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Modelling seasonal effects of temperature and precipitation on honey bee winter mortality in a temperate climate

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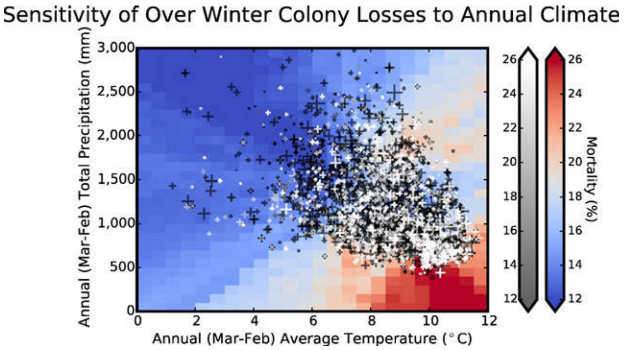
HIGHLIGHTS

- Climate variability in Austria was found to influence over winter colony losses.
- Warmer and drier regions often accompanied higher mortality rates.
- A statistical model using climate inputs improved colony loss prediction.

GRAPHICAL ABSTRACT



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ABSTRACT

Insect pollinators are essential to global food production. For this reason, it is alarming that honey bee (*Apis mellifera*) populations across the world have recently seen increased rates of mortality. These changes in colony mortality are often ascribed to one or more factors including parasites, diseases, pesticides, nutrition, habitat dynamics, weather and/or climate. However, the effect of climate on colony mortality has never been demonstrated. Therefore, in this study, we focus on longer-term weather conditions and/or climate's influence on honey bee winter mortality rates across Austria. Statistical correlations between monthly climate variables and winter mortality rates were investigated. Our results indicate that warmer and drier weather conditions in the preceding year were accompanied by increased winter mortality. We subsequently built a statistical model to predict colony mortality using temperature and precipitation data as predictors. Our model reduces the mean absolute error between predicted and observed colony mortalities by 9% and is statistically significant at the 99.9% confidence level. This is the first study to show clear evidence of a link between climate variability and honey bee winter mortality.

1. Introduction

Current global food production strongly depends on pollinators such as the western honey bee (*Apis mellifera*) (Aizen and Harder, 2009). It is therefore alarming that managed honey bee populations across the world have seen increased mortality rates in the last few decades

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(vanEngelsdorp et al., 2012; van der Zee et al., 2014; Lee et al., 2015). The challenges facing the honey bee threatens the future of our food supply, and thus, research that focuses on the potential causes of honey bee mortality is essential (Potts et al., 2010).

