) were used for analysis. Average monthly temperature and precipitation values were then binned by meteorological season: fall (September, October, November), winter (December, January, February), spring (March, April, May), and summer (June, July, August) (Fig. S3). We similarly obtained monthly 30-year normal temperature and precipitation data (i.e., climate-normal conditions or average temperature and precipitation for 1991–2020) for each of our apiary sites.

Change in colony cluster size

For our study, the honey bee colonies were kept in hive boxes with removable frames, upon which the bees built their nest. Colony cluster size, a proxy for adult population size (Nasr et al. 1990), was determined by counting the number of frames fully covered on either side with adult bees (Nasr et al. 1990). Hives were of various sizes and therefore varied in available frames, introducing the potential for censoring. We used a mixed effects Cox model, through the coxme package in R (Therneau 2022; Therneau and Grambsch 2000) to model change in colony size from July to September. This modeling framework allowed us to indicate that change in colony size was potentially right censored for colonies that had filled all hive frames in September.

Pollen

In every year, two colonies in each apiary were outfitted with pollen traps (Superior Pollen Traps, Mann Lake, Hackensack, MN), which brush pollen loads off returning foragers. Pollen traps were set to collect pollen for 72 h every two weeks from early July through late September. Each of the resulting six pollen collection periods were synchronized ± 3 days each year. In some years there were fewer collections, either due to the managing beekeeper's schedule (moving colonies into the apiaries late in early summer or removing colonies early in fall) or due to actions by the researchers (i.e., a scheduling conflict or mis-labeled samples) (Table S2). In total, we collected 317 pollen samples (2015=46 samples, 2016=79 samples, 2017=96 samples, 2018=96 samples). Pollen samples were transported in coolers from the field to the lab where they were stored at -20 °C until they were weighed.

Capped brood

In September 2018, the two colonies at each apiary from which pollen samples were collected were also inspected for area of capped brood (pupal population size), allowing for direct comparison between average mass of foraged pollen and capped brood. Amount of capped brood was determined by examining both sides of each colony's frames and recording the area of each frame containing capped brood (rounded to

the nearest 1/32 per frame side). A gridded 4×8 piece of clear plexiglass was used to train observers in estimating capped brood (Delaplane et al. 2013) until consistent estimates were made among observers.

Mass

Colony mass (excluding equipment mass) approximates the mass of stored nectar and honey in a colony. Two additional colonies in each apiary were placed on hive scales (Solutionbee LLC, Raleigh, NC) that logged mass every 15 min. Before analysis, colony mass data were cleaned as follows (modified from Smart et al. 2018). First, to remove artifactual spikes or drops in mass that could have resulted from colony management, sudden changes in mass (>2 kg within 15 min) were smoothed, as were absolute mass below 25 kg (approximate mass of two large, empty hive boxes with frames and 2.25 kg of bees). Colonies with extremely sparse data (fewer than 10 logged masses from mid-July to late-September) were excluded. Then, cumulative colony mass change was calculated, starting at 0 kg when the colony was placed on the scale resulting in a continuous, smoothed mass change curve. From this curve, we extracted bi-weekly snapshots of colony mass on the same collection schedule as pollen sampling. Mass was obtained at midnight when we would expect all bees to be inside their colony.

Model development and analysis

All statistical analysis was completed in R version 3.6.3 (R Core Team 2020). In the mixed effects Cox model for change in colony cluster size, apiary and year were included as random effects. Foraged pollen mass and colony mass were each modeled using a generalized linear mixed effects model (GLMM) through the nlme package (Pinheiro et al. 2020). A first-order autoregressive error structure was used to account for repeated measures of bi-weekly sampling rounds on colonies. To accommodate the hierarchical structure of these data sets, year, apiary-within-year, and colony-within-apiary-within-year were each included as nested random effects. Amount of capped brood in September was modeled using a GLMM using the lme4 package (Bates et al. 2015) with a random effect of apiary.

