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Growing stock of nectar- and honeydew-producing tree species determines the beekeepers' profit

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Abstract

Forests and woodlands are considered as the most important sources of honey bee forage in many European countries with several tree species providing nectar and/or honeydew flow. Slovenia boasts with high number of beekeepers and high colony count per square kilometer. We have investigated the impact of availability of natural resources and colony density on honey yield.

Data presented here were collected on 57 locations with monitor hives, equipped with scales, over years 2011 – 2016. Locations were selected according to site vegetation, ensuring identified source of nectar or honeydew flow. The source of the flow was recorded and verified by contract beekeeper. We investigated 1) the relationship between abundance of the flow source expressed as the quantity of growing stock and net mass gain of the monitor colony during the flow and 2) the relationship between colony density expressed as the number of colonies against growing stock volume and net mass gain of the monitor colonies.

We found an asymptotic exponential relationship between colony mass gain and growing stock of the species, providing flow. The exception was the spruce where the relationship was determined as linear ($k = 0.023 \pm 0.009$). The τ of the exponential approach in the case of acacia flow was 9.8 ± 5.6 and in case of linden flow 6.6 ± 3.9 (mean ± SE). Colony density then determined the colony mass gain due to flow. In cases of acacia, linden and spruce flow we have determined the relationship between colony density and mass gain as decaying exponential ($\tau = 283.9 \pm 60.6$, $\tau = 1.6 \pm 0.4$ and 3.0 ± 1.3, respectively, all mean ± SE). Combined linden/chestnut flow was fitted best with linear equation ($k = - 0.08 \pm 0.019$). Most likely, another variable should be used in the case of spruce flow: population of dew-producing insects. Periodical monitoring of eight acacia locations show differences in mass gain between years, thus allowing prediction of colony densities which guarantee profit: these locations are determined as those with colony density less than 50 hives/10^3 m^3 growing stock gained more than 10 kg/hive in 83% of cases, regardless of the year.

Our results indicate that a cap on the total number of colonies at one location should be considered to maximize beekeepers' profit.

Keywords: beekeeping, forage, environment carrying capacity, non-wood forest products

Introduction

Forests and woodlands are considered as the most important sources of honey in many European countries with several tree species providing nectar and/or honeydew flow. Even in regions like sub-Saharan Africa, honey has already been recognized as valuable non-wood forest product (Chikamai et al. 2009). Beekeepers often pursue single-source flows – e.g. linden bloom or spruce honeydew - to obtain honey with distinct sensorical properties (c. f. Persano Oddo & Piro 2004, Crane and Walker 1985) - such honeys achieve higher prices on the market. Beside linden and spruce, honeys like acacia, chestnut and fir honey are recognized as important single-source honeys in Slovenia and neighboring countries. In contrast with many EU and non-EU countries, cultured plants are of lesser importance for honey production in Slovenia (for recognized honey sorts see Official Gazette of the Republic of Slovenia, 2009). Desire to maximize honey yield calls for potential regulation of the colony density in forest stands in which the nectar/dew flow is expected. Such a move may be strongly opposed by beekeeping community, yet data is very scarce. To uphold the regulation a thorough analysis should be made, and a model developed.

Honey bees are forest dwellers, establishing colonies in hollow tree trunks. Natural colony density as determined for both Palearctic and Nearctic forests was established at 0.5 colonies/km^2 (Galton, 1971, Visscher & Seeley, 1982). With the arrival of deadly ectoparasite *Varroa destructor*, feral colonies were thought to be mostly extinct. However, Kohl & Rutschmann (2018) showed a contemporary natural density of 0.11–0.14 honey bee colonies/km^2 in two European beech forests of Germany, which is in agreement with 0.1 colonies/km^2 reported from Poland (Oleksa, Gawroński & Tofilski,

2013) and an order of magnitude less than 1.0 colonies/km^2 in later census in a mature Nearctic hardwood forest (Seeley, 2007). These densities are fairly low compared to the densities of managed colonies reported by national registries for certain countries. For example, there were roughly 160.000 registered colonies on Slovenia's territory of 20.273 km^2 in the years up till 2017, giving densities around 8 colonies/km^2. Most of the colonies (>99%) are registered under 900 m above sea level, taking higher mountainous regions (15 % of total surface) out of the equation. The recalculated density is then 8.64 colonies/km^2 on 11.764 locations, giving an average a bit more than 13 colonies/apiary. Official honey production varies from year to year with maximum of 2047 tons or 12.8 kg/colony in 2015 (Statistical Office RS, 2018).

The natural dispersal of a colony's foragers over the space has been often addressed. In cases with low colony density, a skewed distribution of foragers was reported with median forage range of 1650 m and maximum range of 10,100 m (Visscher & Seeley 1982). A similar report was given by Steffan-Dewenter and Kuhn (2003) who noted median range of 1,181 m and maximum range of 10,037 m. In cases where food patches are more abundant, Waddington et al. (1994) showed that distances and forage pattern can differ significantly between locations and colonies, yet most of foraging happens within 3 km radius. However, in situations with high colony density foragers disperse to places burdened with lesser colony numbers (Gary 1978).

The Slovenian government-sanctioned Queen breeding program for *Apis mellifera carnica* contains provisions for monitoring of the natural resources, namely nectar and honeydew flow monitoring. Monitoring service was established more than 30 years ago and is currently being managed by experts at Slovenian Beekeepers' Association

(SBA). It consists of a network of monitoring colonies (50 – 70, depending on the year), equipped with manual and automatic hive scales at selected locations, which provide certain kind of nectar or honeydew flow (e.g. acacia, linden, spruce, fir...). Contract beekeepers maintain the monitoring colonies and confirm the type of the flow. Selection of locations is based on the geodatabase of forest stands (Slovenia Forest Service, 2015) and monitoring growing stock for different tree species every 10 years.