Previous studies have investigated the predominant challenges facing honey bee populations, which we group into four categories: 1) parasites and diseases, 2) pesticides, 3) nutrition, and 4) habitat dynamics. With respect to parasites and diseases, the most prevalent and detrimental parasite that has been shown to affect the honey bee populations across the globe is the mite *Varroa destructor* (Rosenkranz et al., 2010). Higher levels of Varroa mite infestation in the fall season can dramatically increase winter colony losses (van der Zee et al., 2015; Genersch et al., 2010). Mite infested colonies can quickly develop disease symptoms, which if left untreated commonly leads to colony collapse (Martin, 2001; Genersch et al., 2010). Neonicotinoid pesticides, among other sub-lethal effects, have been shown to reduce foraging efficiency of honeybees (Gill et al., 2012; Henry et al., 2012; Goulson et al., 2015). Nutrition includes factors relating to the quality and the quantity of nectar and pollen resources (Brodschneider and Crailsheim, 2010; Vaudo et al., 2015). These resources are linked to agricultural practices, landscape composition, weather, and climate. Lastly, studies focusing on habitat dynamics include the influence of resource availability, biodiversity, and the impacts of weather and climate variability on colony health. Stressors such as disease, weather and/or climate can lead to precocious foragers (Perry et al., 2015), who were shown to have greatly reduced effective foraging lives. Biodiversity, species richness, and the geographic distribution of insects have been linked to climate and land use change (Williams et al., 2007; Billeter et al., 2008; Dormann et al., 2008; Kerr et al., 2015). Climate has also been shown to affect biological traits in insects (Talavera et al., 2014; Zeuss et al., 2014; Polce et al., 2014; Miller-Struttmann et al., 2015). Weather related impacts such as the intensity of temperature, rain or solar radiation have been connected with the activity of social insects including honey bees (Szabo, 1980; Heard and Hendrickz, 1993; Vicens and Bosch, 2000; Kasper et al., 2008). Particularly rainy periods have been shown to influence the behavior of bees in the nest (Riessberger and Crailsheim, 1997; Schmickl and Crailsheim, 2007), while higher air temperatures have been found to increase colonial net gain rates and raise the efficiency of honey storage rates due to lower metabolic rates (Voorhies et al., 1933; Harris et al., 2003). Ambient air temperature also affects honey bee flight activity (Burrill and Dietz, 1981), honey stores (Szabo, 1980), thermoregulation (Stabentheiner et al., 2010), waggle run frequency (Bräuninger, 1964) and queens provisioning and egg laying rate (Alhaddad and Darchen, 1995). These studies were not designed to relate these shorter-term weather events with longer-term effects on colony survival. In response to surveys taken in the United States, beekeepers often name “weather”, or “poor winter” as a top factor for honey bee colony winter losses (vanEngelsdorp et al., 2012; Steinhauer et al., 2014). Despite this ranking, little detailed information is available on how and under which conditions weather has an impact on the epidemiology of diseases or honey bee colony mortality. Honey bee populations in Europe are shaped by ecological and climatic factors, but also by the lines traditionally bred or purchased elsewhere (Coroian et al., 2014; Wallberg et al., 2014). A series of experiments has demonstrated that honey bees adapted to the local environment and climate outperform bees not adapted to this environment (Dražić et al., 2014; Meixner et al., 2015). Le Conte and Navajas (2008) had a qualitative discussion that pointed to the potential connections between climate variability, climate change and colony mortality. Others have presented a more quantitative link with an inverse correlation between fall to winter (September–March) temperatures and the proportion of colonies lost in different regions of Pennsylvania, United States (vanEngelsdorp et al., 2008). However, a robust investigation into the link between longer-term weather or climate and colony health is absent.

In this study, we investigate the impact that longer-term weather and/or climate conditions have on honey bee colony survival. Initially, we find the monthly climate variables that have the greatest influence on colony mortality rates. Then, we construct a statistical model to predict mortality rates using climatic data as input. The skill of the model is evaluated to ascertain whether the climatic data can be used to provide better predictions. Ultimately, we want to investigate if predictions of winter mortality rates can be improved if we include information on the weather or climate of the preceding months.

2. Methods

2.1. Austrian meteorological and honey bee mortality data

This study uses Austrian honey bee mortality data for the period 2009–2014 (Brodschneider et al., 2010; Brodschneider and Crailsheim, 2013). Mortality rates are calculated as the percentage of lost colonies out of the total number of colonies wintered for each individual beekeeper. The geographic locations of the beekeepers and their colony mortality rates, for each year in the period 2009–2014, are shown in Fig. 1. These 6 years of record is comprised of a total of 4983 participating beekeepers. The number of contributing beekeepers varies from year to year with a minimum of 310 (year 2010) to a maximum of 1533 (year 2012). Each of these beekeepers had between 1 and 520 individual colonies. The combined total number of individual colonies over the 6 years of record was 106,675. Climate data is derived from the Integrated Nowcasting through Comprehensive Analysis (INCA) meteorological data set (Haiden et al., 2011) from the Austrian Department of Meteorology and Geodynamics (ZAMG). The data used in this study consists of temperature, precipitation, global radiation and wind speed. The meteorological data was interpolated to a 5 × 5 km resolution and aggregated to monthly climatic values. The 5 × 5 km resolution was chosen to coincide approximately with the 90th percentile foraging distance (Couvillon et al., 2015). An inverse distance weighting algorithm was then used to generate a time series of climate data at each of the geographic locations of the beekeepers.

Within the honey bee mortality data set, beekeepers only specified if they had migratory colonies or not, but information concerning when colonies had moved and where they were moved to was not collected. When we did remove migratory beekeepers from the data set, in contrast to treating all beekeepers as stationary, we found no significant change to our model results. Therefore, we make the assumption that the beekeepers are stationary, and the climate record for each beekeeper is the climate record of their main apiary location.