To understand the importance of our landscape metrics and weather to describe each of our four colony outcomes, we developed 17 increasingly complex candidate models (Table 1) that followed the basic model structures described above. Those candidate models which included weather variables always included summer temperature and precipitation because we expected summer weather to have a direct effect on colonies. Spring or fall temperature and precipitation were included in more complex candidate models (in addition to summer weather) because we expected them to have a less pronounced, indirect effect on colonies beyond that of summer weather. Ten of the candidate models included a land use variable, summarized using principal components analysis. Additionally, land use Shannon diversity and mean patch size were each included along with (1) land use; land use and each seasonal weather combination (i.e., (2) summer, (3) summer/ spring, (4) summer/ fall); and (5) together (Shannon diversity and mean patch size) with land use.

Change in cluster size and capped brood models also included a set of null predictor variables (fixed effects that were the same across all eight candidate models). For change in colony cluster size, varroa mite infestation in September was included as null predictors in every candidate model, as we expected varroa mites to have potentially confounding effects on colony growth. For the capped brood model, mean mass of pollen collected across all sampling events and July colony size were included as null predictor variables. No fixed effects were included as null predictors in either the pollen mass or colony mass models, resulting in each null candidate model being an intercept-only model. In all candidate models, each predictor variable was scaled and centered prior to analysis, enabling comparisons of coefficient estimates (β) within each model.

We used Akaike's Information Criterion, corrected for small sample size (AICc) and model weights to rank these candidate models (Burnham and Anderson 2002) and report parameter estimates and 95% confidence intervals (CI) for supported models. We did this using the MuMIn package (Bartoń 2019). Models are considered substantially different at $\Delta\text{AICc} > 2$ per additional variable (Burnham and Anderson 2001). Given the exploratory nature of our model comparisons, we chose not to report p-values, which by their nature suggest hypothesis testing, and would

Table 1 Akaike information criterion corrected for small sample size (AICc), showing the difference in AICc values (Δ AICc) among 17 different candidate models for honey bee colony outcomes

	Null	Land			Weather (Temperature + Precipitation)			Δ AICc	df	Model Weight
	Varroa	Land Use	Shannon Diversity	Mean Patch Size	Summer (T_0)	Spring (T_0)	Fall (T_{-1})			
Change in Colony Cluster Size	Y	Y	Y		Y	Y		0	12.0	0.36
	Y				Y	Y		0.7	14.4	0.26
	Y	Y			Y	Y		1.0	14.6	0.22
	Y	Y		Y	Y	Y		1.6	15.1	0.16
	Y				Y		Y	14.9	16.8	0.00
	Y				Y		Y	18.6	17.1	0.00
	Y				Y			21.6	13.9	0.00
	Y	Y	Y		Y			21.7	11.1	0.00
	Y	Y			Y			22.2	14.3	0.00
	Y	Y		Y	Y			23.3	14.7	0.00
	Y	Y	Y	Y				25.9	10.9	0.00
	Y		Y					26.1	11.4	0.00
	Y	Y	Y					27.3	10.1	0.00
	Y							27.5	12.7	0.00
	Y	Y						27.7	13.3	0.00
	Y	Y		Y				27.8	13.9	0.00
	Y			Y				28.3	13.2	0.00
	Intercept	Land Use	Shannon Diversity	Mean Patch Size	Summer (T_0)	Spring (T_0)	Fall (T_{-1})	Δ AICc	df	Model Weight
Summer-long Foraged Pollen	Y				Y			0	8	0.26
	Y							0.2	6	0.24
	Y	Y			Y			2.1	9	0.09
	Y	Y						2.3	7	0.09
	Y				Y	Y		3.5	10	0.05
	Y	Y		Y				3.5	8	0.05
	Y	Y	Y					3.6	8	0.04
	Y	Y		Y	Y			3.7	10	0.04
	Y	Y	Y		Y			3.9	10	0.04
	Y				Y		Y	4.2	10	0.03
	Y	Y	Y	Y				5.3	9	0.02
	Y	Y			Y	Y		5.6	11	0.02
	Y	Y			Y		Y	6.3	11	0.01
	Y	Y	Y		Y	Y		7.4	12	0.01
	Y	Y		Y	Y	Y		7.5	12	0.01
	Y	Y		Y	Y		Y	8.0	12	0.00
	Y	Y	Y		Y		Y	8.2	12	0.00

Table 1 (continued)