In this paper we discuss growing stock as determinant of the resource availability and the colony density's bearing on colony mass gain and colony honey production.

Methods

Data sources

Presented data about nectar and honeydew flow were collected in years 2011 – 2016 with monitoring hives in care of contract beekeepers. Mass changes of these hives were recorded daily by means of commercially-available automatic GSM-equipped hive scales (Ames d.o.o and Eldema d.o.o, both Slovenia). The data collection was and still is organized and coordinated organized by Slovenian Beekeepers' Association; daily changes are available to public via online portal (https://ecebelar.czs.si). All measurements collected are stored in the database maintained at the Agricultural Institute of Slovenia. We have extracted daily data for selected acacia, linden, mixed linden/chestnut nectar flows and spruce honeydew flow. While botanical sources of linden, chestnut and spruce flows are clear (*Tilia spp.*, *Castanea sativa*, *Picea abies*, correspondingly), the acacia nectar flow is actually provided by black locust tree (*Robinia pseudacacia*) which in beekeeping community is termed "acacia". We will maintain this term through the paper when discussing flow and/or honey. Type of the flow is verified by contract beekeeper who took care of the hive. Determination of the source was based on timing, vegetation around the hive and sensory qualities. No palynological validation was performed. In cases where overlap in time was possible (linden/chestnut), care was taken either to exclude any doubt about the flow purity or to assign the measurements to mixed category. Monitoring hives are strategically placed at the locations interesting for beekeepers (expert judgement, Fig 1A). Depending on the situation, some locations are kept for years, others are changed yearly (Table 1). Beekeepers must report establishment of a new apiary as well colony counts at the apiaries under their care; colony counts are collected twice a year. Apiary coordinates and corresponding yearly colony counts were obtained from database of national veterinary administration (UVHVVR). We have counted colonies within 3 km radius of the monitoring colonies, using custom-written Python script.

Data about growing stock of certain tree species within a forest stand around apiary (in m^3) were calculated based on the data of forest stand map, produced every ten years by Slovenian Forest Service for forest management plans. Based on remote sensing data (orthophoto images at 1:5.000 scale) and field survey, homogenous forest stands were delineated (Slovenian Forest Service, 2015). In each delineated forest stand, several temporary sampling plots (minimum 7 per stand) are established during field work. The growing stock for each tree species in each plot was estimated with Bitterlich's angle-count method and measurement of average tree height per different tree species (Bitterlich 1948). Finally, sample plot data were averaged for each forest stand and growing stock per tree species (in m^3/ha) was calculated. To obtain information on growing stock per tree species per stand level (in m^3), the growing stock of certain tree species within a forest stand was calculated according to the area of specific forest stand.

Growing stocks per tree species were later evaluated in 3 km radius around the monitoring colonies. Both, forest stand map and apiary coordinates were imported into GIS (ArcMAP 10.6; ESRI, 2018) and only forest stands within 3 km buffer (function *Buffer*) around each apiary was selected for further analyses (function *Clip*). For forest stands on border of 3 km, growing stock per tree species per stand level were corrected according to the proportion of the forest stand inside / outside buffer of 3 km. Growing stock per tree species inside buffer of 3 km was finally calculated by summarizing data from selected forest stands (Fig 1B).

We have defined colony density as a number of colonies per volume of growing stock of selected tree species to offset different amount of resources at different locations. Colony density was calculated using custom-written Python script.

Table 1. Number of monitor colonies per year for each type of flow. Time interval in which flow appears is also marked.

	Acacia	**Linden**	**Linden/Chestnut**	**Spruce**	**N**
2011	13	12	9	8	42
2012	15	10	9	15	49
2013	14	9	12	5	40
2014	14	9	20	4	47
2015	15	10	19	3	47
2016	14	12	19	4	49
N data	**85**	**62**	**88**	**39**	**274**
N unique locations	**18**	**19**	**26**	**18**	
Observed flow period	end of April-end of May	end of May-early July	end of May-early July	end of April-early July	