2.2. Model predictors

Prior to implementing any statistical model, we investigated the relevance of the relationships between monthly climatic variables and colony mortality rates. The process to establish climatic predictor relevance is illustrated in Fig. 2. As an example, Fig. 2a shows scatter points corresponding to observed winter colony mortality, for each beekeeper, and mean temperature of the preceding September. The scatter is split into two equal sized halves along the x-axis (approximately <14 °C and $>=14$ °C) and weighted averages of the percentage mortality are calculated for these halves (seen as the white squares). When the vertical distance between these two white squares is large, there is a stronger relationship between that particular climatic variable and beekeeper colony mortality rates. Fig. 2b shows the range of these distances for all climate variables and the 12 months investigated. The color intensity of the grid cells, in Fig. 2b, highlight the climatic predictors that have the greatest impact on colony mortality.

2.3. Model validation and selection

Model validation was performed by calculating the mean absolute error (MAE) of retrospective forecasts. Model performance was evaluated using cross-validation, where each year's mortality rates were

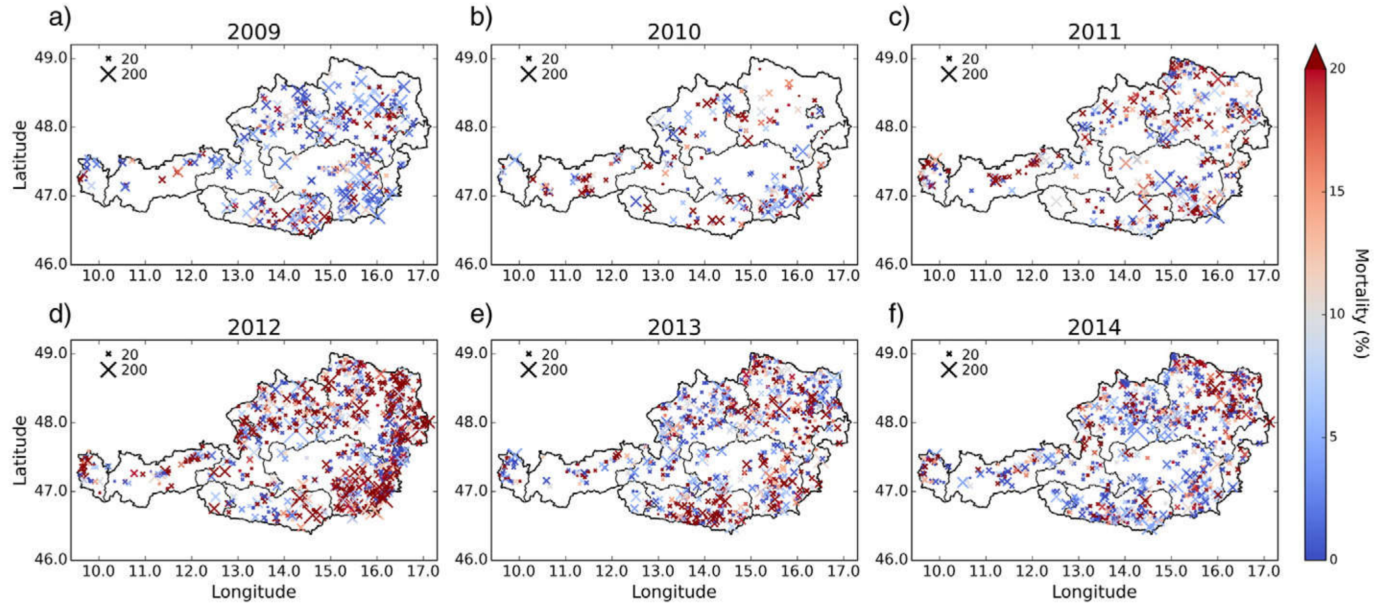

Fig. 1. The geographic locations of each individual beekeeper from the period 2009–2014. The number of colonies that the beekeeper had entering into the winter is shown as the size of each X, while the colorbar shows the observed over-winter percentage mortality of colonies. The shapefiles were extracted from GADM version 1.0 (http://www.gadm.org).

predicted using the data from the other years. Retrospective forecasts were made using four different models. These were multiple linear regression, support vector machine regression (Cortes and Vapnik, 1995), decision trees regression (Breiman et al., 1984) and k-nearest neighbors regression (Altman, 1992). The models used 24 predictors, which were the average monthly temperatures and the precipitation sums (shown as rows T and P of Fig. 2b). Model performance did not improve with the inclusion of additional predictors (e.g., global radiation, wind speed, maximum temperature). Ultimately, we selected to use the k-NN regression model (kNNM) because it was found to outperform the other models (F-test showed the improvement of the kNNM to be statistically significant with $p < 0.01$).