	Average Pollen Mass +Cluster Size	Land Use	Shannon Diversity	Mean Patch Size	Summer (T ₀)	Spring (T ₀)	Fall (T ₋₁)	ΔAICc	df	Model Weight
September Capped Brood	Y	Y						0	6	0.65
	Y	Y	Y					2.5	7	0.18
	Y	Y		Y				4.0	7	0.09
	Y				Y			5.7	7	0.04
	Y	Y	Y	Y				7.0	8	0.02
	Y	Y			Y			7.5	8	0.02
	Y				Y	Y		10.2	9	0.00
	Y							11.4	5	0.00
	Y	Y	Y		Y			12.3	9	0.00
	Y	Y		Y	Y			12.9	9	0.00
	Y	Y			Y	Y		13.7	10	0.00
	Y				Y		Y	14.2	9	0.00
	Y	Y			Y		Y	18.3	10	0.00
	Y	Y	Y		Y	Y		21.2	11	0.00
	Y	Y		Y	Y	Y		21.4	11	0.00
	Y	Y		Y	Y		Y	25.8	11	0.00
	Y	Y	Y		Y		Y	25.9	11	0.00
	Intercept	Land Use	Shannon Diversity	Mean Patch Size	Summer (T ₀)	Spring (T ₀)	Fall (T ₋₁)	ΔAICc	df	Model Weight
Summer-long Colony Mass	Y	Y			Y		Y	0	11	0.23
	Y	Y	Y		Y		Y	0.1	12	0.22
	Y				Y		Y	0.4	10	0.19
	Y	Y		Y	Y		Y	1.3	12	0.12
	Y	Y	Y					2.0	8	0.08
	Y	Y						3.0	7	0.05
	Y	Y		Y				3.7	8	0.04
	Y	Y	Y	Y				4.1	9	0.03
	Y							5.7	6	0.01
	Y	Y	Y		Y			6.1	10	0.01
	Y	Y			Y			7.0	9	0.01
	Y	Y		Y	Y			7.7	10	0.00
	Y	Y			Y	Y		8.1	11	0.00
	Y	Y	Y		Y	Y		8.3	12	0.00
	Y				Y			8.7	8	0.00
	Y	Y		Y	Y	Y		9.8	12	0.00
	Y				Y	Y		11.2	10	0.00

Candidate models include null predictor variables (first column), landscape variables (a forest versus agricultural land use variable derived through Principal Components Analysis, land use Shannon diversity, and/or mean land use patch size), and/or weather variables (seasonal temperature and precipitation). Boxes containing “Y” indicate that a variable (column) is included in candidate model (row). This suite of 17 candidate models is proposed for each honey bee colony metric along with fixed and random effects described in the statistical analysis section of the methods. Total number of degrees of freedom (df) for each model are also shown. Weather data are from the year preceding each summer inspection, such that fall weather includes data from the previous calendar year (T₋₁) of the colony inspection (T₀)

therefore be misleading in this context (Tredennick et al. 2021).

Results

Landscape metrics

Based on the CDL, there were an average of 36 ± 2 (mean \pm standard error (S.E.)) unique land use types per 4 km buffer. Correcting for land area evenness, the Shannon diversity of these landscapes ranged from 1.6 to 2.5, with an average score of 2.0 ± 0.1 . The mean patch size of land use classifications ranged from 3551 to 8173 m² and averaged 5259 ± 326 m².

The first land use principal component (PC1) explained 65.4% of variance in simplified land use surrounding our sites and had a standard deviation of 11.07. The first principal component was negatively correlated with area of staple crops ($\rho = -0.69$) and non-staple crops ($\rho = -0.16$) and positively correlated with area of forests ($\rho = 0.69$). All other land cover loadings had a magnitude of 0.10 or less. Thus, PC1 can be thought of as an axis of agriculture to forest, with high values representing landscapes dominated by forests and low values representing landscapes dominated by agriculture. Sites ranged in PC1 values from -15.3 to 16.6 . The next principal component (PC2) only explained an additional 14.2% of the variance.

Weather

There was significant variation in seasonal temperature and precipitation among the years of our study (Fig. S3). Across the four seasons, 2017 and 2018 were generally wetter than 2015 and 2016, with summer precipitation showing the most variation across sites. 2016 and 2017 were the warmest years in our study, with temperatures remaining relatively consistent across sites within each season.