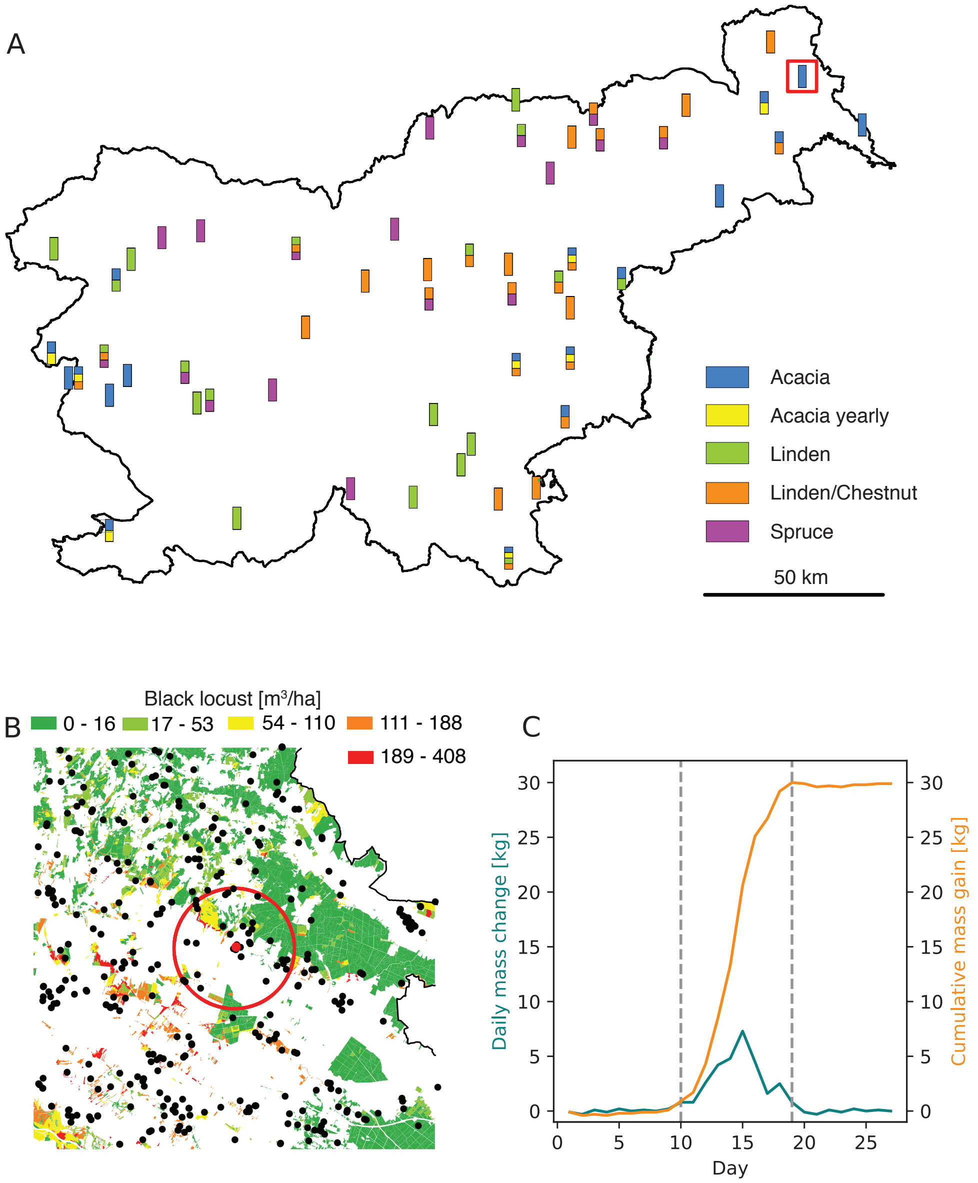

Figure 1. A: locations of monitoring hives within Slovenia, providing data for this study. In several locations, monitoring hive provided data for different nectar flows (see legend). Locations marked as "Acacia yearly" were used in the analysis of yearly differences in acacia nectar flow. Location "Bogojina" marked with a red square. B: Neighborhood of monitoring hive at location "Bogojina". Red circle marks 3 km radius around the hive. Black dots represent apiaries in the surroundings. Black locusts' growing stocks are color coded. See legend within figure. C: Daily mass changes (green) and cumulative mass gain (orange) at the location "Bogojina" in 2015 due to the acacia nectar flow.

Data analysis

The analysis was made for the selected time interval for relevant locations. Time interval of nectar flow was determined by both the beekeeper charged with care of the station and deviation of daily mass gain from the baseline (Fig 1C) during the time of bloom. Data within this interval was then summed for each location and each year.

We have investigated relationship of growing stock on monitoring colony mass gain, and the relationship between the colony density and the colony mass gain. Python's *lmfit* package was used in our custom-written scripts (DOI: 10.5281/zenodo.3248183) to perform fits and evaluate the quality of the fit.

We describe the relationship between quantities by fitting the recorded values by either exponential approach (Eq 1; in case of growing stock, custom-written) or exponential decay for colony density (Eq 2; included in *lmfit* package) using least-squares minimization (LSM) method. Alternatively, a linear regression built in *lmfit* package was used, using LSM as well.

Eq 1: $$y = A \times \left(1 - e^{-\frac{x}{\tau}}\right) + B$$

Eq 2: $$y = A \times e^{-\tau \times x} + B$$

To decide between the exponential or linear approach we used Akaike information criterion (AIC), implemented in *lmfit* package, selecting the model with lower AIC score. Goodness of fit is reported with standard error, also implemented within *lmfit* package.

Results

Acacia nectar flow

Flow begins in late April/early May - depending on the geographical location - and lasts between 2 and 16 days in years observed. Eighty-five measurements were collected at 18 locations over the years 2011 – 2016 (Table 1). Range of mass gain during acacia nectar flow in the years 2011 – 2016 was between 0.0 and 44.6 kg, with median 14.1 kg and interquartile range of 15.3 kg. First and most evident thing are the differences in median mass gain between years: from 5.8 kg in 2014 to 21.85 kg in 2013. We present values in Fig 2A. Average yearly durations of the flow were between 5.2 and 6.9 days with the exception of 2014, in which the flow was cut short to 2.4 days.