2.4. kNN model

To illustrate the kNNM methodology, the mortality rate of one beekeeper in the year 2014 is predicted using the data from 2009 to 2013. Of the total number of beekeepers (4983), there were 3960 for the years 2009–2013. As previously mentioned, the predictors are the average temperature and precipitation sums, corresponding to the locations of the beekeepers, for the 12 months preceding the counting of winter colony losses. This set of predictors can be referred to as matrix A, and it is 3960 rows by 24 columns. The temperature and precipitation predictors were first normalized by month. To do this, the means and the standard deviations for each column of matrix A were obtained first. Then, for each respective column of matrix A, we subtract the means and divide by the standard deviations from the prior step. As a result, the climatic data is normalized across time and space with respect to the years other than 2014. Similarly, there are the average temperature and precipitation sums corresponding to our example beekeeper. This array of these 24 values, from here on referred to as B_1, were also normalized by the means and standard deviations of matrix A. Next, the values in each column of matrix A and the values of array B_1 were multiplied by the corresponding predictor weights, where the predictor weights are simply the absolute values of the quantities shown in rows T and P of Fig. 2b. Due to this step, the kNNM more heavily weights March precipitation and September temperature (seen as dark blue and red, respectively) than it does June precipitation and July temperature (very light blue and red, respectively). As a result, we weight our 24 climatic predictors by the influence, or relevance, each has on colony mortality. Then, the differences are calculated between the normalized, weighted climatic array B_1 and each row of the normalized, weighted matrix A. These differences are subsequently used to find the corresponding Euclidean distance between each beekeeper in the 2009–2013 period and the example beekeeper in 2014. The Euclidean distance for a given beekeeper x can be calculated as:

$$\mathrm{ED}_x = \sqrt{\sum (B_1 - A_x)^2} \tag{1}$$

In this example, a unique *ED* is calculated for each beekeeper between the period 2009–2013 (for a total of 3960 *ED* values). Smaller values of *ED* correspond to beekeepers that have more climatically similar conditions. The kNNM was optimized to use the nearest 400 neighbors. Therefore, the model uses the mortality rates from the 400 beekeepers that were nearest to the climate of the example beekeeper (where the 400 nearest neighbors correspond to the 400 smallest *ED* values). We want to calculate the total mortality rate accounting for the varying numbers of colonies for these 400 beekeepers. These nearest neighbor beekeepers had a total of 9492 colonies of which 1586 colonies experienced mortality. Finally, the predicted mortality rate is $1586/9492 = 0.167$ or 16.7%. Our example beekeeper had 100 colonies, and therefore our model would predict approximately 17 of these colonies to experience mortality through the winter. Lastly, the same procedure is applied to make retrospective forecasts for the rest of the beekeepers by excluding the data from the year from which the beekeeper was sampled.

3. Results

3.1. Modelling winter mortality

For the most part, higher values of temperature and global radiation are associated with increased mortality (positive relationship, seen in Fig. 2b as red colors). November and February temperatures are the exceptions, which are inversely correlated. On the other hand, greater amounts of precipitation for all of the months investigated (with the exception of October) were accompanied with lower rates of mortality. Global radiation and wind speeds in the zonal and meridional directions were seen to have minimal influence on the observed mortality rates.