Change in colony cluster size

In July, colony cluster sizes ranged from 3 to 38 frames of bees, with a mean of 17 frames (± 0.4 frames; S.E.). By September, colonies ranged in cluster size from 2 to 26 frames of bees, averaging 14 frames (± 0.2 frames). Colony populations showed a

large range of change between sampling rounds, from -25 to 19 frames. On average, colonies decreased in size by 2 frames (± 0.4 frames) throughout the summer. This decrease in colony size, on average, is likely in part due to right censoring by available hive equipment (many colonies had honey supers removed in August). Of 367 analyzed colonies, 98 were at maximum capacity provided by available hive equipment at the September inspection.

We found that apiary locations that experienced more spring precipitation had a greater risk of population size loss by September. The four most parsimonious models for describing change in colony cluster size each included spring weather. Together, these models made up 100% of candidate model weights (Table 1), indicating high certainty in the importance of spring weather for describing change in colony cluster size within our set of candidate models. Furthermore, the CI for spring precipitation did not contain zero ($\beta = 0.46$, CI 0.31, 0.61), based on estimates from our top model. It should be noted that for the top model, the assumption of proportional hazards was violated for the summer weather variables. We report on the original model here and show that alternative models, aimed at resolving the violation, yield very similar results (Table S3).

Low to moderate precipitation, estimated to maximize colony growth, fell within the historic range (30-year normal) of spring precipitation for our region whereas higher-than-normal spring precipitation was associated with population loss. Some of the smallest colonies we observed, however, were in locations that experienced normal spring precipitation (Fig. 1a). There was a negative correlation between spring temperature and the hazard of change in colony cluster size, suggesting apiary locations that experienced warmer spring temperatures supported greater colony growth by the following September ($\beta = -0.87$; CI $-1.10, -0.65$) (Fig. 1b). Both spring precipitation and temperature trends seemed to be driven by two years of data; colonies grew more in 2015 (a warm spring with intermediate precipitation) and less in 2018 (a cool spring with abnormally high precipitation in some sites), so caution should be taken in over interpreting these results. While both spring models also included summer weather by default, there was no evidence of a correlation between summer weather and change in colony size (summer temperature: $\beta = 0.11$; CI $-0.05, 0.28$; summer precipitation:

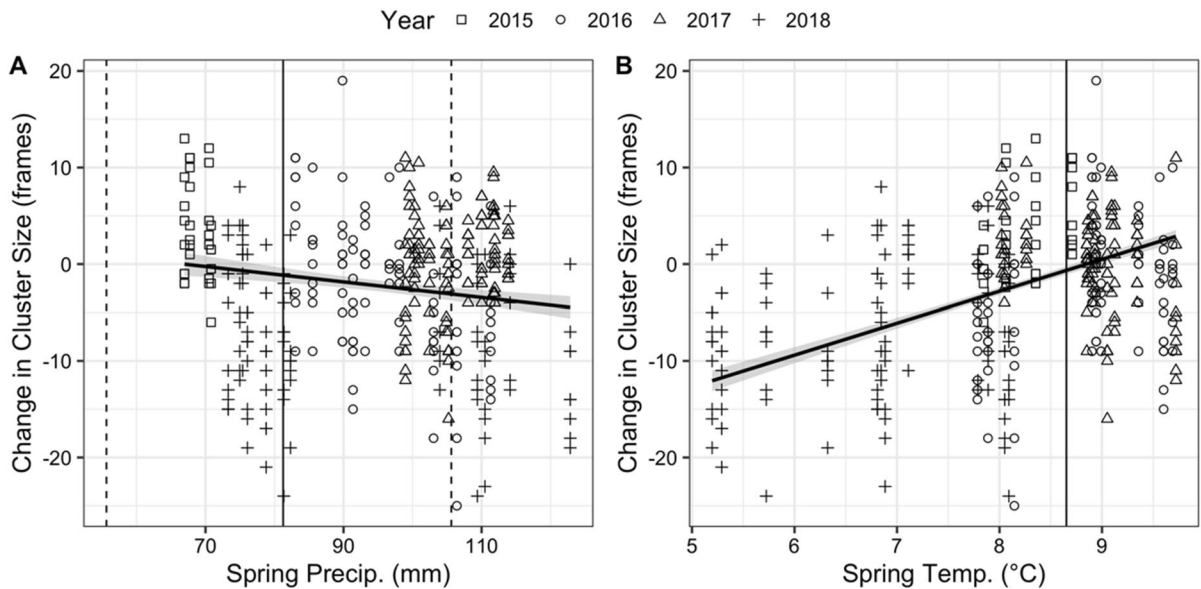


Fig. 1 Correlation between change in colony cluster size of honey bees in Michigan, USA from 2015 to 2018 and average spring (March–May) precipitation (**A**), and average spring temperature (**B**). Each line of best fit, with shaded confidence interval, shows the relationship between model-fitted values

of change in cluster size and each predictor variable. Vertical lines show the 30-year normal spring precipitation range (maximum and minimum as dashed lines) and median (solid line) across all apiary locations in this study

$\beta=0.09$; CI $-0.07, 0.24$). Land use composition ($\beta=-0.37$; CI $-0.64, -0.10$) and Shannon diversity ($\beta=-0.33$; CI $-0.56, -0.10$) were each positively correlated with colony growth in the top model. However, the addition of these land use covariate did not improve upon the top model ($\Delta\text{AICc}<1.6$), indicating that land use was not important for describing change in colony cluster size. Models without spring weather each had a model weight of $<1\%$ and were therefore not considered further.

All candidate models included varroa infestation rates, but there was no evidence for an association with varroa infestation on change in cluster size ($\beta=0.07$; CI $-0.07, 0.20$). We found an average of fewer than 3 varroa mites per 100 bees which is commonly considered the treatment threshold for this parasite (Jack and Ellis 2021). However, the distribution of mite infestation was heavily right skewed, with 26% of colonies above this threshold and some colonies showing very high infestation (the most infested colony had 29 mites/ 100 bees).

Pollen

On average, colonies collected 76.6 g (± 4.9 g) of pollen per biweekly 72-h sampling round. The mass of foraged pollen was heavily right skewed, with the majority ($\sim 70\%$) of colonies collecting less than 100 g of pollen per sampling round. The maximum amount of pollen foraged within 72 h was 725.9 g. None of our proposed candidate models were better than the null intercept model ($\Delta\text{AICc}=0.2$), suggesting that colony pollen collection was not related to our weather and landscape covariates. In our top model, apiaries intercepts had a standard deviation of 1.7 and colonies had a standard deviation of 1.4. The standard deviation of intercepts among years was zero, indicating low variation among years when considering other variables in the model.

Capped brood

When we assessed capped brood in September 2018, an average of 1.5 frames (± 0.2 frames) were capped, with a maximum of 3.3 frames and a minimum of 0.3 frames. Our model selection results indicate a single