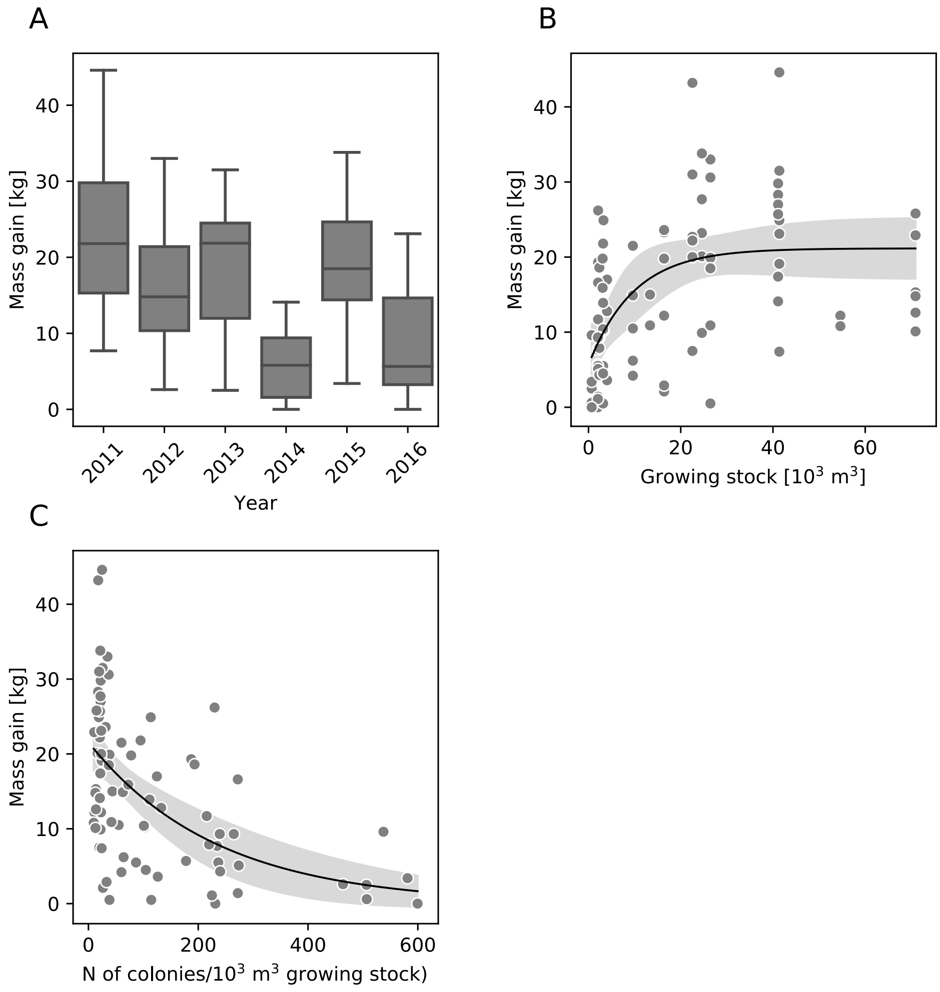

Figure 2. A: Mass gains during acacia nectar flow. Boxplots show huge variability between years. B: Impact of black locust's growing stocks on measured mass gain. Figure shows mass gains reaching ceiling at approximately 40 x 10^3 m^3 of growing stocks (τ = 9.8 ± 5.6, mean ± SE). C: Mass gain during nectar flow depends on colony density. Colony density was computed as number of hives on 10^3 x m^3 of black locust growing stocks (τ = 283.9 ± 60.6). Each dot in B and C represents a single data point. Shaded areas in B and C mark 95% confidence interval.

Relationship between *Robinia*'s growing stock and colony mass gain during acacia nectar flow was best described by exponential approach function (Eq 1; τ = 9.8 ± 5.9, mean ± SE; AIC_{expapp} = 370 vs. AIC_{lin} = 383), reaching ceiling around 200.000 m^3 of growing stock (Fig 2B). Finally, Fig 2C shows importance of colony density. Locations burdened with more than 200 colonies per 1000 m^3 of black locust growing stock gained more than 10 kg only in 3 cases (16%) and locations, burdened with 400 colonies per 1000 m^3 without single exception harvested less than 10 kg/hive. The relationship between density and colony mass gain is not linear either: exponential decay fits best (Eq 2; $\tau = 233.9 \pm 60.6$, mean ± SE; $AIC_{expdec} = 368$ vs. $AIC_{lin} = 372$). Locations burdened with less than 50 hives/1000 m^3 had harvested 10 kg/hive and more in 85 % of cases.