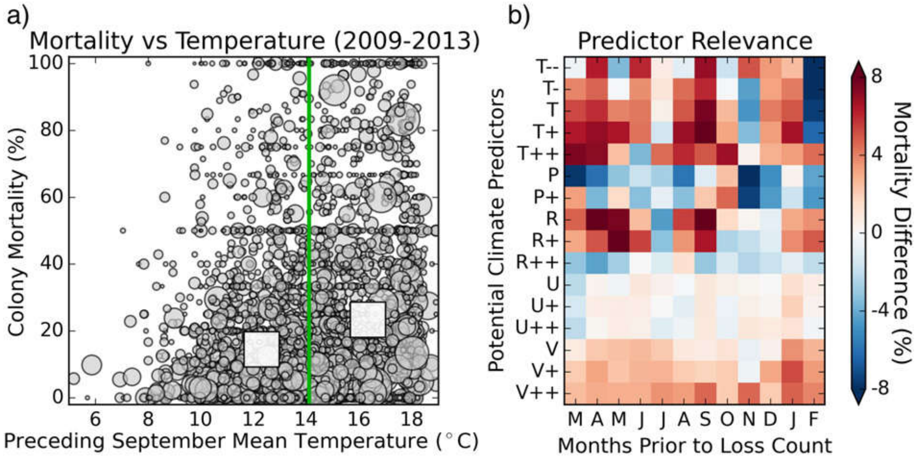

Fig. 2. Subplot (a) shows the winter mortality percentages of each beekeeper plotted against the preceding mean temperature in September. The size of the circles corresponds to the number of colonies being wintered by each beekeeper. The white squares are weighted averages of the two halves of the data (split by the green line), sorted along the x-axis. Subplot (b) illustrates the differences between mortality percentages for the chosen climate variables and months. The values on the y-axis are temperature (T), precipitation (P), global radiation (R), zonal wind speed (U), and meridional wind speed (V), while the --, -, +, and ++ are the monthly minimum, average minimum, average maximum, and monthly maximum values, respectively. At month S and climate predictor T, we can see the darker red grid cell corresponding to the vertical distance between the two squares in subplot (a). Warmer colors and cooler colors respectively show positive and negative relationships between the climate predictor and winter colony mortality.

Model predicted values of MAE were compared between kNNM and a set of reference predictions. Reference predictions, for each year, were the average colony mortality rate, or percentage, of all other beekeepers in the excluded years (where the mortality rate was the total number of colonies that experienced mortality divided by the total number of colonies being wintered). The kNNM and reference predictions of mortality rates were subsequently multiplied by their respective number of colonies being wintered to obtain the predicted number of colonies to experience mortality. This gives us a more accurate estimate of our skill, where we are not biased by a model that better predicts mortality rates for beekeepers with a small number of colonies and poorly predicts beekeepers with a large number of colonies. The MAE of the reference predictions is 3.48, while the MAE for kNNM is 3.18 (shown by more scatter points falling to the right of the one-to-one line in Fig. 3b). kNNM reduces our error and improves predictive skill. To test for statistical significance, we performed a Monte Carlo simulation by running the kNNM with randomly generated climatic data (sampled from the data of the excluded years). The kNNM was run a total of 1000 times with the randomly generated data (400 randomly sampled beekeepers instead of the 400 nearest neighbors) in place of the actual observed climate data. Of these 1000 model runs, the average MAE was 3.54 ± 0.07 (95% confidence interval), while the best performing MAE equal to 3.43. As a result, the skill of the kNNM, using the observed climatic data, is found to be statistically significant at the 99.9% confidence level.

3.2. Sensitivity of winter mortality to annual climate

Fig. 4 gives a more general overview of how the average yearly climate relates to colony mortality rates. As depicted by the figure, the beekeepers with warmer and drier annual averages experienced increased levels of colony mortality. It should be noted that the sensitivity map in Fig. 4 was obtained without knowledge of the climate for individual months contributing to the annual values, and is therefore not as skillful as the kNNM (its MAE is equal to 3.44 which is only slightly better than the reference predictions, though still statistically significant at the 99.8% confidence level). However, the results can be a useful tool for beekeepers by clearly illustrating the expected mortality rate as a function of their annual climate.