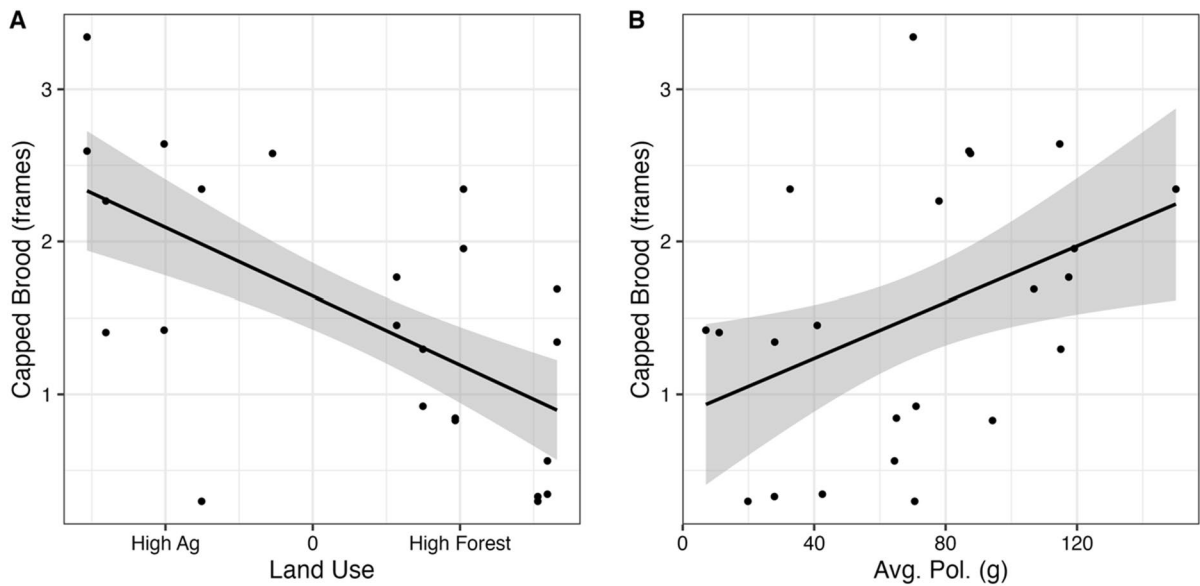


Fig. 2 Area of capped brood in honey bee colonies in Michigan, USA in summer 2018, plotted against agriculture versus forest land use within 4 km of the apiary (**A**) and against average mass of foraged pollen throughout summer (**B**). Lines of

best fit and shaded confidence intervals are shown for model-fitted capped brood values and actual capped brood values are plotted as points

model as the most parsimonious (land use+averaged foraged pollen mass+July cluster size). This model accounted for 65% of model weights and the next best model was different based on a threshold of $\Delta\text{AICc} \geq 2$ (Burnham and Anderson 2002) ($\Delta\text{AICc}=2.5$). Model estimates indicate that apiaries surrounded by more agricultural land and less forested land supported a greater amount of capped brood in September ($\beta = -0.65$; CI $-0.90, -0.40$) (Fig. 2). In addition to the correlation with land use, mean mass of foraged pollen throughout summer was positively correlated with area of capped brood in September ($\beta = 0.43$; CI $0.17, 0.69$), whereas July cluster size was not ($\beta = 0.09$; CI $-0.17, 0.35$).

Mass

Colonies on average gained 3.57 kg from early July to late July and 5.48 kg from early July to early August. By late August, colonies were only 2.70 kg heavier on average than they were in early July. In early September, colonies were only 0.42 kg heavier than early July, and were 0.37 kg lighter in late September than early July.

Candidate models for colony mass that included fall weather (September – November of the previous year) all ranked highly. The four models that included fall weather accounted for 76% of total model weights ($\sim 20\%$ each). In the top model, fall precipitation showed a strong negative correlation with colony mass ($\beta = -2.91$; CI $-4.01, -1.80$) (Fig. 3). As with change in colony cluster size, however, this trend seems to be driven by the 2016 and 2018 data, which fell outside of the 30-year-normal fall precipitation range for the region. Most apiaries in 2016 experienced drought-like conditions the previous fall, while the 2018 apiaries experienced excessive rainfall. Colonies put on slightly more mass in 2016 when fall precipitation was low and lost mass in 2018 when fall precipitation was extremely high (Fig. 3).

There was little support for the importance of land use composition in describing colony mass. While land use was included in both top models, it did not sufficiently improve the model based on AIC, and it was only weakly correlated with colony mass ($\beta = 0.87$; CI $-0.23, 1.97$).

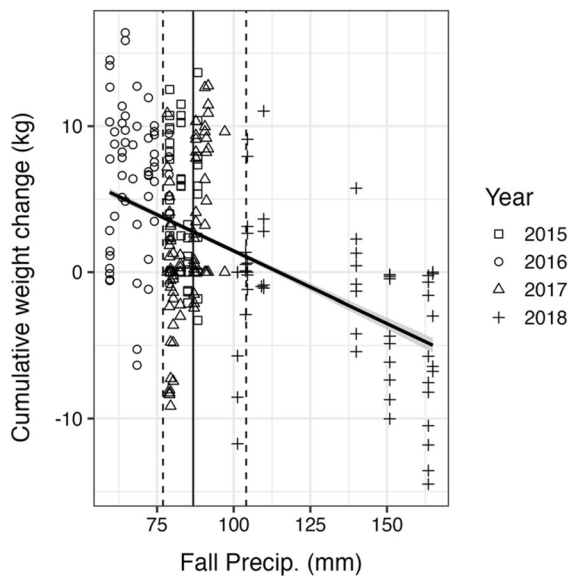


Fig. 3 Plot of cumulative mass change in honey bee colonies in Michigan, USA, versus fall (September–November) precipitation from the year before. Colony mass is plotted for every two weeks from early July to late September. Points representing mass observations are shaped according to year. The line of best fit, with shaded confidence interval is shown for model-fitted mass change values. Vertical dashed lines show the range (maximum and minimum), and the vertical solid line shows the median 30-year normal fall precipitation across all apiary locations