Linden and mixed linden/chestnut nectar flow

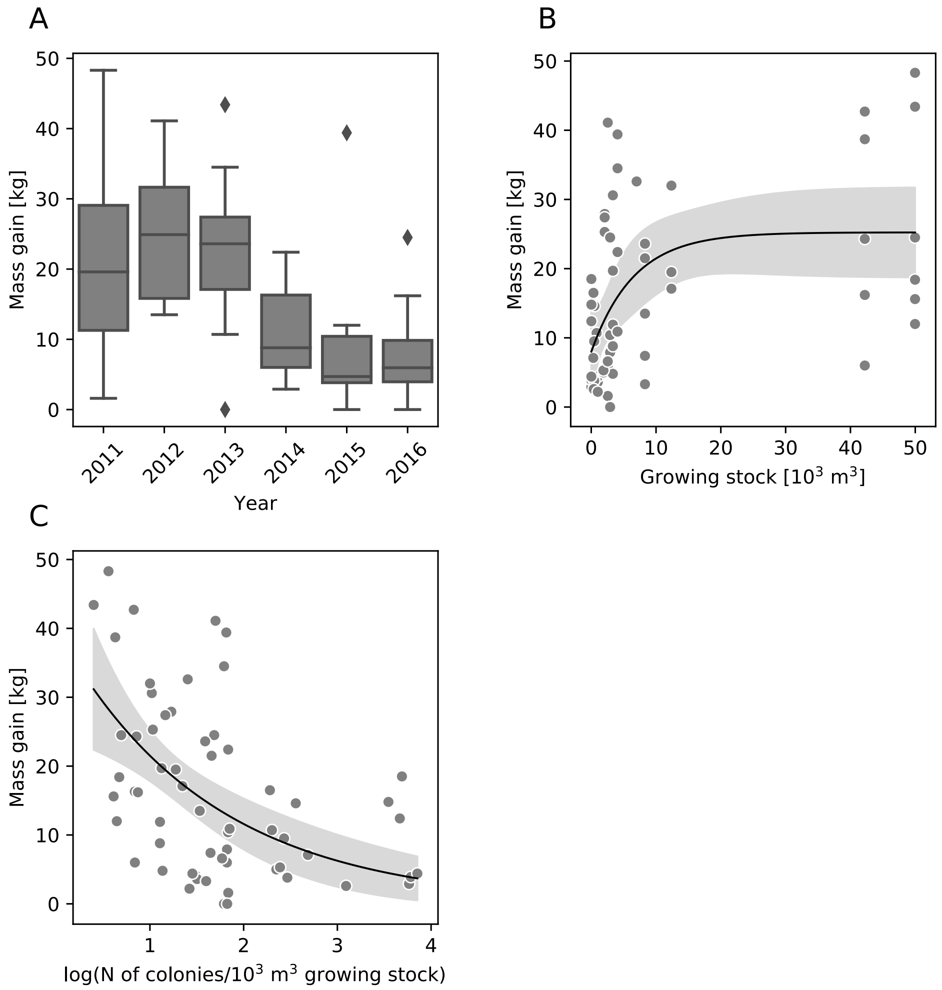

Figure 3. A: Colony mass gain during linden nectar flow. Boxplots show variability between years. B: Dependence of mass gain on linden growing stock ($\tau = 6.6 \pm 3.9$, mean ± SE). C: Dependence of mass gain on log colony density ($\tau = 1.6 \pm 0.4$, mean ± SE). Each dot in B and C represents a single data point. Shaded areas in B and C mark 95% confidence interval.

Linden nectar flow (*Tilia* spp.) is usually due in June and in many locations overlaps at least partially with chestnut (*Castanea sativa*) flow. We took data from linden-only locations and combined locations for years in which flow did not overlap, all together 62 measurements from 19 locations (Table 1). Nectar flow differed between years, with overall median being 12.95 kg and interquartile range 19.05 kg (Fig 3A). Asymptotic exponential approach offered best description between mass gain and growing stock

(Eq 1; $\tau = 6.6 \pm 3.9$, mean ± SE; $AIC_{expapp} = 303$ vs. $AIC_{lin} = 305$; Fig 3B). To examine the impact of hive density on mass gain during linden flow, we have log-transformed colony density and fitted data with exponential decay (Eq 2; $\tau = 1.6 \pm 0.4$, mean ± SE; $AIC_{expdec} = 299$ vs. $AIC_{lin} = 304$; Fig 3C).

Overlapping of linden and chestnut nectar flow was recorded in 88 occasions in 26 locations during last six years (Table 1). Again, mass gains of the monitoring colonies differed between years: median mass gain of years 2014, 2015 and 2016 combined was only 59 % (9.65 kg) compared to combined median mass gain recorded in years 2011, 2012, 2013 (16.35 kg; Fig 4A). Colony density had negative impact on the mass gain of the monitoring colonies: negative trend due to higher colony density is evident in figure Fig 4B. Linear regression fitted data points ($R^2 = 0.17$; $k = -0.08 \pm 0.019$, mean ± SE;). Both the exponential decay and linear model had similar AIC values (345 and 345, respectively); we decided for more parsimonious linear model. Data recorded in locations with colony density higher than 50 colonies per 1000 m^3 gained more than 10 kg of mass only in 8 out of 26 cases. With colony densities less than 50 per 1000 m^3 of wood, 37 out of 62 gained more than 10 kg mass during the flow.

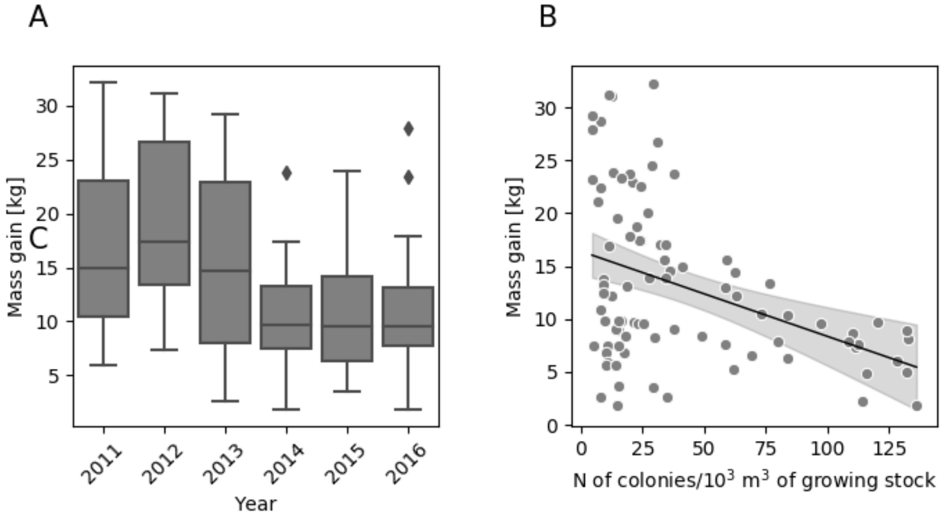

Figure 4. A: Mass gains during combined linden/chestnut nectar flow. Boxplots show large variability between years. B: Increase of colony density shows decrease of colony mass gain ($R^2 = 0.17$; $k = -0.08 \pm 0.019$, mean ± SE). Each dot in B represents a single data point. Shaded area in B marks 95% confidence interval.

Spruce honeydew

Spruce honey is one of the two types of single-source honeydew honeys recognized in Slovenia. 39 data points collected in years from 2011 to 2016 at 18 locations are shown (Table 1). Median mass gains of the monitor colonies range from 11.4 kg in 2015 and 20.9 kg in 2010 (Fig 5A).