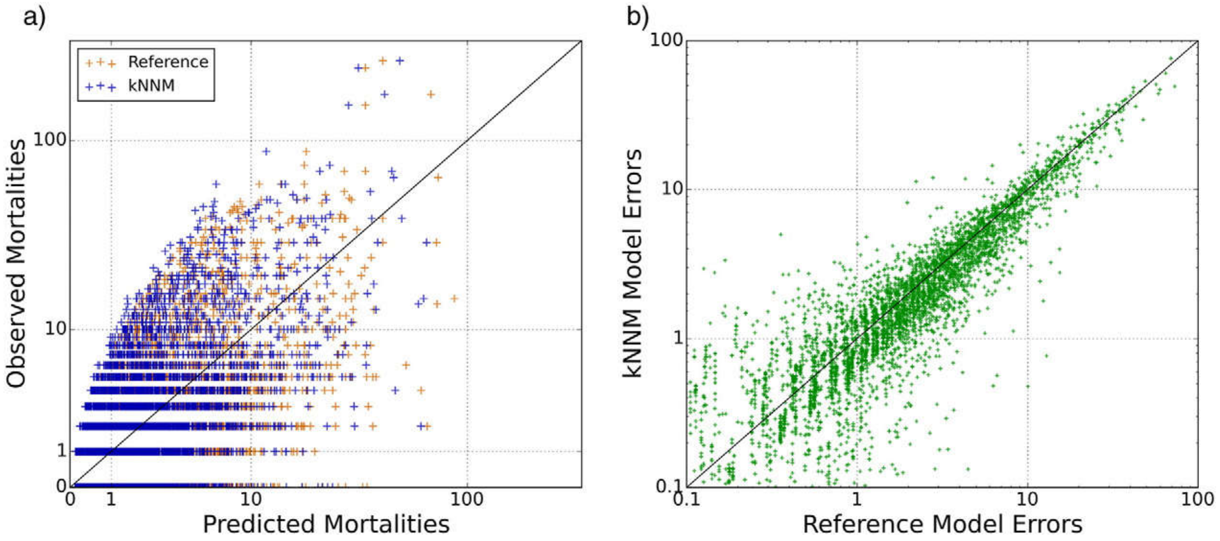

Fig. 3. Subplot (a) shows the predicted colony losses versus observed colony losses, for kNNM and the reference. The absolute errors of these predictions are illustrated in subplot (b).

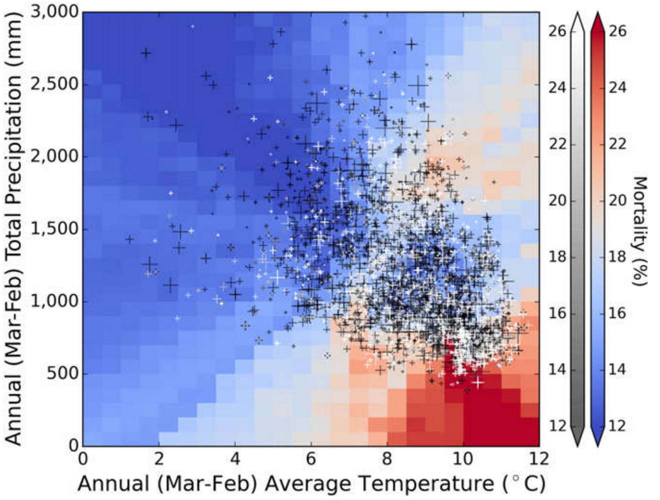

Fig. 4. Average annual (March–February) temperature and precipitation values for the beekeepers in the period 2009–2014. The plus signs are located according to the beekeeper's observed climatic values, while the gray colorbar shows their winter mortality percentages. The blue to red colorbar reflects the modelled mortality sensitivity to climate. The colored grid cells are obtained with a simplified kNNM that is run using annual temperature and precipitation as predictors.

4. Discussion

This study first investigated the correlations between climatic variables and winter honey bee colony mortality. We then developed a k-nearest neighbors model (kNNM) to predict the expected colony mortality rate conditioned by a region's climate. The model used mean monthly temperature and monthly precipitation sums, from the preceding year, as predictors. Compared to temperature and precipitation, we found a rather weak link between global radiation, wind speed and colony mortality. This model was evaluated using a yearly cross-validation. Predictions, using kNNM, were more skillful than the reference predictions and were found to be statistically significant at the 99.9% confidence level. Our analysis and modelled results show higher winter mortality for colonies across Austria when the preceding months are, on average, warmer and drier. The month of February is the exception, which shows lower temperatures coinciding with increased colony mortalities. This result is intuitively appealing, because February is a crucial month for honey bee colonies when they are particularly susceptible to cold spells, as colonies usually are already breeding and first forage sources are available in Austria. However, we should not over-interpret this finding, as we cannot pinpoint the time when colony mortality occurred (measured colony mortality could for example have taken place in November). Additionally, we presented a more generalized annual sensitivity of colony mortality to climate which was illustrated in Fig. 4. These results can be interpreted in two ways. First, there is the influence of climate on colony mortality rates in a regional context; colonies in cooler and wetter climates, or at higher elevations, on average have historically seen less losses than those of warmer and drier regions. Second, expected temperature increases, across Austria in the decades to come (IPCC, 2013; Haslinger et al., 2015), could lead to an increase in colony mortality rates (moving to the right in Fig. 4).