Discussion

Through this four-year assessment of honey bee colonies in Michigan, USA we demonstrate connections between multiple colony productivity outcomes and environmental factors, including seasonal precipitation and landscape metrics. In particular, we highlight the negative correlation between extreme spring and fall precipitation and change in colony mass and cluster size the following summer, respectively. Our results also indicate that colonies that collect more pollen and that are in more agricultural landscapes (as opposed to more forested landscapes) have more capped brood by September.

Weather

There was considerable variation around each of our observed correlations. Although models that included the influence of precipitation on colony growth and colony mass were selected based on AICc,

uncertainty in effect sizes and model selection suggests these findings should be interpreted with caution. Furthermore, reports in the literature on the relationship between precipitation on honey bee colonies are mixed. Similar to our findings, a survey of honey bee colonies across the Northcentral U.S. showed that spring precipitation was negatively correlated with colony mass gain (Quinlan et al. 2022). However, other studies have found that winter precipitation is positively correlated with honey production (Báez et al. 2019) and that annual precipitation is positively correlated with colony survival (Switaneck et al. 2017).

It may not be the magnitude (high or low) of precipitation, but how extreme it is (different from the norm). Excessive amounts of fall and spring precipitation appear to negatively impact honey production and colony growth in the following season, respectively. Similar to our colony growth finding, Calovi et al. (2021) reported links between both high and low summer precipitation and decreased winter colony survival. Since colonies in our study did not arrive to apiaries until July of each year, the association between extreme precipitation on colony mass and change in colony size is likely caused by indirect effects of precipitation on floral resource abundance and quality. Dudney et al. (2017) found that in annual grasslands, high precipitation the previous fall decreased forb abundance while increasing grass abundance. The same authors found a similar trend for current-year spring precipitation, but the negative correlation between spring precipitation and forb abundance was not significant. This evidence from the literature, along with our findings, suggests that extreme weather may have unexpected impacts on colony development the subsequent year, mediated through floral resource abundance. Therefore, managing landscapes with climate-resilient floral resources may support pollinator health. Based on our findings, future studies should examine the relationship between precipitation in the preceding fall and spring on floral resources to better understand summer colony outcomes.

While summer precipitation was included in our models for change in colony size and mass, it had a comparatively small effect size and large uncertainty in model estimates. Rain can directly inhibit bees' ability to forage, can damage flowers, and it impedes other aspects of plant-pollinator interactions

(reviewed by Lawson and Rands 2019). Because of this, we would have expected to see a negative correlation between hive mass change and growing season (summer) precipitation. There may not have been sufficient variation in summer precipitation among years to observe a difference. This reinforces the need for continued field monitoring of honey bee colonies to capture relationships between a range of seasonal weather conditions on colony productivity. Given that extreme weather events (heat waves and extreme precipitation) are expected to increase in this region due to climate change (Gao et al. 2012), such data could allow us to predict colony health and honey crop production in a changing climate. Predictions of suitable honey bee habitats based on weather could also provide migratory beekeepers with decision support tools to avoid poor-weather regions and give stationary beekeepers information on when and how to manage their colonies (e.g., by supplementing feed in years with extreme weather). Additionally, crop insurance is available to beekeepers to mitigate losses associated with extreme precipitation (USDA 2017). A better understanding of lagged correlations with extreme weather could assist beekeepers in selecting the best insurance options for their region.