Spruce is one of the most important tree species in Slovenian forests, yet the relationship between spruce growing stock and mass gain of monitor colonies is moderate at best. AIC values suggested use of linear model ($AIC_{expdec} = 187$ vs. $AIC_{lin} = 185$); we described relationship by a linear equation ($R^2 = 0.15$; $k = 0.023 \pm 0.009$, mean ± SE; Fig 5B). Relationship between colony density and monitor colonies' mass gain was described by decay exponential (Eq 2; $\tau = 3.02 \pm 1.4$, mean ± SE; $AIC_{expapp} = 184$ vs. $AIC_{lin} = 185$; Fig 5C).

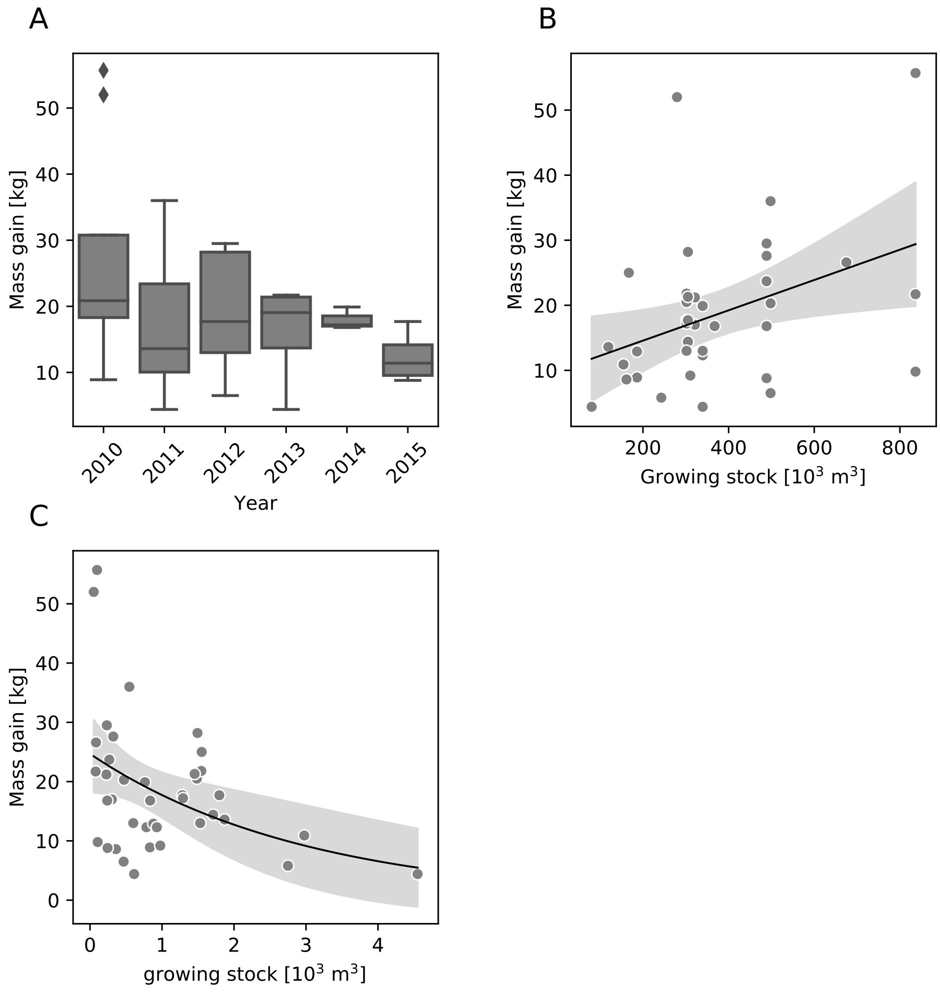

Figure 5: Colony mass gain during spruce honeydew flow. Boxplots show variability between years. B: Dependence of mass gain on spruce growing stock ($R^2 = 0.15$; $k = 0.023 \pm 0.009$, mean ± SE). C: Dependence of mass gain colony density ($\tau = 3.0 \pm 1.3$, mean ± SE). Each dot in B and C represents a single data point. Shaded areas in B and C mark 95% confidence interval.

Yearly differences in acacia nectar flow

Eight out of eighteen acacia locations were monitored in all six years. We used this subset for detailed analysis of inter-seasonal variation. In years with normal or good nectar flow (2011, 2012, 2013 and 2015), an approach to ceiling could be observed regardless of the growing stock. Exponential approach (Eq 1) reached ceiling regardless of black locust density and limiting honey yield at around 200,000 m^3 of black locust stocks ($\tau = 4.1 \pm 3.3$ in 2012, mean ± SE). In years with low nectar flow however, the relationship is still asymptotic and relatively flat ($\tau = 24.6 \pm 15.4$ in 2014, mean ± SE), almost linear (Fig 6A).

Colonies in the environment burdened with less than 50 colonies per 1000 m^3 of black locust growing stock gained more than 10 kg/hive in 83 % of cases. On the other hand, colonies in the locations burdened with more than 200 colonies per 1000 m^3 of black locust growing stock would not gain more than 10 kg mass during the flow, regardless of the year. The maximum mass gain range was 37.2 kg in one of the locations ("Šempeter"), while minimum mass gain range was 9.3 kg in location "Mokronog". The relationship between density and colony mass gain was described by exponential decay: τ values were between 17.2 ± 6.5 (2014) and 164.1 ± 43.9 (2015; mean ± SE; Eq 2).