The climate data used in this study was on a grid with a 5 × 5 km resolution. However, this resolution does not reflect the precise microclimatic conditions at the apiary (e.g. orientation, slope or if the colonies are placed in the shade). Temperature, humidity, wind speed and light intensity at the apiary have an impact on foraging flights (Szabo, 1980), and microclimate at the foraging site affects the net energy gain of forager bees (Stabentheiner and Kovac, 2016). However, we made the assumption that the microclimate that applies at the apiary location has limited influence on colony survival because of the colonies' ability to maintain a relatively stable temperature (Stabentheiner et al., 2010).

Next to honey bee colony mortality, climate has a much more pronounced impact on vegetation, which also affects the honey bee foraging season, colony development and vitality of the colony. Together with changes in land use due to agriculture, the expected shift of Austria's climate towards warmer conditions (IPCC, 2013; Haslinger et al., 2015) will have an impact on apiculture. This applies to hive management such as the treatment against the *Varroa*-mite. Therefore, the climate-mortality relationship that is observed, and is used in our model, might not be directly causal. The links that we found between climate and mortality could, in fact, be due to indirect influences. Additional drivers of colony mortality, such as *Varroa destructor*, are strongly impacted by the climate predictors used by our model (Moretto et al., 1991; Harris et al., 2003). As a result, changing weather and climatic conditions can provide better/worse conditions for the reproduction, spread, and virulence of honey bee parasites and diseases. Moreover, the climate could have a greater influence on the parasites and diseases than on the bees themselves (Gisder et al., 2010). Similarly for *Varroa*-mite mitigation strategies, formic acid or products based on essential oils, which are commonly used to fight the parasite in Austria in July and August (Brodschneider and Crailsheim, 2013) are strongly dependent on ambient temperature and humidity (Imdorf et al., 1999; Underwood and Currie, 2003). Other treatments, like oxalic acid treatment, need brood-free colonies to be effective. With warmer autumn/winter conditions, the colonies are less likely to be completely free of brood, which hinders proper treatment. Additionally, the treatment in summer, which is mainly accomplished with formic acid, and which is sensitive to temperature and humidity, is a challenge for apiculture.

The effects of pesticides or available forage could also be playing a significant role in this study (Goulson, 2013; Budge et al., 2015). Agricultural production in Austria is more intensive in the regions where the climate is warmer and drier. As a result, these regions are generally characterized by greater pesticide use. Data specifying pesticide use is not in the public domain, so the role of pesticides over this period is difficult to establish. Increased disease or changes in the distribution of forage plant species could also partly explain what we observe. However, whether it is due to direct or indirect influences, we have shown that using climatic data can improve the predictions of expected winter losses.

5. Conclusions

Honey bee colony winter mortality can be attributed to complex interactions between several factors, including parasites, hive management, chronic sublethal stress, pesticides, and habitat loss (Potts et al., 2010; vanEngelsdorp et al., 2012; Goulson, 2013; Becher et al., 2014; van der Zee et al., 2014; Budge et al., 2015; Clermont et al., 2015; Lee et al., 2015; McMahon et al., 2016). In our case, we have attempted to isolate the influence of weather and climatic variability on honey bee mortality rates in Austria, though we do support the idea that multiple synergistically acting drivers are responsible for bee decline or high winter mortality of honey bees (Le Conte and Navajas, 2008; Goulson et al., 2015).

This is one of the first studies to robustly show how honey bee colony over-winter survival relates to climatic variables. Our results on winter mortality are in opposition to the assumption that warmer weather, and/or climate, is better suited for brood development and bee activity (Szabo, 1980; vanEngelsdorp et al., 2008). Follow up studies, in Austria and other climate regions around the world, are required to help gain a clearer picture of the impact that climatic variability has on honey bee mortality. Efforts to further improve projections of colony mortality will invariably include other factors such as *Varroa destructor*, mite treatment and pesticide exposure. However, this study illustrates the importance of climate variability when quantitatively modelling colony dynamics and health. A better understanding of the effect of climate variability on honey bee and parasite population dynamics would help improve hive management.

Competing financial interests

The authors do not have any competing financial interests that would gain or lose by this publication.

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