Landscape metrics

In our study, apiaries spanned a gradient of agricultural to forested land, and those in more agriculturally dominated landscapes had more capped brood by September. This is expected, given that dense deciduous forests in this region provide very limited nutritional resources for bees by late summer (Mola et al. 2021) and colonies in our study were not positioned in study apiaries during spring forest nectar flow. Agricultural landscapes can support honey bee colonies (Naug 2009; Sponsler and Johnson 2015; Danner et al. 2016). Using a model selection approach, Sponsler and Johnson (2015) found that in Ohio, honey bee colony wax and honey production were positively associated with area of cropland around research apiaries. These authors suggest that weeds in crop margins support honey bee colonies' nutritional needs (Sponsler and Johnson 2015). Indeed, studies assessing honey-bee foraged pollen in the Midwestern U.S. found a high proportion of non-native, weedy species in pollen collected by bees (Smart et al. 2017; Quinlan et al. 2021a, b). The crops themselves may also

provide resources to honey bee foragers. Other studies have identified potentially detrimental relationships between agricultural land on honey bee colony outcomes, from inconsistent availability of resources to the risk of pesticide exposure (Dolezal et al. 2016, 2019; Colwell et al. 2017; McArt et al. 2017; Graham et al. 2021). While our results suggest that agricultural land is more supportive of honey bee colonies than forested land (which provides few late-season floral resources) agriculture may only be less harmful than forests in late summer. We are not able to draw conclusions on correlations with other types of land use based on apiary locations in our study and our analytical approach. Based on potential risks posed by agricultural land, and landscape scale studies in the literature (Smart et al. 2016, 2018), we expect that natural and semi-natural forage land use would be even more supportive of honey bee colonies than agricultural land. Overall, these results highlight the importance of temporally consistent floral resources for pollinators at a landscape scale.

While land use was related to capped brood area, land use was not an important factor in either the colony mass or foraged pollen models. There are several factors that could have confounded this mechanism. For example, the relationship between pollen foraging and brood production is bidirectional. That is, colonies that collect more pollen raise more brood, and colonies with more brood collect more pollen (Pankiw et al. 1998). Pollen hoarding is also a genetic trait that is associated with the proportion of pollen foragers in the colony (Page et al. 1995), which may explain colony-level variation in pollen foraging that we observed. Additionally, variation in pollen mass could have been introduced by moisture content. To avoid this potentially confounding factor, future studies should consider lyophilizing pollen samples before weighing. Likewise, neither Shannon diversity of land covers nor mean patch size improved any of the models. Honey bees' ability to communicate the location of high quality resource patches within the surrounding landscape through dance may make them particularly resilient to land fragmentation and habitat heterogeneity (Beekman and Lew 2008; Nürnberg et al. 2017). Future studies that capture an even broader gradient of these landscape metrics could be useful for understanding the extent of this adaptation.

Colony-level metrics

Varroa mites are recognized as one of the leading stressors of honey bee colonies in the USA (Rosenkranz et al. 2010), but there was not support in our model for an association with varroa mites. This may be due to the timing of our study, as many of the negative effects of varroa are seen later in the season (Amdam et al. 2004; Rosenkranz et al. 2010), or because colonies in this study also received standard management, limiting variation in mite levels.

Conclusion

Our models identified several variables, particularly weather, as important for describing multiple colony productivity outcomes. Honey bee colonies are subjected to a complex assembly of biotic and abiotic stressors in the field (Goulson et al. 2015; Potts et al. 2010; Vanengelsdorp and Meixner 2010), which can manifest across levels of colony organization, from foraged resources, to developing brood, to colony growth. The synergy of these factors makes drawing conclusions on drivers of overall honey bee colony productivity extremely difficult. Our observational study points to excessive precipitation across multiple seasons as important to describing colony outcomes. To support overall colony productivity, land managers, researchers, and beekeepers may need to consider multiple weather, land use, and colony conditions and their potential interactions. By taking an integrated perspective, our findings provide a roadmap for future studies to develop interventions (such as climate-resilient, temporally consistent floral resources) based on a mechanistic understanding of overall honey bee colony productivity and to enhance inference on broad-scale stressors such as extreme weather associated with climate change.

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Author contributions All authors (GMQ, RI, CRVO, AHS, and MOM) contributed to the study design, contributed to the interpretation of the data, and provided substantive revisions to the work. MOM and GMQ acquired the data; GMQ analyzed the data; GMQ drafted the work.

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Declarations

Competing interests None to declare.

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