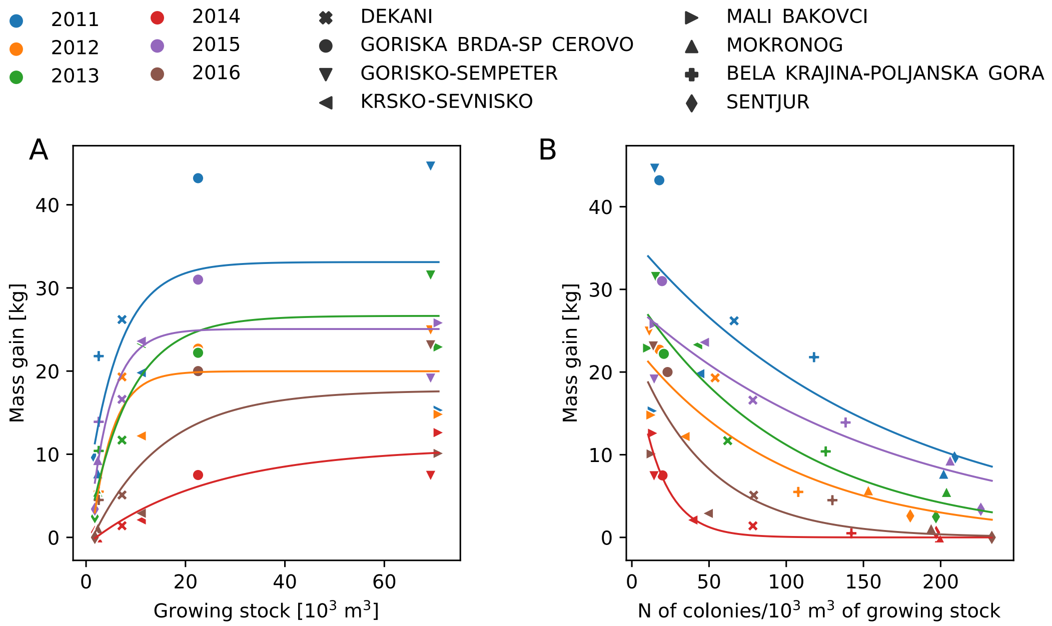

Figure 6. Mass gain due to acacia nectar flow, recorded every year on eight locations. A: Dependence of mass gain due growing stock in 3 km range. Mass gain reaches ceiling in "normal" years regardless of available growing stock. B: Mass gain during nectar flow depends on colony density. Colony density was computed as number of hives on 10^3 x m^3 of R. pseudacacia *growing stocks. Each dot in A and B represents a single data point.*

Discussion

Beekeeping is very much woven into the fabric of the Slovenian nation. Consequently, a lot has been invested in research of various aspects of nectar and honeydew flows in the past. Unfortunately, most of the collected data hasn't been digitized and/or centralized. We used the available data to show the importance of natural resource scarcity and the environment capacity for honey bee colony density in connection with availability of nectar and honeydew flow.

Colony mass changes

We have analyzed mass gains in the monitoring hive during the bloom, yet the observed gains were not due to the nectar flow only. Honey bees seem to condense collected nectar already on the return flight (Nicolson & Human, 2008), a change that does not register on hive scales. Commercial hive scale system usually reports mass once a day. Beside water evaporation, calculated mass changes include also consumption for colonies' own needs; these needs vary with the state of the colony (Brodschneider & Creilsheim, 2010). Non-linear relationship between stored honey and colony mass was determined as polynomial, variability between locations ascribed to differences in moisture and temperature (McLellan, 1977). It is possible to separate daily needs of the colony using smoothing average of hourly mass measurements as a reference line. Amplitudes of hourly changes against such background show colonies' physiological needs, water evaporation etc. It is possible to discern trends in gaining/losing food stores over longer period e.g. week (Meikle et al. 2008). For all these reasons it is impossible to use linear relationship to predict honey harvest directly. Yet it is possible to use the measured mass changes to get rough ball-park estimation.

Availability of resources

In this paper we use absolute growing stock (in m^3) to describe available resources. Alternative to complex data of growing stock would be land use data e.g. percentage of forest area. While percentage of forest area might be directly comparable to growing stock in pure mono-cultures or forests with single forest tree species, percentage of forest area is much less reliable in diverse and natural forests of eastern and southern part of Europe (Pirnat, 2017).

Sites providing single-source flows are sought for – local single-source honeys have their unique characteristics and usually achieve higher market prices. Black locust (*R. pseudacacia*) blooms early in season, usually in late April or early May, giving so-called acacia honey. Honey potential for one hectare of black locust was reported to be between 48 and 1600 kg, range depending on the country (Crane et al., 1984). For consideration, 36 years old and very pure black locust forest stands can contain 282 m^3/ha (Redei and Meilby, 2000). A noteworthy observation (Fig 2B) is the existence of ceiling: increase of resource availability over 200.000 m^3 does not improve mass gain considerably. Linden trees (*Tilia* spp.) have similar honey potential as black locust, 90 – 1000 kg, again, depending on the country (Jašmak, 1973; Crane et al., 1984); however, one should take into the account that linden trees are rarely dominant tree species in forest stands of Slovenia in contrast to black locust (Brus, 2012). The effective foraging radius in Europe was estimated to about 2 – 3 km (von Frisch 1965), yet there is no way to tell how far from the hive did the colony forage. In the dense and floristically monotonous associations where black locust is dominant, and in which colony density is high, it is easy to assume dispersal of the foragers to places burdened with lesser colony numbers, like observed in the orchards (Gary 1978).

On the other hand, linden and chestnut trees are normally found in floristically diverse associations in which they do not represent major component. Due to sparsity of linden trees in such associations, one could assume that colonies forage in patch-like fashion, focusing on single patch and switching only when quality of the patch drops (c.f. Waddington et al., 1994). Chestnut grows on acidic soil as the main supporting species of several associations and does not form continuous forests (Brus, 2007).

Honeydews are dependent on insects sucking sap, adding another variable to the equation. Spruce trees host two important species *Physokermes piceae* and *P. hemicryphus*, which are one of the most important sources of dew. These insects are univoltine and overwinter as larvae, making them susceptible to weather conditions (Rihar, 1992). Proper explanation of mass gain during honeydew flow would then require knowledge of the insect's population and poor fits are likely consequence of the lack of knowledge about this component.

Colony density and economic consequences

Regardless of the flow source, our results show importance of colony density: higher the density, lower the mass gain. This is especially important in the seasons with weak nectar flow when the carrying capacity of the environment could be reached already at low colony densities (Fig 6B, years 2014 and 2016). While it is difficult to predict a weak season without very evident reason like spring frost, it is clear that seasons differ in mass gains and honey yield. There seem to be several parameters, influencing nectar flow, among them weather conditions during the preceding winter. In case of acacia, the most important seem to be temperature requirements: > 25 ºC during daytime and > 15 ºC during the night (for review, see Farkas and Zajácz, 2007). Figures 3A and 4B show a drop in median mass gains for linden and combined linden/chestnut flow in years 2014 – 2016. Average colony density did not change much: quick calculation for linden flow shows average density of 68 colonies/1000 m^3 for years 2011, 2012 and 2013 against 74 colonies/1000m^3 in years 2014, 2015, 2016. Most likely alternative could be weather conditions, e.g. severe storms. Unfortunately, we have no precipitation or other weather-related data for most of the locations.

Attempts to limit the colony numbers at the popular locations are being fiercely objected by local beekeeping community as pointless during main flow. Our study demonstrates that resources, in our case growing stock, define the reasonable colony density at the location. In related study, environment carrying capacity was investigated in Saudi Arabia, an arid country where vegetation outside oases is not particularly rich. Two most popular flow sources are *Acacia tortilis* and *Ziziphus spina-christi*. The authors calculated availability of the resources by dividing number of flowering plants with number of the colonies, concluding that increase of the colony numbers in the last 20 years more than halved the harvest in some cases (Al-Ghamdi et al., 2016).

A neighboring country, Croatia, has reported 11,500 tons of honey harvested on roughly 56,600 km^2 from 406,000 colonies (7.2 colonies/km^2). Calculations returned

28.3 kg/colony and 2.03 kg/ha (European Commission, 2015). The hectare yield is more than double with roughly 10% less colonies per square kilometer. The question is whether increasing colony density would increase honey harvest per hectare of surface or is the carrying capacity already reached? In terms of geography, climate and vegetation, Slovenia is perhaps more similar to another neighbor, Austria. Official statistics of EU shows that Austria reported 370,000 colonies - 4.4 colonies/km^2 – and 4,300 tons of harvested honey in 2015, giving 11.6 kg/colony or 0.51 kg/ha (European Commission, 2015). This is roughly half the density and half the yield per hectare in comparison with Slovenia, which, as noted above, reported similar honey yield per colony (12.8 kg). In Austria at half of the density the average colony yield is already at the level of Slovenia. Therefore, we speculate that domestic increase of colony number to increase honey yield is probably not the option. On the other hand, decreasing the colony numbers in Slovenia might improve the yield of individual beekeeper. Out of 10,000+ registered beekeepers there are less than hundred professionals, making living exclusively out of honey production, which gives additional weight to such argument.

Majority of forest owners value their woodland property mostly as the source of timber. In hypothetical case, there are 244 colonies within 3 km radius at 8.64 colonies/km^2 in Slovenia. In case of acacia honey harvest of 10 kg per hive and back-yard retail price of 10 €/kg, this represents revenue of 24,400 €. On the other hand, black locust timber is valued at 50 €/m^3 (Slovenian State Forests pricelist, April 2019). Assuming consistent growing stock of 282 m^3/ha within 3 km radius, maximum revenue of one hectare of black locust forest would reach one-time value of 14,100 €. After such consideration, forest owners might be encouraged to become stakeholders in beekeeping operations.

Competition for resources

Last but not least, honey bees share available resources with other species. Overcrowding environment with honey bee colonies could have consequences on wild bees (bumblebees and other bees not belonging to genus *Apis*) and non-bee pollinators. The researchers seem to be divided on the topic: one study, for example, found no direct competition between honey bees and wild bees for forage, e.g. wild bees mostly depend on the coverage of non-cultivated vegetation in Central Europe (Steffan-Dewenter & Tscharntke, 2000). On the other hand, Thomson (2004) showed honey bees (*Apis mellifera*), non-native to the New world, as a threat to native pollinators from genus *Bombus*. Another report made by Roubik and Wolda (2001) show that in native bees on the island in the Panama Canal did not suffer from introduction of Africanized *Apis mellifera*. Yet none of the above studies considered such high colony numbers at the location.

Conclusions

Woodlands and forests are important resources for honey bees and beekeepers. Quantity of the resource – e.g. growing stock around the apiary – is the most important parameter when considering the carrying capacity of the environment in terms of honey bee colony numbers. Consequently, colony density requires both ecological and economic considerations. Both have a common denominator: (too high) density has negative consequences for both beekeepers and most likely for other nectar-feeders as well. While relationships between nectar flows and colony mass gain is clear, the relationships between honeydew flows and colony mass seem to be more complex and not as clear. Most likely, another variable should be built in the equation, explaining the yield: population of dew-producing insects. Nevertheless, our models could be used to develop recommendations for management of beehive density, providing that there are both colony density and growing stock data available.

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Declaration of interest

Declarations of interest: None.

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